

Research Article

Phylogeny and systematics of the tribe Sonerileae (Melastomataceae) in Africa: A revised taxonomic classification

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Abstract The tribe Sonerileae in tropical Africa and Madagascar is a morphologically diverse lineage that consists of 239 species in 10 genera. In this study, we present the first in-depth phylogenetic analysis of African Sonerileae to test monophyly of the currently recognized genera. Phylogenetic analyses were performed using sequence data from two nuclear (nrITS and nrETS) and three plastid loci (*accD-psal*, *ndhF* and *psbK-psbL*). Sampling consisted of 140 accessions including 64 African, 27 Malagasy, 46 Asian, and three neotropical Sonerileae together with a broad outgroup sampling (105 spp.). Phylogenetic relationships were inferred using maximum likelihood and Bayesian inference approaches, and a careful reassessment of morphological characters was carried out. Our results neither support the monophyly of the Old World nor African Sonerileae. The monospecific African genus *Benna* is partially supported as sister to *Phainantha*, one of the basal neotropical lineages, while African and Malagasy *Medinilla* are nested among the SE Asian genera. *Gravesia* (116 spp.), the most species-rich and morphologically diverse genus in Madagascar, is recovered as monophyletic. The African genera of Sonerileae *Calvoa*, *Dicellandra*, and *Preussiella* form well-supported clades. In contrast, *Amphiblemma* (including *Amphiblemma molle*) and *Cincinnobotrys* s.l. (including *Cincinnobotrys felicis*) are not monophyletic. To accommodate the caulescent *C. felicis* we propose reinstatement of the monospecific genus *Bourdaria*. For the distinctive *A. molle* a new genus *Mendelia* is described. *Calvoa hirsuta* is designated here as the type of genus *Calvoa*, lectotypes are designated for *Medinilla engleri* and *Veprecella lutea*, and a neotype is designated for *Preussiella kamerunensis*.

Key words: Africa, Malagasy, Melastomataceae, morphology, new genus, phylogeny, Sonerileae, taxonomy.

1 Introduction

The advent of molecular phylogenetics has greatly changed our understanding of natural plant groups. This is the case for Melastomataceae s.l. (including Memecylaceae), a

pantropical lineage that consists of ca. 5857 species in 176 genera (Michelangeli et al., 2020; Ulloa Ulloa et al., 2022). Melastomataceae s.l. are mostly herbs or shrubs, with some climbing lianas, epiphytes, hemiepiphytes, or small to emergent trees (Renner, 1993). Recent phylogenetic analyses

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have greatly increased our understanding of tribal relationships within Melastomataceae (Fritsch et al., 2004; Michelangeli et al., 2004, 2011, 2013; Penneys et al., 2010; Penneys & Judd, 2013; Veranso-Libalah et al., 2017, 2020; Bacci et al., 2019; Bochorney et al., 2019; Kartonegoro et al., 2021). However, except for the subfamily Olisboeideae (Stone, 2006, 2014; Stone & Andreasen, 2010) and the African Melastomataceae tribe (Veranso-Libalah et al., 2017, 2020), the rest of the Afrotropical tribes are still sparsely sampled in a phylogenetic context.

Over the years, the tribal circumscription of the paleotropical Melastomataceae has greatly changed. Following Triana (1866, 1872), several authors recognized four tribes within the paleotropical Melastomataceae: Osbeckieae (= paleotropical Melastomataceae), Oxysporeae, Sonerileae (= Cassebeerieae) and Dissochaeteae (= Medinilleae) (see Table 1; Hooker, 1867; Cogniaux, 1891; Krasser, 1893; Gilg, 1898; Engler, 1921). Baillon (1877) recognized all tribes listed above except Sonerileae, which he included within the neotropical Bertolonieae, and additionally proposed a new monogeneric tribe, Rousseauxiae (for the genus *Rousseauxia* DC. currently treated in Melastomataceae). Based on wood anatomical studies, Van Vliet (1981) and Van Vliet et al. (1981) recognized Osbeckieae, Dissochaeteae, and proposed a broad circumscription of Sonerileae to include the paleotropical Oxysporeae and the neotropical Bertolonieae. Renner (1993) merged two segregated tribes, Tibouchineae (= neotropical Melastomataceae) and Osbeckieae (= paleotropical Melastomataceae) into the Melastomataceae. She also treated Oxysporeae and Bertolonieae in Sonerileae, and Dissochaeteae in the Miconiae (Table 1). Within the Sonerileae, Renner (1993) recognized two provisional alliances: the *Oxyspora* DC.-*Anerincleistus* Korth. alliance and the *Sonerila* Roxb.-*Bertolonia* Raddi-*Gravesia* Naudin alliance, but the distinction between them was very weak, with some genera, for example, *Bredia* Blume and *Driessnia* Korth. fitting morphologically into both. The *Oxyspora*-*Anerincleistus* alliance comprises mainly shrubs with terminal or axillary, umbellate, fasciculate, or thyrsoid paniculate cymes (scorpioid in some *Neodriessnia* M.P.Nayar) and 8- or 10-ribbed, occasionally quadrangular capsules (in *Bredia*). On the other hand, the *Sonerila*-*Bertolonia*-*Gravesia* alliance consists mainly of herbs with often uniparous (scorpioid) inflorescences, rarely with paniculate cymes or flower clusters, and typically triangular or quadrangular capsules (Renner, 1993).

Previous molecular phylogenetic analyses have shown that Bertolonieae are a monophyletic lineage unrelated to the Dissochaeteae-Oxysporeae-Sonerileae complex (Bacci et al., 2019). Bertolonieae s.s. are now treated as a monogeneric tribe (*Bertolonia*), excluding *Monolena* Triana ex Hook.f. and *Triolena* Naudin which are now placed in the Trioleneae. Two other genera, *Macrocentrum* Hook.f. and *Salpinga* Mart. ex DC. now belong to Merianiae (Bacci et al., 2019, 2020). Kartonegoro et al. (2021) have recently shown that Dissochaeteae are endemic to Southeast Asia and composed of six genera and ca. 90 species. Several molecular studies have supported the monophyly of the Oxysporeae-Sonerileae s.l. complex (including *Medinilla* and allied genera) (Bacci et al., 2019, 2020; Zhou et al., 2019, 2022; Kartonegoro et al., 2021). Three neotropical genera, *Boyania* Wurdack, *Phainantha* Gleason and *Tryssophyton* Wurdack are

supported as the basal lineages of the Sonerileae-complex (Bacci et al., 2019; Maurin et al., 2021). Nevertheless, these studies sparsely sampled the African and Malagasy endemic members of Sonerileae; it is still not known if the currently recognized genera are natural lineages.

The Oxysporeae-Sonerileae s.l. complex (hereafter the Sonerileae complex) comprises ca. 1079 species in 43 genera, distributed mainly in the Paleotropics (Southeast Asia and Oceania [31 gen./828 spp.], Madagascar [2/184], and Africa [7/55]), with a few neotropical entities (6/12) (Liu et al., 2022; Ulloa Ulloa et al., 2022). It is a morphologically heterogeneous assemblage mainly characterized by apically crowned ovaries, a feature present in two-thirds of the genera (Renner, 1993). They also have angular fruits, a persistent hypanthium and non-cochleate seeds with a tuberculate testa (Triana, 1866). Many Sonerileae are acaulous herbaceous plants with basal rosettes and grow in shaded habitats (Figs. 1–3). Few species have tubers (*Cincinnobotrys* Gilg and *Phyllagathis* Blume) and often a basal whorl of large, somewhat turgescent leaves. *Anisophylly* is also very common in the Sonerileae (Renner, 1993; Fig. 1). Berries and dry capsular fruits from inferior ovaries are also present in the tribe (Figs. 1–3).

Circumscriptions of the African genera have been more-or-less similar among the different monographs and taxonomic treatments (Hooker, 1867; Triana, 1872; Krasser, 1893; Gilg, 1898). Within Oxysporeae, two Malagasy genera were treated, *Veprecella* Naudin (= *Gravesia*) and *Rousseauxia* (Hooker, 1867; Triana, 1872). Krasser (1893) additionally included *Phornothamnus* Baker (= *Gravesia*). Gilg (1898) also included *Urotheca* Gilg and *Petalonema* Gilg (= *Neopetalonema* Brenan), both now treated as additional synonyms of *Gravesia*. Within the African Sonerileae, three genera were recognized: *Amphiblemma* Naudin, *Calvoa* Hook.f. and *Gravesia* (Hooker, 1867; Triana, 1872; Krasser, 1893). Dissochaeteae (= Medinilleae) were composed of *Dicellandra* Hook.f., *Medinilla* and *Sakersia* Hook.f. (= *Dichaetanthera* Endl., now treated in Melastomataceae) and sometimes *Gravesia* (Hooker, 1867; Triana, 1872; Krasser, 1893; Gilg, 1898). Four new genera *Cincinnobotrys*, *Myrianthemum* Gilg (= *Medinilla*), *Phaeoneuron* Gilg (= *Ochthocharis* Blume) and *Tetraphyllaster* Gilg (= *Tristemma* Juss.) were later placed in the Sonerileae by Gilg (1898).

The family-wide classification of Renner (1993) recognized the following genera within African Sonerileae: *Amphiblemma*, *Calvoa*, *Cincinnobotrys* (= *Gravesiella* A.Fern. & R.Fern, *Haplophyllophorus* A.Fern. & R.Fern. and *Primularia* Brenan), *Dicellandra*, *Gravesia* (= *Orthogoneuron* Gilg and *Neopetalonema*), *Feliciademia* Bullock (= *Adamia* Jacq.-Fél.), *Ochthocharis* (= *Phaeoneuron*) and *Preussiella* Gilg. She also transferred *Medinilla* from Dissochaeteae to Miconiae. Apart from *Ochthocharis* placed in the Oxyspora alliance, the remaining African and Malagasy genera were treated in the Sonerila-Bertolonia-Gravesia alliance (Renner, 1993). The last classification proposed for the African Sonerileae and Dissochaeteae was by Jacques-Félix (1995). He treated *Ochthocharis*, *Medinilla* and *Dinophora* Benth. in Dissochaeteae and proposed a monogeneric tribe, *Feliciademiae*, for *Feliciademia*. He retained the rest of the genera in Sonerileae. *Dinophora* and *Ochthocharis* are neither part of the Dissochaeteae s.s. nor the Sonerileae complex; they are instead in a polytomy with

Table 1 Classification history of African Sonerileae

	Cogniaux, 1891, based on Triana, 1872	Krasser, 1893	Hooker, 1867	Baillon, 1877	Gilg, 1898; Engler, 1921	Renner, 1993	Jacques-Félix, 1995 and his earlier publications	This study
Dissochaetiae					Dissochaeteae	Melastomatae	Dissochaetiae	Sonerileae
<i>Dicellaandra</i>	<i>Dicellaandra</i>	<i>Medinillinae</i> (= <i>Dissochaetiae</i>)	<i>Bertoloniinae</i> (incl. <i>Sonerileae</i>)	<i>Bertoloniinae</i> (incl. <i>Sonerileae</i>)	<i>Dicellaandra</i>	<i>Dinophora</i>	<i>Medinilla</i>	<i>Amphiblemma</i>
<i>Sakertia</i>	<i>Sakertia</i>	<i>Dicellaandra</i>	<i>Amphiblemma</i>	<i>Sakertia</i>	<i>Sakertia</i>	<i>Rousseauxia</i>	<i>(+ Myrianthemum)</i>	<i>Benna</i>
(= <i>Dichaetanthera</i>)	(= <i>Dichaetanthera</i>)	<i>Sakertia</i>	<i>Calvoa</i>	<i>Medinilla</i>	<i>Medinilla</i>	<i>Tristemma</i>	<i>Dinophora</i>	<i>Boundaria</i>
<i>Medinilla</i>	<i>Medinilla</i>	<i>Medinilla</i>	<i>Gravlesia</i>	<i>Myrianthemum</i>	<i>Myrianthemum</i>	<i>(= Tetraphylaster)</i>	<i>Ochthocharis</i>	<i>Calvoa</i>
Osbeckiae				Dissochaeteae	Dissochaeteae	Miconiae	Cincinnobotrys	
(= <i>Melastomatae</i>)				<i>Dicellaandra</i>	<i>Dicellaandra</i>	<i>Tetraphylaster</i>	<i>(= Phaeoneuron)</i>	<i>Dicellaandra Gravlesia</i>
<i>Dinophora</i>	<i>Dinophora</i>	<i>Oxysporae</i>	<i>Sakertia</i>	<i>Phaeoneuron</i>	<i>Phaeoneuron</i>	<i>Feliciadaniæa</i>	<i>(in Africa and Madagascar)</i>	
Oxysporae		<i>Veprecella</i>	<i>Medinillinae</i>	<i>Preussiella</i>	<i>Medinilla</i>	<i>Feliciadaniæa</i>	<i>Medinilla</i>	
<i>Veprecella</i>	<i>Ochthocharis</i>	<i>Ochthocharis</i>	<i>Medinilla</i>	<i>Orthogoneuron</i>	<i>Sonerileae</i>	<i>(= Adamea)</i>	<i>Medinilla</i>	(in Africa, Madagascar and Asia)
<i>Ochthocharis</i>	<i>Rousseauxia</i>	<i>Rousseauxia</i>	<i>Melastomatae</i>	<i>Melastomatae</i>	<i>Oxyspora Alliance</i>	<i>Melastomatae</i>	<i>Dinophora</i>	<i>Mendelia gen. nov.</i>
<i>Rousseauxia</i>	<i>Sonerileae</i>	<i>Sonerileae</i>	<i>Dinophora</i>	<i>Dinophora</i>	<i>Ochthocharis</i>	<i>Ochthocharis</i>	<i>Preussiella</i>	
Sonerileae		(incl. <i>Bertoloniinae</i>)	<i>Oxysporae</i>	<i>Sonerileae</i>	<i>(= Phaeoneuron)</i>	<i>Sonerila-Bertolonia-</i>	<i>Feliciadaniæa</i>	
<i>Amphiblemma</i>	<i>Amphiblemma</i>	<i>Amphiblemma</i>	<i>Ochthocharis</i>	<i>Amphiblemma</i>	<i>Ochthocharis</i>	<i>Gravesia Alliance</i>	<i>Feliciadaniæa</i>	
<i>Calvoa</i>	<i>Calvoa</i>	<i>Calvoa</i>	<i>Rousseauxia</i>	<i>Calvoa</i>	<i>Amphiblemma</i>	<i>Amphiblemma</i>	<i>Calvoa</i>	<i>Melastomatae</i>
<i>Gravlesia</i>	<i>Gravlesia</i>	<i>Gravlesia</i>	<i>Rousseauxia</i>	<i>Oxysporae</i>	<i>Calvoa</i>	<i>Cincinnobotrys</i>	<i>Rousseauxia</i>	
				<i>Urotheca</i>	<i>Oxyspora</i>	<i>(+ Boundaria)</i>	<i>Dinophoreæ</i>	
				<i>Petalonema</i>	<i>Haplophyllophorus</i>	<i>Dicellaandra</i>	<i>Dinophora</i>	
					<i>and Primularia</i>	<i>Preussiella</i>	<i>Ochthocharis</i>	
					<i>Gravlesia</i>	<i>Dicellaandra</i>		
						<i>Feliciadaniæa</i>		
						<i>Preussiella</i>		
						<i>Gravlesia</i>		

Author names of genera: *Adamea* Jacq.-Fél., *Amphiblemma* Naudin, *Benna* Burgt & Ver-Lib., *Boundaria* A.Chev., *Calvoa* Hook.f., *Dichaetanthera* Endl., *Dinophora* Benth., *Feliciadaniæa* Bullock, *Gravlesia* Naudin, *Gravlesia* Brenan, *Haplophyllophorus* A.Fern. & R.Fern., *Mendelia* Ver-Lib. & G.Kadereit, *Myrianthemum* Gilg, *Neopetalonema* Blume, *Orthogoneuron* Gilg, *Petalonema* Gilg, *Phaeoneuron* Gilg, *Phornothamnus* Baker, *Preussiella* Gilg, *Primuluria* Brenan, *Rousseauxia* DC., *Sakeria* Hook.f., *Tetraphylaster* Gilg, *Tristemma* Juss., *Urotheca* Gilg, *Veprecella* Naudin.



Fig. 1. Representatives of African Sonerileae. **A–E**, *Benna alternifolia*. **F–H**, *Amphiblemma soyauxii*. **I, J**, *Amphiblemma cymosum*. **K**, *Amphiblemma ciliatum*. **L, M**, *Amphiblemma heterophyllum*. **N, O**, *Amphiblemma setosum*. **P, Q**, *Amphiblemma gossweileri*. **R, S**, *Calvoa hirsuta*. **T, U**, *Calvoa pulcherrima*. **V–X**, *Calvoa seretii*. **Y–AB**, *Calvoa monticola*. **AC, AD**, *Calvoa orientalis*. **AE, AF**, *Calvoa crassinoda*. **AG, AH**, *Calvoa jacques-felixii*. **AI**, *Calvoa trochainii*. Photographs by P. Barberá (R, T, U), X.M. van der Burgt (A–E), E. Bidault (F, H, K, M, O, S, V, X–Z, AA, AC, AD), K. Koïogui (I, J), O. Lachenaud (G, N, AE, AF), A.–H. Paradis (D, L), T. Stévert (AI), N. Texier (AB).



Fig. 2. Representatives of the new monospecific genus *Mendelia* and the reinstated monospecific genus *Bourdaria*. **A–G**, *Mendelia mollis* (*Amphiblemma molle*). **H–O**, *Bourdaria felicis* (*Cincinnobotrys felicis*). Photographs by N. Texier (A), E. Bidault (B–C), L. MacKinnon (F, G), X.M. van der Burgt (D, E, H–O).



Fig. 3. Representatives of African and Malagasy Sonerileae. **A, B**, *Dicellandra barteri* var. *barteri*; **C, D**, *Dicellandra barteri* var. *escherichii*; **E–G**, *Dicellandra descoingsii*; **H**, *Cincinnobotrys speciosa*; **I–K**, *Cincinnobotrys oreophilus*; **L–O**, *Preussiella kamerunensis*; **P, Q**, *Medinilla fasciculata*; **R**, *Medinilla torrentum*; **S**, *Medinilla sedifolia*; **T**, *Medinilla occidentalis*; **U**, *Gravesia thymoides*; **V, W**, *Gravesia setifera*; **X, Y**, *Gravesia laxiflora*; **Z**, *Gravesia erecta*. Photographs by F. Almeda (P–R), H. Andriamiarinoro (T), E. Bidault (A, C–F), H. Rasoazanany (S), A–H Paradis (G), M. Schmidt (H–K), A. Sieder (U), T. Stévert (O, L), E. Lerat (N).

Rhexieae, Microlicieae, Marcetieae and Melastomateae. Both of these genera are now placed in a new tribe, Dinophoreae (Penney et al., 2022). A summary of these different classification schemes is provided in Table 1.

More than 99% of the tropical African species currently treated in Sonerileae are unsampled in molecular phylogenetic studies. Therefore, it is unknown if the African and Asian members of Sonerileae are a natural lineage. In addition, it is unknown whether the currently recognized African Sonerileae genera are monophyletic lineages. As such, the present study seeks to: (i) resolve phylogenetic

relationships of the Sonerileae complex using two nuclear (nrETS, nrITS) and three plastid (*accD-psal*, *ndhF*, *psbK-psbL*) markers, based on a broad sampling; (ii) test monophyly of the currently recognized African genera and (iii) propose a revised generic classification for the African species. A key to all currently accepted African Sonerileae genera is provided. For each previously recognized genus, a diagnosis is provided and a list of accepted taxa. For the newly described genera, a diagnosis, etymology, full description and accepted taxa are provided. Notes are provided to explain lecto- and neotypifications.

2 Material and Methods

2.1 Taxon sampling

A total of 245 accessions representing 220 species were included in the phylogenetic analyses to resolve phylogenetic relationships of the Sonerileae complex, with emphasis on the African members. Of the 245 accessions sampled, 91 represent African (64) and Malagasy (27) species. A total of 46 species of Asian Sonerileae and a single species of each of three American Sonerileae genera *Boymania*, *Phainantha* and *Tryssophyton* were also sampled. Except for *Feliciadamia* which is still unsampled, the rest of the African endemic genera (including type species) currently treated in the Sonerileae complex were sampled (*Amphiblemma* 12/15, *Calvoa* 8/19, *Cincinnobotrys* 4/8, *Dicellandra* 2/3 and *Preussiella* 1/2). In addition, 25 *Gravesia* (including 2/5 African spp. and 23/111 Malagasy spp.) and 17 *Medinilla* species (1/3 African spp., 4/73 Malagasy spp., 12/303 Asian spp.) were also sampled. As outgroup, 105 species from other currently accepted tribes [Bertoloniiae (7 spp.), Pyxidantheae (=Blakeeae) (3 spp.), Pyramieae (=Cambessedesiae) (1 sp.), Dissochaeteae (10 spp.), Dinophoreae (3 spp.), Eriocnemeae (1 sp.), Henrieteeae (1 sp.), Marcteiae (11 spp.), Melastomataee (33 spp.), Merianiae (15 spp.), Miconiae (6 spp.), Lavoisiereae (=Microlicieae) (6 spp.), Rhexieae (4 spp.) and Trioleneae (3 spp.)] in the subfamily Melastomatoideae were sampled. GenBank accession numbers are provided in Appendix I.

2.2 DNA extraction, amplification and sequencing

Total genomic DNAs were extracted, amplified and sequenced as described in Veranso-Libalah et al. (2017, 2018, 2020). Two nuclear [the nuclear ribosomal internal transcribed spacers (nrITS) and the nuclear ribosomal external transcribed spacer (nrETS)] and three plastid loci (*accD-psal*, *psbK-psbL* and *ndhF*) were amplified and sequenced. These loci have been widely used in phylogenetic studies across the Melastomataceae (Michelangeli et al., 2004, 2008, 2011, 2013; Kriebel et al., 2015; Reginato & Michelangeli, 2016; Rocha et al., 2016; Veranso-Libalah et al., 2017, 2020; Guimarães et al., 2019; Kartonegoro et al., 2021). All the African Sonerileae sequences were generated in a previous study (Burgt et al., 2022); voucher information is provided in the online supporting information (Table S1). Additional outgroup sequences were obtained from GenBank.

2.3 Phylogenetic inference

Contigs of forward and reverse sequences were assembled and manually edited using SEQUENCER v.4.1.4 (Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were automatically aligned using MAFFT v.7 (Katoh & Standley, 2013) and then manually adjusted in MESQUITE v.3.10 (Maddison & Maddison, 2016) or MEGA v.11 (Tamura et al., 2021). The best-fit partitioning scheme and models of molecular evolution for the data set were determined using PartitionFinder v.2 (Lanfear et al., 2012, 2017), with the following search parameters: linked branch length; models available in BEAST v.2.5 (Bouckaert et al., 2019), AIC model selection; greedy search algorithm. Each of the five markers was set in the input file as a distinct data block, to avoid over-parameterization.

Using maximum likelihood (ML) and Bayesian inference (BI), phylogenetic analyses were separately conducted on the nuclear (nrETS and nrITS) and plastid loci (*ndhF*, *psbK-psbL* and *accD-psal*). Without any well-supported topological conflicts between the nuclear and plastid gene trees (see Supporting information, Figs. S1–S4), all further analyses were performed using the concatenated 5-loci data set (*ndhF*, *psbK-psbL*, *accD-psal*, nrETS and nrITS). Maximum likelihood analyses were performed using RAxML v.8 (Stamatakis, 2014) with a GTRGAMMA model of sequence evolution and 1000 bootstrap replicates (Felsenstein, 1985). The BI analyses were performed using BEAST v.2.5.0 (Bouckaert et al., 2019). Four independent Markov chain Monte Carlo (MCMC) analyses were run, each of 30 million generations sampling every 3000 generations. All xml files were prepared using BEAUTI and run on the CIPRES Science Gateway v.3.3 (<https://www.phylo.org>; Miller et al., 2010). We used TRACER v.1.6 (Rambaut & Drummond, 2013) to assess convergence and effective sampling size (ESS) of all parameters from the output log files. As “burn-in,” 25% of samples were removed prior to combining the independent runs using LOGCOMBINER v.2.5 (Bouckaert et al., 2019). A Maximum Clade Credibility tree was constructed using TREEANNOTATOR v.2.5 (Bouckaert et al., 2019) and node support was expressed as posterior probability (PP). All phylogenetic analyses were performed using the CIPRES Science Gateway v.3.3 (<https://www.phylo.org>; Miller et al., 2010).

2.4 Taxonomic treatment

The morphology of African Sonerileae was studied from herbarium specimens [herbaria visits (BRLU and BR), loans (BR, BRLU, C, K, MO, UPS) and through online repositories from BM (<http://data.nhm.ac.uk/>), LISC (<http://actd.iict.pt/>), P (<https://science.mnhn.fr/all/search>), WAG (<http://bioportal.naturalis.nl/>), Z (<http://www.herbarien.uzh.ch/en/Datenbanken.html>) and COI (raw catalogue of specimens was provided but not yet publicly available online)]. Types and additional morphological information were obtained from literature (Hooker, 1867; Brenan, 1953; Engler, 1921; Fernandes & Fernandes, 1956, 1960; Jacques-Felix, 1952, 1955, 1973, 1974a, 1974b, 1976, 1977, 1981, 1983a, 1983b, 1987, 1995; Wickens, 1975).

3 Results

3.1 Molecular variation

A total of 4814 aligned characters (1911 parsimony-informative sites) were used for the analyses. The combined chloroplast data set of all three markers comprised 3164 aligned base pairs while the combined nuclear data set consisted of 1650 aligned base pairs. The selected substitution model for the nrETS, nrITS and *ndhF* loci was GTR + Γ + I, and for the *psbK-psbL* and *accD-psal* loci was GTR + Γ (Table 2). Additional information and statistics for the data set are provided in Table 2.

3.2 Major phylogenetic relationships

The Sonerileae complex is only weakly supported by the ML analyses (Figs. 4A, 4B; BS 59). Excluding the neotropical

Table 2 Summary statistics of genomic regions sequenced for phylogenetic analyses of African Sonerileae

Marker	Accessions sampled	Aligned			Variable sites	% Variable sites	Parsimony-informative sites		% PIS	Models
		base pairs	% Missing data	Conserved sites			% PIS			
nrITS	131	482	47	41	419	87	376	77	GTR + Γ + I	
nrITS	212	1166	14	293	720	62	515	44	GTR + Γ + I	
accD-psal	148	1418	40	658	638	45	354	25	GTR + Γ	
ndhF	175	1077	29	498	559	52	394	37	GTR + Γ + I	
psbK-psbL	203	609	17	174	367	92	270	44	GTR + Γ	
Combined	245	4818	29	1657	2710	56	1911	40		

Boyania which is weakly supported as sister to the remaining members of the Sonerileae complex, the rest of the genera form a well-supported monophyletic clade (Fig. 4B; BS 97/PP 1). Within this lineage, a clade consisting of the neotropical Phainantha and the African monospecific *Benna* Burgt & Ver.-Lib. is sister to the rest of the species. The next lineage is Tryssophyton, another neotropical taxon which is sister to a large clade of the remaining Sonerileae. This large Sonerileae clade consists of the largely Asian and the African-Malagasy endemic subclades. The largely Asian clade is composed of all the genera previously treated in the tribe Dissochaeteae subtribe Medinillinae (Medinilla-alliance), Oxysporaeae and the Asian Sonerileae s.s. The African (*Medinilla manii* Hook. f.) and Malagasy *Medinilla* species sampled are nested within this largely Asian clade. Although we did not sample the type of *Medinilla* [*M. medinilliana* (Gaudich.) Fosberg & Sachet] the genus as previously circumscribed is polyphyletic (albeit without strong support).

The African-Malagasy endemic clade (excluding *Medinilla*) is recovered as a well-supported monophyletic lineage (Fig. 4B; BS 100/PP 1). Within this clade, *Gravesia* is recovered as monophyletic (Fig. 4B; BS 100/PP 1) and sister to the other genera. *Cincinnobotrys felicis* (A.Chev.) Jacq.-Fél. is sister to a clade composed of *Dicellandra*, *Calvoa*, *Preussiella*, *Amphiblemma* and *Cincinnobotrys* s.s. (excluding *C. felicis*). The genera *Dicellandra* and *Calvoa* are both well-supported lineages (Fig. 4B). *Amphiblemma* on the other hand is paraphyletic with *Preussiella* and some *Cincinnobotrys* species nested within it.

4 Discussion

4.1 Sonerileae s.l.

The molecular results presented herein do not support any of the traditional classifications of the Sonerileae (see Fig. 4B; Table 1). Instead, Sonerileae s.l. (including *Medinilla* and related genera) form a monophyletic lineage. These results are similar to those previously reported (see Bacci et al., 2019; Zhou et al., 2019, 2022; Kartonegoro et al., 2021). Morphologically, Sonerileae s.l. are a very diverse lineage, but most species are characterized by apically crowned ovaries, angular fruits, persistent hypanthia and non-cochleate seeds with a tuberculate testa (Renner, 1993). Although there has been an attempt to resolve phylogenetic relationships within the largely Asian clade (Zhou et al., 2019, 2022), an in-depth sampling with better resolution of the Asian lineages is still

needed. In addition, the two most diverse genera, *Medinilla* (~379 spp.) and *Sonerila* (~184 spp.), are still sparsely sampled with less than 5% of their species included in molecular studies.

4.2 African Sonerileae

4.2.1 *Benna*

Benna is a monospecific genus endemic to Guinea (Burgt et al., 2022). It has large ovate-orbicular alternate leaves and a short paniculate inflorescence appearing somewhat fascicled (Figs. 1A–1E). Together with the neotropical genera sampled, *Benna* is among the basally diverging lineages and unrelated to the other African or Malagasy genera of Sonerileae (Fig. 4B). It is partially supported (BS 74%) as sister to the South American genus *Phainantha*.

4.2.2 *Medinilla*

The species-rich *Medinilla* consists of ca. 379 species found in Asia (303 spp.), Madagascar (73 spp.), Africa (3 spp.) and one in Australia (Perrier de la Bâthie, 1951; Wickens, 1975; Jacques-Félix, 1983a; Regaldo, 1990, 1995; Renner, 1993; Bánki et al., 2021). Malagasy species of *Medinilla* have been treated in two sections, *Septatae* H.Perrier and *Adhaerentes* H.Perrier based on ovary adnation. Section *Septatae* was further divided into three groups, and sect. *Adhaerentes* into six groups (Perrier de la Bâthie, 1951). In Africa, three species are currently accepted: the Tanzanian endemic *Medinilla engleri* Gilg, *M. mirabilis* (Gilg) Jacq.-Fél. which is restricted to Cameroon, Equatorial Guinea, and Gabon, and the widespread *M. manii* (occurring in the Guinean-Congolian rainforest from Cameroon to Guinea and extending to Uganda).

In this study, we sampled 17 *Medinilla* species, including four from Madagascar, one from Africa (*M. manii*), and 12 from Asia. We found that *Medinilla* is polyphyletic and nested within the Asian Sonerileae. Although the backbone within the largely Asian clade is unresolved, *M. manii* from Africa is sister to three of the four Malagasy species sampled (Fig. 4B). Based on morphological evidence, *Medinilla* was previously treated in Dissochaeteae (Hooker, 1867; Baillon, 1877; Cogniaux, 1891; Krasser, 1893; Gilg, 1898; Engler, 1921; Jacques-Félix, 1995), Medinilleae (Baillon, 1877) or Miconiaeae (Renner, 1993). Our current molecular phylogeny rejects the inclusion of *Medinilla* in any of the above tribes. These results are similar to those of previous molecular studies (Clausing & Renner, 2001; Bacci et al., 2019; Zhou et al., 2019). Our current phylogenetic sampling does not provide any insight into the

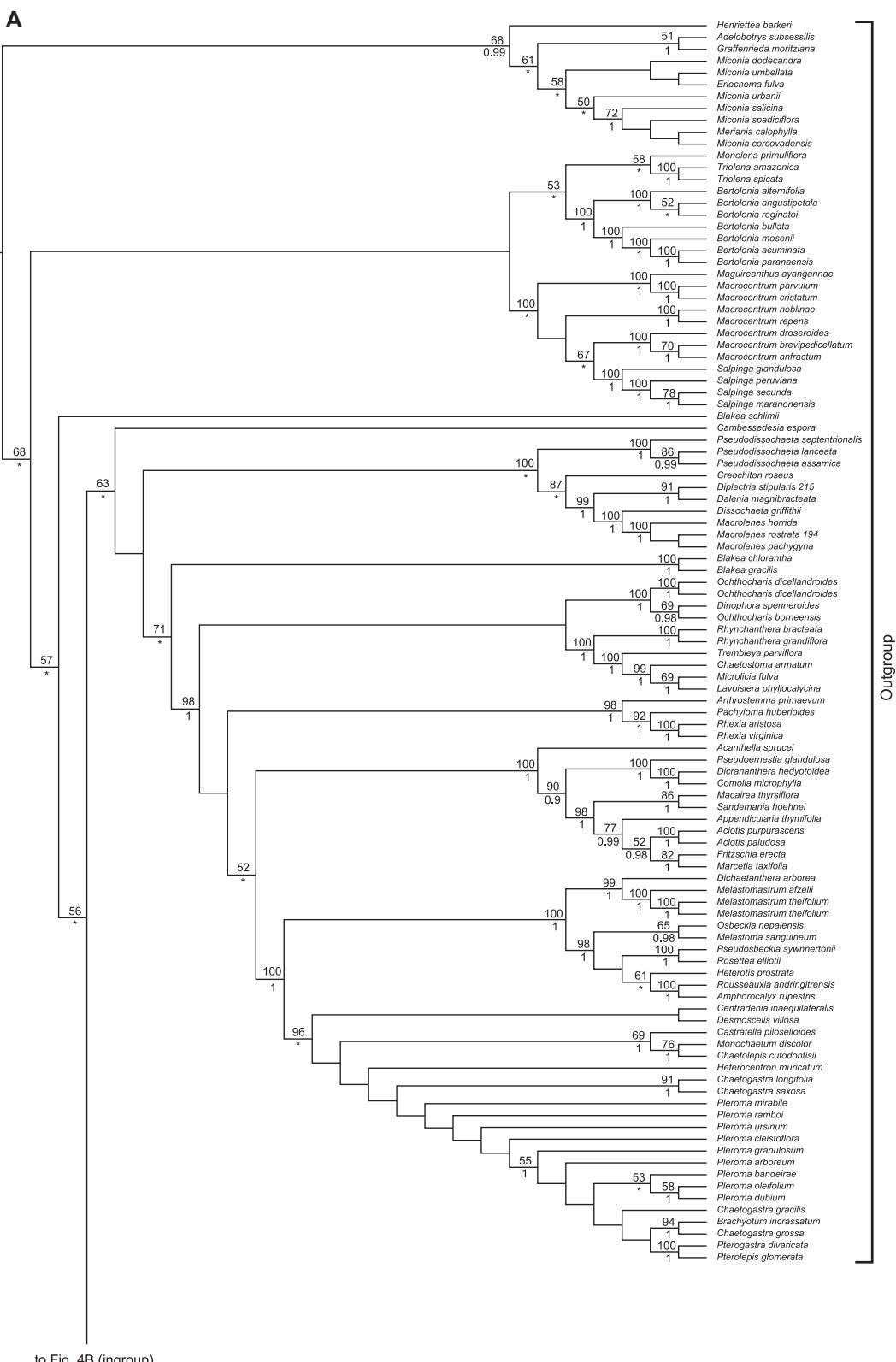


Fig. 4. A, B, Maximum likelihood (ML) phylogenetic cladogram of African Sonerileae with representatives of Asian and Malagasy Sonerileae and outgroups derived from the combined data matrix (nrITS, nrETS, accD-psal, ndhF, psbK-psbL). Values above branches refer to bootstrap values resulting from the ML analysis (only values ≥ 50), and values below branches refer to the posterior probabilities resulting from Bayesian inference (only values ≥ 0.90). An asterisk (*) denotes a branch supported by either bootstrap or posterior probability only.

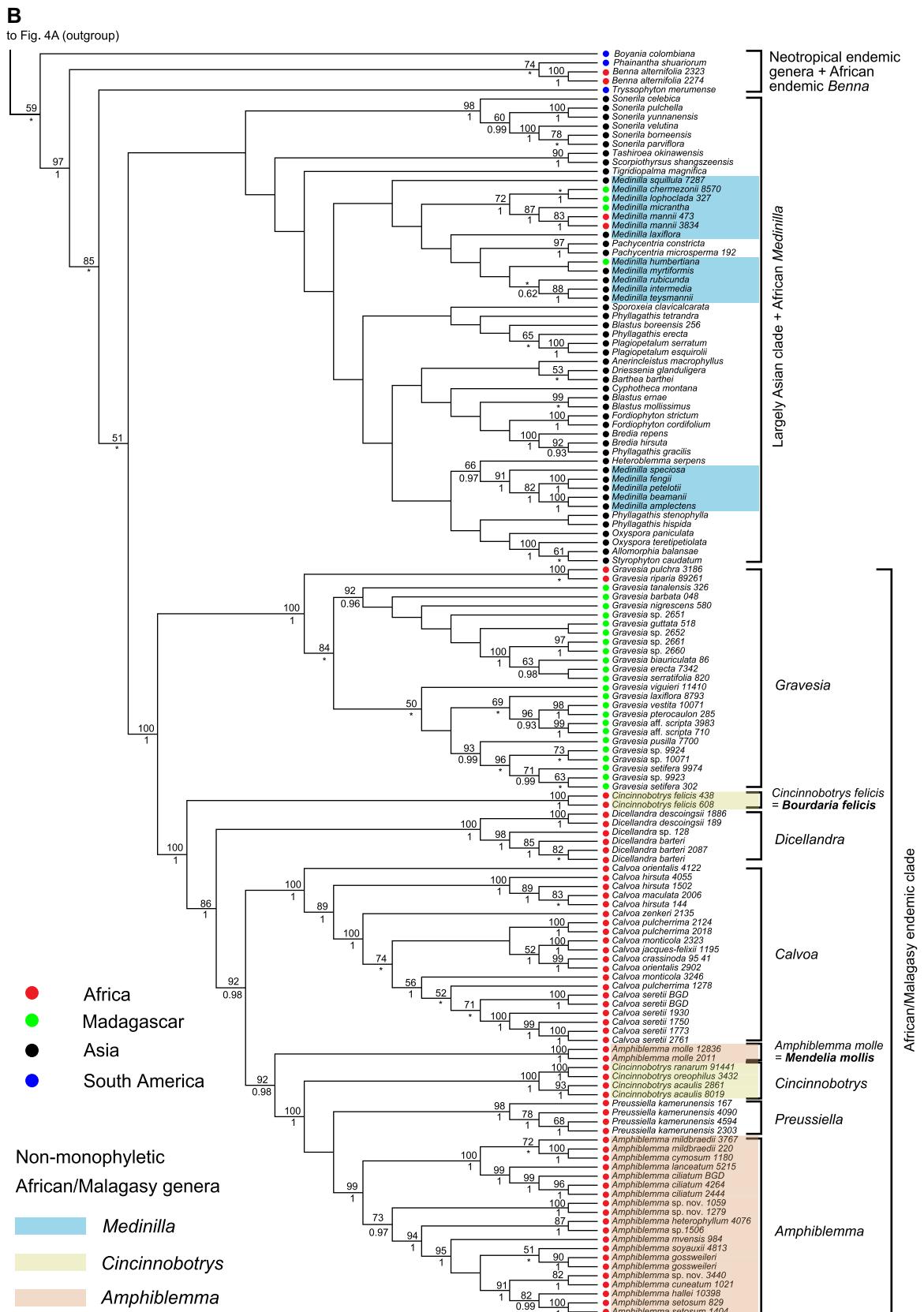


Fig. 4. Continued

monophyly or infrageneric classification of African and Malagasy *Medinilla*.

Medinilla is a morphologically heterogeneous genus of acaulescent or caulescent herbs, scandent climbing epiphytic or terrestrial shrubs, and rarely small trees to 9 m tall (*M. whitfordii* Merr.). The fruits are globular, baccate and bacciform with many oblong-cuneate seeds (Jumelle & Perrier de la Bâthie, 1914; Perrier de la Bâthie, 1951; Fernandes & Fernandes, 1956; Wickens, 1975; Regaldo, 1990, 1995).

4.2.3 *Gravesia*

Gravesia is also rich in species (ca. 116), most of which are endemic to Madagascar with only five endemic species in Africa. It is a morphologically diverse genus of acaulescent or caulescent plants ranging from erect or prostrate herbs to erect shrubs or scandent climbing vines with adventitious roots. The capsule is more-or-less angular and crowned by conspicuous accrescent often slightly woody plates or wedge-like scales. The seeds are oblong to obpyramidal (Perrier de la Bâthie, 1951; Fernandes & Fernandes, 1956; Jacques-Félix, 1983a; Figs. 3U–3Z).

Due to the large morphological diversity of Malagasy *Gravesia*, three subgenera *Eugravesia* (*Gravesia*) (= 100 spp.), *Peltivesia* H.Perrier (6 spp.) and *Amphorovesia* H.Perrier (1 sp.) were proposed by Perrier de la Bâthie (1932, 1951). The subg. *Eugravesia* was further divided into four sections: sect. *Macrophyllae* H.Perrier, sect. *Primuloidae* H.Perrier, sect. *Pauciflorae* H.Perrier and sect. *Scandentes* H.Perrier (Perrier de la Bâthie, 1951). Although Africa has few species of *Gravesia*, the taxonomy of this genus has been problematic. Three monospecific African genera [*Neopetalonema* (= *Petalonema*), *Orthogoneuron* and *Urotheca*] are now considered synonyms of *Gravesia*. In Africa, three of the five species are endemic to Tanzania [*G. hylophila* (Gilg) A.Fern. & R.Fern, *G. pulchra* (Gilg) Wickens and *G. riparia* A.Fern. & R.Fern.]. *Gravesia gabonensis* Jacq.-Fél. is endemic to Gabon while *G. lebrunii* Jacq.-Fél. is endemic to DR Congo.

In our combined molecular analyses, 25 accessions of *Gravesia* were sampled (2 from Africa and 23 from Madagascar). Our results recovered both the African and Malagasy *Gravesia* forming a clade (Fig. 4B). The African *Gravesia* species sampled are sister to the Malagasy species. With the current limited sampling, we are unable to provide any insights into the infrageneric classification of the Malagasy members.

4.2.4 *Bourdaria felicis* (*Cincinnobotrys felicis*)

The genus *Bourdaria* was described by Chevalier (1932) and distinguished from *Cincinnobotrys* by the fasciculate flowers and distinctly appendiculate stamens. *Bourdaria felicis* A.Chev., the only species in this genus, was transferred to *Cincinnobotrys* by Jacques-Félix (1976) based on its staminal morphology, despite its morphological uniqueness and distribution in West Africa, while all other species of *Cincinnobotrys* occur in Central and East Africa. *Cincinnobotrys felicis* is endemic to rocky hills in Guinea and Sierra Leone (a single collection at Kew is from Gbengbe Hills) where it grows in humid crevices on vertical rock (Figs. 2H–2O).

According to Jacques-Félix (1976), unlike the other *Cincinnobotrys* species in which new plants grow from lateral buds on the tubers or rhizomes, in *C. felicis* the stem arises vertically from the thickened base which is usually attached to the substrate. During its growing season, a few rosette leaves and sessile, axillary and terminal cymes are produced, so that the stem immediately acquires its final diameter and nodular appearance. Vertical elongation is very slow with an 8–10 cm long stem for a plant nearly 20 years old. Small plantlets may arise from either the base or the top of the tuber as the mother plant approaches senescence. All the same, the stem remains short, and it is this unicaulous characteristic that makes the species unique. Although not very visible, the growth is certainly sympodial, as indicated by the position of the apical flowers (Jacques-Félix, 1976).

Excluding *C. felicis*, *Cincinnobotrys* species have a single peduncle with a solitary flower or cymose inflorescence. In *C. felicis*, the inflorescences are axillary fascicles with one to several flowers borne on long and slender pedicels (Figs. 2H–2O). Like most *Cincinnobotrys* species [except for *C. acaulis* (Cogn.) Gilg and *C. pulchellus* (Brenan) Jacq.-Fél. with pentamerous flowers], *C. felicis* has tetramerous flowers (Jacques-Félix, 1976). In *C. felicis* the ovary is adherent to the hypanthium for its entire length with the calyx lobes peripherally accrescent and the placentas clearly displaced on the apex. The crown forms acute margins from the concave ovary. The fruits are tetragonal, marked with four calyx ribs and four weaker intermediates. The seeds are 0.5 mm long, with a slender and fragile funicle, obovoid, asymmetric, and finely tuberculate (Jacques-Félix, 1976).

In our molecular analyses, *C. felicis* is excluded from *Cincinnobotrys* s.s. and instead recovered as sister to a clade consisting of *Dicellandra*, *Calvoa*, *Preussiella*, *Amphiblemma* and *Cincinnobotrys* s.s. (Fig. 4B). Together with its unique morphology and geographical distribution, our molecular analyses support reinstating the monospecific genus *Bourdaria*.

4.2.5 *Dicellandra*

Dicellandra was described by Hooker (1867), but over the decades its species composition grew doubtful (Jacques-Félix, 1974a). A total of ten species have been described in *Dicellandra* with only three species currently accepted [*D. barteri* Hook. f., *D. descoingsii* Jacq.-Fél. and *D. glanduligera* (Pellegr.) Jacq.-Fél.]. Four varieties for *D. barteri* [var. *barteri*, var. *erecta* Jacq.-Fél., var. *escherichii* (Gilg ex Engl.) Jacq.-Fél. and var. *magnifica* Jacq.-Fél.] are also currently accepted (Jacques-Félix, 1974a, 1983a, 1983b). Morphologically, *Dicellandra* are erect or creeping, ascending to leaning single-stemmed perennials or shrubs with a sympodial branching habit. The inflorescences are compound uniparous terminal cymes. The capsules are ellipsoid-oblong to globular and remain enveloped by the hypanthium and persistent calyx. Dehiscence occurs by rupture of the capsule walls, which are apparently hygroscopic and mucilaginous (Figs. 3A–3G). The seeds are probably dispersed by water (Jacques-Félix, 1974a). The chromosome number of *D. barteri* is either $n = 32$ or $n = 34$ (Favarger, 1952, 1962), but the other species are still uncounted.

In our molecular analyses, we included six accessions representing two *Dicellandra* species (*D. barteri* and *D. descoingsii*). We recovered *Dicellandra* as a monophyletic lineage and sister to a clade consisting of *Calvoa*, *Preussiella*, *Amphiblemma* and *Cincinnobotrys* s.s. (Fig. 4B). *Dicellandra* was treated in *Dissochaeteae* (*Medinilleae*) by several authors based on its irregular capsule dehiscence and wedged-shaped seeds (Hooker, 1867; Triana, 1872; Cogniaux, 1891; Gilg, 1898; Engler, 1921; Jacques-Félix, 1955). In the revision of *Dicellandra* and later taxonomic treatments, it was treated in *Sonerileae* (Jacques-Félix, 1974a, 1983a, 1983b). Our molecular results support the inclusion of *Dicellandra* in *Sonerileae*.

Dicellandra barteri is widespread in the Guinean-Congolian region from Cameroon to Liberia. *Dicellandra barteri* var. *magnifica* is found almost throughout the eastern DR Congo to Kivu and Uganda but also in Mayombe. The other varieties have narrower distributions. *Dicellandra barteri* var. *erecta* is restricted to the southern region of Cameroon and the Biafran region while var. *escherichii* extends from southern Cameroon to the mouth of the Congo. *Dicellandra glanduligera* and *D. descoingsii* are only known from a few sites in the Ngounié basin in Gabon. Jacques-Félix (1974a) suggested that *Dicellandra* are humicolous and either hygro-sciaphilous or hemisaprophytes. However, this interesting phenomenon is still being monitored in the field.

4.2.6 *Calvoa*

The genus *Calvoa* was established by Hooker (1867) and was never disputed by subsequent authors in various floristic and revisionary treatments (Hooker, 1871; Hutchinson & Dalziel, 1927; Keay, 1954; Wickens, 1975; Jacques-Félix, 1983b; Figueiredo, 2001).

Calvoa are understory perennial herbs or shrubs sometimes climbing or decumbent, terrestrial or epiphytic, glabrous or glabrescent, puberulous with minute red hairs on young parts or rarely hirsute. The inflorescence is a terminal (rarely axillary) scorpioid cyme, flowers are pentamerous, brachymorphic and somewhat gamopetalous (Fig. 1R; A1). Sepals are distinctly or inconspicuously 5-lobed. The stamens are diplostemonous (Jacques-Félix, 1981; Figueiredo, 2001). Chromosome numbers in *Calvoa* are variable, for example, *C. monticola* A.Chev. ex Hutch. & Dalziel $n=28$, *C. sinuata* Hook.f. $n=14$, *C. pulcherrima* Gilg & Mildbr. $n=14$ and *C. orientalis* Taub. $n=17$ (Favarger, 1952, 1962; Jacques-Félix, 1952; Solt & Wurdack, 1980; Farron & Favarger, 1983).

We included 20 accessions of *Calvoa* representing nine species in our molecular analyses. All these accessions formed a monophyletic lineage sister to a large clade composed of *Amphiblemma molle* Hook.f., *Preussiella*, *Cincinnobotrys* and *Amphiblemma* s.s. (excluding *A. molle*). *Calvoa* is a morphologically well-defined genus supported by molecular data (Fig. 4B), but its species limits are nevertheless still poorly known. Several species, for example, *C. monticola*, *C. pulcherrima* and *C. orientalis* are not monophyletic (Fig. 4B). The 19 accepted species of *Calvoa* are mainly distributed in West-Central Africa (from Sierra Leone to Angola, through Central Africa) and in the

four islands of the Gulf of Guinea (Annobon, Bioko, São Tomé, and Príncipe). Only the widespread *C. orientalis* extends to East Africa (Ethiopia, Rwanda, Tanzania and Uganda).

4.2.7 *Amphiblemma*

The genus *Amphiblemma* was first described by Naudin (1851) as monospecific based on *Melastoma cymosum* Schrad. & Wendl. [= *A. cymosum* (Schrad. & Wendl.) Naudin]. There are currently 15 accepted species (Jacques-Félix, 1973, 1974b, 1987; Leal, 2008). This shade-tolerant genus is restricted to forest and gallery forest of Central Africa with its highest diversity and endemism in Gabon (10 spp.) and Cameroon (6 spp.). Engler (1921) proposed the first infrageneric classification of *Amphiblemma* and recognized three sections: sect. *Cincinnatae* Engl., sect. *Corymbosae* Engl., and sect. *Axillares* Engl. Later, Brenan (1953) proposed an additional section, *Amphiblemma* sect. *Haplophyllophora* Brenan. He distinguished this section from sect. *Amphiblemma* as follows: acaulous species, which usually have one or rarely two leaves per plant with the leaves and inflorescences arising directly from the rootstock or tuber (Brenan, 1953). On the other hand, *Amphiblemma* is composed of species with elongate stems bearing pairs of leaves separated by internodes, stems not enlarged and rooting laterally (Brenan, 1953). He transferred two species previously treated in *Cincinnobotrys* [*C. acaulis* (Cogn.) Gilg and *C. seretii* De Wild.] to sect. *Haplophyllophora*. Only the sect. *Cincinnatae* and sect. *Corymbosae* were accepted by Jacques-Félix (1973).

In this study, we sampled 22 accessions representing 12 species of *Amphiblemma*. Our results show that *Amphiblemma* is not monophyletic since one species, *A. molle*, is recovered outside of the *Amphiblemma* s.s. lineage (Fig. 4B). Excluding *A. molle*, a morphologically unique species and the lone species in sect. *Cincinnatae*, the remaining species of *Amphiblemma* (treated in sect. *Corymbosae*) are morphologically well characterized. Unlike the species in sect. *Corymbosae*, *A. molle* is characterized by solitary, erect, elongated, uniparous cymes with many flowers, sepals with a linear subapical appendage and an epigynous crown protruding at maturity. The species of sect. *Corymbosae* have uniparous cymes with two to five digitate branches forming a corymb or sometimes panicles. The cymes are at times reduced or pauciflorous, forming a contracted umbel or sometimes axillary cymes. The sepals lack linear appendages, and the epigynous crown is included (Figs. 1F–1Q).

We did not recover the two distinct morphological groups within sect. *Corymbosae* suggested by Jacques-Félix (1973), nor sect. *Axillares* Engl. (for *A. soyauxii*) by Engler (1921). Jacques-Félix (1973) had earlier rejected sect. *Axillares* since *A. ciliatum* (= *A. lateriflorum* Cogn.) like *A. soyauxii* may also have axillary flowers. Like Jacques-Félix (1973), our molecular results clearly suggest that *Amphiblemma* sect. *Haplophyllophora* and other closely related species should be treated in *Cincinnobotrys* and not *Amphiblemma*. Most *Cincinnobotrys* (including *Amphiblemma* sect. *Haplophyllophora*) species, even though acaulescent also have isomorphic anthers (except in *Cincinnobotrys oreophilus* Gilg, the type species) with the

connective base having a thickened ring, broader dorsally and slightly lobed. *Amphiblemma* species have dimorphic stamens that markedly differ in size and structure (diplostemonous), with a well-developed and prolonged connective; the larger, alternipetalous anthers usually have a dorsal appendage. *Amphiblemma cymosum* has a chromosome number of $n=38$ and *A. ciliatum* $n=19$ (Favarger, 1952, 1962; Jacques-Félix, 1952; Solt & Wurdack, 1980; Farron & Favarger, 1983). The chromosome numbers of the remaining species are still unknown.

Amphiblemma as treated here consists of 14 species mainly distributed in the Congolian region with only one species, *A. cymosum*, extending to the Guinean region. Morphological and molecular evidence suggest excluding *A. molle* from *Amphiblemma*.

4.2.8 *Mendelia mollis* (*Amphiblemma molle*)

Amphiblemma molle was described by Hooker (1871). Although its inflorescence would suggest that it belongs to *Amphiblemma* sect. *Cincinnatae*, Engler (1921) treated this species in *Amphiblemma* sect. *Corymbosae* on the basis of its leaves. He placed two species (*A. erythropodium* Gilg & Lederm. and *A. riparium* Gilg) from Cameroon in sect. *Cincinnatae*. Jacques-Félix (1973) in his revision of *Amphiblemma* treated *A. riparium* as a synonym of *A. molle* while he was unable to identify *A. erythropodium* and suggested it might be another synonym. He treated *A. molle* as the lone species in sect *Cincinnatae*. The type specimen of *A. erythropodium* was destroyed in Berlin during World War II.

In addition to its erect, elongated, uniparous cymes bearing alternate subsessile flowers, the mucronate sepal tip in *A. molle* develops into distinct linear appendages (Figs. 2A–2G). Also, the corolla is clearly reduced and inconspicuous. Most *Amphiblemma* species have capsules with loculicidal dehiscence via valves: the tip splits along the five valves dividing the epigynous crown into many segments. In the case of *A. molle*, the placentas separate from the axis and extend somewhat to the tip. The reduplicated membranous crown does not split over its entire length but opens in a star around the five branches of the placenta.

Based on morphological uniqueness and our molecular phylogenetic results (see Figs. 2A–2G, 4), we propose that *A. molle* should be treated in a new genus, *Mendelia* Ver.-Lib. & G.Kadereit (see taxonomic section for additional information). This monospecific genus is distributed in Angola, Cameroon, DR Congo, Congo Republic, Equatorial Guinea and Gabon.

4.2.9 *Cincinnobotrys*

Cincinnobotrys was described by Gilg (1898) as a monospecific genus based on *C. oreophilus*, an epiphytic acaulescent species with a bulbil-bearing rhizome, roots forming tubers, solitary leaves and tetramerous flowers. Gilg (1898) retained *A. acaule* Cogn. in *Amphiblemma* even though this species morphologically resembles *C. oreophilus*, differing from it only by having pentamerous flowers. The second species of *Cincinnobotrys*, *C. seretii* De Wild., was described by De Wildeman (1908) as very close to *A. acaule*.

After a comprehensive review of African Sonerileae, Brenan (1953) treated *A. acaule* and *A. seretii* Brenan in *Amphiblemma* sect. *Haplophyllophora* [*A. acaule* is now

Cincinnobotrys acaulis while *A. seretii* is *Cincinnobotrys acaulis* var. *seretii* (De Wild.) Maluma & Geerinck]. He also established the genus *Primularia* with type *P. pulchella* Brenan from a collection by W. Eggeling from southeastern Tanzania. Fernandes & Fernandes (1960) described the genus *Gravesiella* based on *G. speciosa* A.Fern. & R.Fern. collected by J. E. Procter from Tanzania. *Amphiblemma* sect. *Haplophyllophora* was then raised to the rank of genus, *Haplophyllophorus* by Fernandes & Fernandes (1972). Jacques-Félix (1976) in his revision of *Cincinnobotrys* treated *Bourdaria* (see above), *Haplophyllophorus*, *Gravesiella* and *Primularia* as synonyms of *Cincinnobotrys* due to their morphological resemblance.

Cincinnobotrys s.s. are acaulescent perennial herbs with one or two leaves and inflorescences arising from a bulbil-bearing rhizome (Figs. 3H–3K). They are epiphytes or epiliths that attach to their substrates using rhizomes, tubers or more rarely by a small napiform stump supporting an erect stem. Apart from *C. felicis*, the species usually have one cyme and one leaf (rarely two or more), with further growth emerging only from axillary buds. In *Cincinnobotrys* s.s., the lateral bud at the base of the leafy-flowering internode is also likely to produce a lateral branch. These species therefore have the ability to propagate and disperse vegetatively. Several collectors have reported them as being very abundant in their habitats (Jacques-Félix, 1976).

Anisophylly is also well-developed in *Cincinnobotrys* s.s., with a strong size reduction in one of the two leaves. The flowers are always small, except for the corolla which is sometimes well-developed. The receptacle is largely campanulate, turbinate or rarely urceolate. The petals are widely inserted and often asymmetrical. Except for *C. acaulis* with regularly pentamerous and *C. pulchellus* with tetra- or pentamerous flowers in the same small population, the rest of the species are tetramerous. *Cincinnobotrys* s.s. have either four (haplostemonous) equal, or eight (diplostemonous) dimorphic stamens in two whorls with well-developed appendages. The ovary has four or five locules that adhere to hypanthium/receptacle nearly to the top, which is apically depressed with a narrow glandular-ciliate crown or conspicuous scales. The seeds are generally obtuse with or without a minute papillate testa (Jacques-Félix, 1976).

For the molecular analyses, we sampled six accessions representing the following *Cincinnobotrys* s.l.: *C. acaulis* [= *Haplophyllophorus acaulis* (Cogn.) A.Fern. & R.Fern], *C. felicis* (= *Bourdaria felicis*), *C. oreophilus* (type species)] and *C. ranarum* Pócs. Excluding *C. felicis*, *Cincinnobotrys* is resolved as a monophyletic clade but in a polytomy with *Preussiella* and *Amphiblemma* s.s. (Fig. 4B) As here defined, *Cincinnobotrys* s.s. (excluding *C. felicis*) consists of seven species mainly distributed in the Zambezian region with three species extending to the Congolian region. Tanzania seems to be the centre of diversity of *Cincinnobotrys* s.s., with five of the seven species occurring there, two of them being endemic.

4.2.10 *Preussiella*

Preussiella are glabrous epiphytic shrubs, with thick and swollen nodes. Anisophylly is present in *Preussiella* although

not very pronounced. Inflorescences are large terminal or apical uniparous cymes. The lax inflorescence of *Preussiella* is similar to those of *Dicellandra barteri* var. *magnifica* but have an opposite-decussate branching pattern. *Preussiella* flowers are pentamerous, large and colorful. The hypanthium is narrowly obconical. The stamens are diplostemonous, isomorphic to sub-equal. The fruit is ellipsoid-oblong (Jacques-Félix, 1974a, Figs. 3L–3O).

The two species in this genus, *P. kamerunensis* Gilg and *P. gabonensis* Jacq.-Fél. are mainly differentiated by the leaf shape, attachment and venation. The leaves of *P. kamerunensis* are oval to ovate-lanceolate with two pairs of acrodromous veins and long petioles. In *P. gabonensis* the leaves are elliptic, subsessile with one pair of acrodromous veins. These epiphytic species are restricted to the Guinean-Congolian region with their primary substrate being tree trunks. The widespread *P. kamerunensis* is found in Guinea and extends to Gabon and DR Congo while *P. gabonensis* is endemic to Gabon. *Preussiella kamerunensis* is the only member of African Melastomataceae with a chromosome number of $n=22$ (Favarger, 1952, 1962; Farron & Favarger, 1983). The chromosome number of *P. gabonensis* is still unknown.

We included four accessions of *P. kamerunensis* in our molecular analyses. These formed a well-supported monophyletic clade, but in a polytomy with *Cincinnobotrys* s.s. and *Amphiblemma* s.s. (Fig. 4B). Morphologically, *Preussiella* is a very distinct genus and can be clearly separated from the other Sonerileae genera. Our molecular results support the treatment of *Preussiella* in Sonerileae as was done by Jacques-Félix (1977), not in Dissochaetaceae (see Gilg, 1898; Engler, 1921).

5 Taxonomic Treatment

In this section, we focus on the African Sonerileae. All 10 currently accepted genera have been sampled in the molecular phylogeny and in combination with morphology, we here provide an updated classification at the generic rank. The monospecific genus *Bourdaria* is reinstated, and a new monospecific genus *Mendelia* is described. To complete the realignment of the African Sonerileae, three lecto- or neotypes are designated. We also provide a key to the 10 African genera of Sonerileae.

Key to African genera of Sonerileae

- 1a. Perennial evergreen herbs, growing on vertical rocks; leaves alternate, leaf petiole to 45 cm long; flowers tetramerous..... *Benna*
- 1b. Habit diverse, mainly restricted to forests or shaded habitats; leaves opposite or rosettes, leaf petioles less than 25 cm long; flowers tetra- or pentamerous..... 2
- 2a. Fruit a berry, ovoid or globose..... *Medinilla*
- 2b. Fruit capsular, variously shaped (mostly angular or distinctly ribbed) but not ovoid or globose..... 3
- 3a. Stamens lacking a well developed pedoconnective, thecae not extended, anterior appendages absent but a posterior spur present..... *Gravesia*

- 3b. Stamens with a pedoconnective or with thecae extended, anterior appendages present, especially on the antepetalous stamens, posterior spur may be present..... 4
- 4a. Herbs, rhizomatous or forming a tuberous or cormose base..... 5
- 4b. Herbs or shrubs, scandent or epiphytic, non-rhizomatous, lacking tubers or corms..... 6
- 5a. Stem short, vertically rising from a tuberous or cormose base, internodes short; leaves 2–6 in rosettes, narrowly ovate-lanceolate, petioles up to 4 cm long; flowers tetramerous, borne in axillary fascicles with short peduncles; capsule distinctly tetragonal..... *Bourdaria*
- 5b. Small acaulescent rhizomatous herbs, internodes none; leaves 1–few, broadly ovate-cordate, petioles long, up to 15 cm; flowers mostly tetramerous (pentamerous in *C. acaulis*), the peduncle arising directly from the rhizomatous base; capsule turbinate or campanulate but distinctly ribbed..... *Cincinnobotrys*
- 6a. Herbs; inflorescence solitary, erect, elongated, uniparous cymes with many flowers; two protuberant interfoliar lenticels present on each node; sepal tips mucronate, developing into distinct linear appendages; epigynous ovary crown protruding out of the receptacle at maturity..... *Mendelia*
- 6b. Habit diverse (herbs or shrubs, scandent or epiphytic); inflorescence not as above (simple or bifurcating cymes or thyrses); interfoliar lenticels absent; sepal tips not developing into distinct linear appendages; epigynous ovary crown non-protruding..... 7
- 7a. Inflorescence of simple or bifurcating scorpioid cymes; petals asymmetrical; stamens isomorphic to slightly unequal, brachymorphic; capsules crowned by accrescent woody wedge-like scales exserted well above..... *Calvoa*
- 7b. Inflorescence not as above (few-flowered cymes or thyrses); petals symmetrical; stamens markedly dimorphic, non-brachymorphic; capsules crowned by sepals or not as above..... 8
- 8a. Robust herbs or shrubs, unicaulous or sympodial, erect, scandent or epiphytic, rooting at the nodes; hypanthium glabrous or densely furfuraceous; anterior appendages claviform or linear (especially on the antepetalous stamens); capsule ellipsoid, ribbed; seeds obconical, with raphe forming a lateral spur at the tip..... *Dicellandra*
- 8b. Mostly terrestrial perennial herbs and shrubs or epiphytes not rooting at the nodes; hypanthium glabrous or with simple/glandular hairs; anterior appendages bilobed (especially on the antepetalous stamens); capsule oblong-ellipsoid, obconical, crateriform, campanulate, sometimes ribbed; seeds oblong, oblong-ovoid with an appendiculate-membrane at apex or at both ends..... 9
- 9a. Mostly terrestrial perennial herbs or shrubs with glandular hairs very frequent on the floral organs; hypanthium with variable pubescence but mostly of glandular hairs, turbinete, campanulate-oblong; calyx lobes conspicuous; ovary adnate to the calyx and produced into a crown at the apex; capsule obconical, crateriform, campanulate, sometimes ribbed; dehiscence valvate..... *Amphiblemma*

- 9b. Epiphytic (sometimes epilithic) shrubs, more or less glandular; hypanthium obconical; calyx lobes conspicuous or minute; ovary adnate to the calyx at the apex, with no crown produced; capsule oblong-ellipsoid, weakly pentagonal, 5 (-10)-ribbed, dehiscence loculicidal or septicidal.....
.....*Preussiella*

1. *Amphiblemma* Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 50. 1850 [1851] – Type: *Amphiblemma cymosum* Naudin.

Morphological diagnosis: Mostly terrestrial perennial herbs and shrubs with glandular hairs very frequent on the floral organs; flowers pentamerous; stamens dimorphic; ovary inferior to semi-inferior, with an epigynous crown with five lobes; fruit dehiscence valvate. *Amphiblemma* differs from *Mendelia* by the following characters: cymes with two to five digitate branches forming a corymb, panicle, contracted umbel or sometimes axillary cymes (vs solitary, erect, elongated, uniparous cymes with many flowers); sepals lack linear appendages, and the epigynous crown is included (vs sepals with a linear subapical appendage and an epigynous crown protruding at maturity). See also Figs. 1F–1Q.

Accepted taxa: *Amphiblemma amoenum* Jacq.-Fél., *Amphiblemma ciliatum* Cogn., *Amphiblemma cuneatum* Jacq.-Fél., *Amphiblemma cymosum* Naudin, *Amphiblemma gossweileri* var. *gossweileri* Exell, *Amphiblemma gossweileri* var. *humifusum* Jacq.-Fél., *Amphiblemma hallei* Jacq.-Fél., *Amphiblemma heterophyllum* Jacq.-Fél., *Amphiblemma lanceatum* Jacq.-Fél., *Amphiblemma letouzei* Jacq.-Fél., *Amphiblemma mildbraedii* Gilg ex Engl., *Amphiblemma monticola* Jacq.-Fél., *Amphiblemma mvensis* M.E.Leal, *Amphiblemma setosum* Hook. f., *Amphiblemma sovauxii* Cogn.

Note: Engler (1921) described *Amphiblemma mildbraedii* from Bioko (historically Fernando Po) in the northernmost part of Equatorial Guinea, "bei Musota oberhalb San Carlos (a. d. Westküste) in niedrigem Wald um 600—1200 m," but he did not cite a collector or collection number. Like most of the other melastome types that he designated, these were destroyed in Berlin during WW II. However, there is a collection by J. Mildbraed 705 in Hamburg (HBG), HBG509099 matching the locality described by Engler (1921). It seems likely that the specific epithet was in honor of the collector, J. Mildbraed. We therefore suspect that the material housed in HBG (HBG509099!) is an isotype.

2. **Benna** Burgt & Ver.-Lib., Willdenowia 52(1): 31. 2022—
Type: *Benna alternifolia* Burgt & Ver.-Lib.

Morphological diagnosis: *Benna* can be morphologically identified by the following combination of characters: it is a herb with alternate leaves, margins dentate; inflorescence cymose, paniculate, axillary, branching alternate; flowers actinomorphic, 4-merous, stamens 8, dimorphic; fruit a capsule, apically dehiscent, numerous seeds; seeds obovoid or nearly so, glossy, testa smooth. *Benna* differs from all other African Melastomataceae genera by the following: Leaves alternate (vs opposite or whorled); seeds obovoid or nearly so, glossy, testa smooth (vs seeds diverse but not as in *Benna*). See also Figs. 1A–1E.

Accepted taxon: *Bennia alternifolia* Burgt & Ver.-Lib.

3. *Bourdaria* A.Chev., Bull. Mus. Hist. Nat. (Paris) sér. 2, 4: 681. 1932—Type: *Bourdaria felicis* A. Chev. (\equiv *Cincinnobotrys felicis* (A. Chev.) Jacq.-Fél.).

Morphological diagnosis: *Bourdaria* differs from all other African Sonerileae by its short vertically rising stems that arise from a tuberous or cormose base; plant usually not epiphytic; flowers tetramerous, borne in axillary fascicles with one to several flowers on long slender pedicels; seeds small with a slender and fragile funicle, obovoid, asymmetric, and finely tuberculate. *Bourdaria* differs from *Cincinnobotrys* by having a short stem (vs acaulous); leaves 2–6 in rosettes (vs leaves 1–few, broadly ovate- cordate, petioles long and borne directly from the base); capsule distinctly tetragonal (vs capsule turbinate or campanulate but distinctly-ribbed).

Description: Perennial herbs with a short, erect and thickened stem, 5–12 cm high, from a bulbo-tuberous (cormose) base, anchored to the substrate; branches absent or few, with persistent traces of old leaves and hirsute with long, black bristles. Leaves 1–6 in a contracted apical rosette, petiole slender, 2–4 cm long, glabrous or with a few bristles; blade lanceolate to oblanceolate, base cuneate to rounded, apex acute to acuminate, adaxial surface glabrescent, abaxial surface pubescent, primary ascending veins 3–5, transverse veins widely spaced, margins obscurely serrate at the base and visibly biserrate-ciliate at the apex. Inflorescence a fascicle of one to several axillary flowers subtended by contracted apical rosette leaves. Flowers tetramerous, pedicel slender with capitate hairs. Hypanthium glabrous or with a few capitate hairs, campanulate to sub-urceolate, 4-ribbed; sepals broadly triangular and thickened-keeled on the abaxial surface; petals pink, obovate. Stamens slightly dimorphic (sub-equal). Antepetalous stamens with a short pedoconnective, ventral appendage bilobed, truncate-emarginate, dorsal appendage spatulate. Antesepalous stamens with a pedoconnective and appendages like those of the antepetalous ones but only slightly shorter. Ovary adnate to the hypanthium for its entire length; epigynous crown apically depressed (convex), cupular; stigma capitate; placenta restricted to the upper part of the axis. Fruit tetragonal, marked with four sepal-ribs and four weaker intermediates. Seeds small with a slender and fragile funicle, ovoid, asymmetric, finely tuberculate. See also Figs. 2H–Q.

Accepted taxon: *Bourdaria felicis* A. Chev., Bull. Mus. Hist. Nat. (Paris) sér. 2, 4: 681. 1932 ≡ *Cincinnobotrys felicis* (A. Chev.) Jacq.-Fél., Adansonia sér. 2, 16(3): 377. 1976—Holotype: Guinée, Kalifayagbé; rochers sur les rives du Bady de Tabili à Tondon, Jacques-Félix 163 (P00057510!); isotypes: P00057511!, P00057512!).

4. *Calvoa* Hook.f. in Benth. & Hook.f., Gen. Pl. 1 (3): 732, 755. 1867—Lectotype: *Calvoa hirsuta* Hook.f. (designated here).

Morphological diagnosis: Perennial herbs, shrubs (often suffrutescent), sometimes climbing or decumbent, terrestrial or epiphytic, subglabrous, puberulous with minute red hairs on young parts or rarely hirsute; inflorescences terminal (rarely axillary) scorpioid cymes with up to 60 flowers or sometimes solitary, simple or bifurcating scorpioid cymes; flowers pentamerous, brachymorphic and somewhat gamopetalous; petals asymmetrical; stamens in two whorls, brachymorphic, isomorphic to slightly unequal, alternipetalous

anthers having ribbon-like filaments; ovary 5-locular, inferior to semi-inferior, with an epigynous crown; capsules distinctly ribbed, dehiscence generally apical or loculicidal; seeds oblong or ovoid, papillose, sometimes with well-developed subulate appendages at both ends. *Calvoa* differs from *Amphiblemma* by the following characters: floral organs mostly glabrous (vs floral organs frequently covered with glandular hairs); petals asymmetrical (vs symmetrical). See also Figs. 1R–1AI.

Accepted taxa: *Calvoa angolensis* A.Fern. & R.Fern., *Calvoa crassinoda* Hook.f., *Calvoa grandifolia* Cogn., *Calvoa hirsuta* Hook.f., *Calvoa integrifolia* Cogn., *Calvoa jacques-felixii* Figueiredo, *Calvoa leonardii* Jacq.-Fél., *Calvoa maculata* M.E.Leal, *Calvoa monticola* A.Chev. ex Hutch. & Dalziel, *Calvoa orientalis* Taub., *Calvoa pulcherrima* Gilg & Mildbr., *Calvoa sapini* De Wild., *Calvoa seretii* De Wild. subsp. *seretii* De Wild., *Calvoa seretii* De Wild. subsp. *wildemaniana* (Exell) E.Figueiredo, *Calvoa sinuata* Hook.f., *Calvoa sitaeana* Jacq.-Fél., *Calvoa stenophylla* Jacq.-Fél., *Calvoa subquinquenervia* De Wild., *Calvoa trochainii* Jacq.-Fél., *Calvoa zenkeri* Gilg ex Engl.

Note: In the original description of *Calvoa*, Hooker (1867) did not designate a species as the type. Neither did later authors. We here designate *Calvoa hirsuta* as the type species of the genus.

5. *Cincinnobotrys* Gilg, Nat. Pflanzenfam. Nachtr. II-IV [Engler & Prantl] 1: 265. 1897—Type: *Cincinnobotrys oreophilus* Gilg

= *Amphiblemma* *sensu* Cogn. (non Naudin), Bol. Soc. Brot. 11: 89. 1893, p.p., tant. *Amphiblemma acaule* ≡ *Amphiblemma* sect. *Haplophyllophora* Brenan in Kew Bull. 8: 86. 1953—Type: *Amphiblemma acaule* Cogn.

= *Primularia* Brenan, Kew Bull. 8: 88. 1953—Type: *Primularia pulchella* Brenan (≡ *Cincinnobotrys pulchella* (Brenan) Jacq.-Fél.)

= *Gravesiella* A.Fern. & R.Fern., Bol. Soc. Brot., Sér. 2, 34: 69 (tab. 9). 1960—Type: *Gravesiella speciosa* A.Fern. & R.Fern. (≡ *Cincinnobotrys speciosa* (A.Fern. & R.Fern.) Jacq.-Fél.)

= *Haplophyllophorus* (Brenan) A.Fern. & R.Fern., Bol. Soc. Brot., Sér. 2, 56: 70. 1972—Type: *Haplophyllophorus acaulis* (Cogn.) A.Fern. & R.Fern. (≡ *Cincinnobotrys acaulis* (Cogn.) Gilg ≡ *Amphiblemma acaule* Cogn.).

Morphological diagnosis: Small acaulous rhizomatous herbs, ablastosphyllous (no buds); leaves haplophyllous (simple), 1–few, palmate, petioles long; flowers mostly tetramerous (pentamerous in *C. acaulis*), in scorpioid cymes, hypanthium campanulate. Stamens isomorphic or slightly unequal. Ovary 4 or 5-locular, inferior to semi-inferior, with an epigynous crown of 4 (–8) lobes. Capsules with a persistent crown of slightly exserted scales. *Cincinnobotrys* differs from *Bourdaria* by being acaulous (vs having a short stem); leaves 1–few, broadly ovate-cordate, petioles long and borne directly from the base (vs leaves 2–6 in rosettes); capsule turbinate or campanulate but distinctly-ribbed (vs capsule distinctly tetragonal). See also Figs. 3H–3K.

Accepted taxa: *Cincinnobotrys acaulis* (Cogn.) Gilg, *Cincinnobotrys acaulis* var. *seretii* (De Wild.) Maluma & Geerinck, *Cincinnobotrys letouzeyi* Jacq.-Fél., *Cincinnobotrys oreophilus* Gilg, *Cincinnobotrys pauwelsiana* Maluma & Geerinck, *Cincinnobotrys pulchella* (Brenan) Jacq.-Fél., *Cincinnobotrys ranarum* Pócs, *Cincinnobotrys speciosa* (A.Fern. & R.Fern.) Jacq.-Fél.

Note: Gilg (1897) described *Cincinnobotrys oreophilus* from Tanzania, Uluguru Mts, Mt Nglewenu, based on the collection Stuhlmann 8804 housed in Berlin and destroyed during WW II. However, a leaf fragment and illustration from the collection is at BR and designated *Typus* with no specification of the type. We therefore interpret this collection at BR to be an isotype (BR0000006260330!).

6. *Dicellandra* Hook. f., Gen. Pl. 1 (3): 732, 757. 1867—Type: *Dicellandra barteri* Hook.f.

Morphological diagnosis: Robust erect or creeping, ascending to leaning single-stemmed perennial herbs or shrubs with a unicaulous or sympodial branching habit, epiphytic, rooting along the nodes; inflorescences multi-flowered thyrses; flowers pentamerous, calyx and corolla short, already well exposed before anthesis; hypanthium glabrous or densely furfuraceous. The stamens are either dimorphic or isomorphic but with two anterior appendages or one posterior appendage. Ovary 5-locular, inferior, apex concave with an epigynous membranous crown; style linear, though somewhat thickened toward the top, often bearing glandular tannic hairs toward the base; stigma punctiform to subcapitate. Capsules ellipsoid-oblong to globular and remaining enveloped by the hypanthium and persistent calyx, seeds obconical, with an aril or raphe forming a lateral spur at the tip, dehiscence irregular. *Dicellandra* differs from *Amphiblemma* by the following characters: hypanthium glabrous or densely furfuraceous (vs hypanthium pubescence variable but mostly with glandular hairs); capsule ellipsoid; seeds obconical, with a raphe forming a lateral spur at the tip, dehiscence irregular (vs capsule, obconical, crateriform, campanulate, dehiscence valvate). See also Figs. 3A–3G.

Accepted taxa: *Dicellandra barteri* Hook.f. var. *barteri*, *Dicellandra barteri* var. *erecta* Jacq.-Fél., *Dicellandra barteri* var. *escherichii* (Gilg ex Engl.) Jacq.-Fél., *Dicellandra barteri* var. *magnifica* Jacq.-Fél., *Dicellandra descoingsii* Jacq.-Fél., *Dicellandra glanduligera* (Pellegr.) Jacq.-Fél.

7. *Gravesia* Naudin, Ann. Sci. Nat., Bot., sér. 3, 15: 333. 1850 [1851]—Type: *Gravesia bertolonioides* Naudin

= *Veprecella* Naudin, Ann. Sci. Nat., Bot., sér. 3, 15: 312. 1850 [1851]—Lectotype (**designated here**): *Veprecella lutea* Naudin (≡ *Gravesia lutea* (Naudin) H. Perrier)

= *Phornothamnus* Baker, J. Linn. Soc., Bot. 21: 342. 1884 — Type: *Phornothamnus thymoides* Baker (≡ *Gravesia thymoides* (Baker) H.Perrier)

= *Urotheca* Gilg, Nat. Pflanzenfam. Nachtr. II-IV [Engler & Prantl] 1: 263. 1897—Type: *Urotheca hylophila* Gilg (≡ *Gravesia hylophila* (Gilg) A.Fern. & R.Fern)

= *Neopetalonema* Brenan, J. Arnold Arbor. 26: 213. 1945 ≡ *Petalonema* Gilg in Nat. Pflanzenfam. Nachtr. [Engler & Prantl] I. 264. 1897, non Correns (1889), nec Schlechter (1915), nec A. Peter (1928) – Type: *Neopetalonema pulchrum* (Gilg) Brenan (≡ *Gravesia pulchra* (Gilg) Wickers).

Morphological diagnosis: Perennial herbs or shrubs, erect, scandent or prostrate, sometimes acaulous (in Madagascar); inflorescences of terminal cymes, umbelliform, corymbose, paniculate or sometimes contracted into fascicles or flowers solitary; flowers (4–)5-merous; hypanthium turbinate, ± angled, smooth or ribbed, truncate or variously toothed or

lobed; stamens (8–)10, equal; pedoconnective with ventral appendage and posterior spur-like appendage scarcely produced; ovary 5-locular, inferior; capsule ± angular, crowned by the conspicuous accrescent often slightly woody plate- or wedge-like scales; seeds narrowly oblong to obpyramidal. *Gravesia* differs from other genera of African Sonerileae by having stamens lacking a pedoconnective and anterior appendages but a posterior spur present (vs stamens with a pedoconnective or extended thecae, anterior appendages present, especially on the antepetalous stamens, posterior appendages maybe present or absent). *Gravesia* also differs from *Medinilla* by having capsular fruits (vs berry). See also Figs. 3U–3Z.

Accepted taxa from Africa: *Gravesia gabonensis* Jacq.-Fél., *Gravesia hylophila* (Gilg) A.Fern. & R.Fern., *Gravesia lebrunii* Jacq.-Fél., *Gravesia pulchra* (Gilg) Wickens, *Gravesia riparia* A.Fern. & R.Fern.

Note: The original description of *Veprecella* Naudin (1851) did not designate a type species, and neither did later authors. We here designate *Veprecella lutea* (≡ *Gravesia lutea*) as the type species of *Veprecella*.

8. ***Medinilla*** Gaudich., Voy. Uranie, Bot., 484. 1830—Type: *Medinilla rosea* Gaudich., nom. illeg. (≡ *Medinilla medinilliana* (Gaudich.) Fosberg & Sachet).

Morphological diagnosis: Erect, climbing or epiphytic shrubs, glabrous or pubescent, nodes often thickened; leaves usually coriaceous or fleshy and quite entire; flowers tetra-, penta- or hexamerous; bracts and bracteoles usually present; inflorescences terminal or axillary cymes or panicles; hypanthium ovoid, campanulate or cylindric and widened at the top, thin or fleshy, entire, minutely dentate or with irregular small lobes; stamens 8–12, isomorphic, dimorphic or subequal, opening by 1(–2) pores; pedoconnective not or hardly produced at the base, dorso-basally terminating in a subulate or subulate-clavate spur, ventrally terminating in two lobes or two linear appendages or exappendiculate; ovary adnate to the calyx, usually with 8, 10 or 12 septa above the middle (in African species wholly adnate for most of its length), 4–5–6-locular; fruit a berry enclosed within the persistent calyx, globular; seeds many and minute, semi-ovate to irregularly ovoid or angular; hilum basal, raphe often evident. *Medinilla* differs from the other African Sonerileae by having berry fruits that are ovoid or globose (vs fruits capsular, mostly angular or distinctly ribbed, of various shapes but not as above). See also Figs. 3P–3T.

Accepted taxa from Africa: *Medinilla engleri* Gilg, *Medinilla mannii* Hook.f., *Medinilla mirabilis* (Gilg) Jacq.-Fél.

Note: Gilg (1904) described *Medinilla engleri* from Tanzania, Lushoto District, Amani based on the following syntypes: Engler 570 & Warnecke in Herb. Amani 387. All the collections housed in B were destroyed during WW II. However, there is a duplicate of Warnecke at EA (cited by Wickens, 1975). We therefore designate this collection as the lectotype.

Medinilla engleri Gilg, Bot. Jahrb. Syst. [Engler] 34: 99. 1904—Lectotype (designated here): Tanzania, Lushoto District, Amani, Warnecke in Herb. Amani 387 (EA, not seen).

9. ***Mendelia*** Ver.-Lib. & G.Kadereit, gen. nov.—Type: *Mendelia mollis* (Hook.f.) Ver.-Lib. & G.Kadereit (≡ *Amphiblemma molle* Hook.f.).

Morphological diagnosis: *Mendelia* are perennial herbs with erect, elongated, uniparous cymes; the mucronate sepal tip develops into distinct linear appendages. *Mendelia* differs from *Amphiblemma* by the following characters: solitary, erect, elongated, uniparous cymes with many flowers (vs cymes with two to five digitate branches forming a corymb, panicle, contracted umbel or sometimes axillary cymes); sepals with a linear subapical appendage and an epigynous crown protruding at maturity (vs the sepals lacking linear appendages, and the epigynous crown is included).

Etymology: In 2022 is the bicentennial birthday of Gregor Johann Mendel. The generic name *Mendelia* is a feminine noun, proposed in his honor.

Description: Perennial herbs or subshrubs, erect, branched, hairy to velutinous in all parts, often reddish in color, twigs slender, subangular or terete, covered with dense bristles or capitate hairs; two protuberant interfoliar lenticels present on each node. Leaves opposite, petiolate, slender, densely velutinous; lamina ovate, base rounded to cordate, apex acuminate to acute, appressed setose hairs on both sides, margins obscurely dentate-ciliate. Flowers white to pink, pentamerous (rarely hexamerous), shortly pedicellate, in solitary or terminal uniparous cymes, shortly penduculate bearing up to 50 biseriate flowers (opposite because of sympodial growth) borne on a densely velutinous rachis. Hypanthium covered with velutinous hairs, ovoid-campanulate; sepals triangular to obtuse, with a linear-subulate appendage on the back, hirsute. Petals pink, rarely white, oblong, apex with setose or capitate hairs. Stamens 10, dimorphic, antesepalous stamens with relatively short pedoconnectives, poorly arched, prolonged ventrally with an obtuse-emarginate appendage and dorsal appendage absent, antepetalous stamens with connective not extended at base into a pedoconnective but ventrally bilobed and dorsal appendage short. Ovary adnate to the calyx for most of its length, forming a free crateriform cavity, cylindrical reaching the hypanthium rim and an epigynous crown. Fruit campanulate, ovary protruding out of the receptacle (convex) and sepals by the veined crowns, pentagonal-reduplicate, margins ciliate, truncate to wavy; dehiscence valvate. Seeds minute and papillose. See also Figs. 2A–2G.

Accepted taxon: ***Mendelia mollis*** (Hook.f.) Ver.-Lib. & G.Kadereit comb. nov. ≡ *Amphiblemma molle* Hook.f., Fl. Trop. Afr. [Oliver et al.] 2: 456. 1871. Holotype: Gabon, Mt Crystal (Sierra del Crystal), Mann 1681 (K000313255!).

10. ***Preussiella*** Gilg, Nat. Pflanzenfam. Nachtr. II-IV [Engler & Prantl] 1: 267. 1897—Type: *Preussiella kamerunensis* Gilg.

Morphological diagnosis: Epiphytic (sometimes epilithic) shrubs, glabrous, stems subquadangular, thick and swollen at the nodes, bark more-or-less corky; leaves large with slender petioles, blades ovate to ovate-lanceolate. Inflorescences axillary or terminal thyrses bearing many flowers; flowers pentamerous, large and colorful; hypanthium narrow to obconical and progressively connected to the pedicel; calyx short, lobes indistinct; stamens 10, dimorphic or isomorphic, pedoconnectives with an anterior appendage, dorsal appendages conspicuous; ovary adnate to the calyx at the apex, with no crown; fruit oblong-ellipsoid, weakly pentagonal, 5 (–10)-ribbed; capsule dehiscence loculicidal or septicidal; placentas sessile over the entire length of the locules having five to six rows of seeds. The

seeds are numerous, perpendicular to the axis, appendiculate at the base by the lamellate funicle, and at the apex by the lamellate-truncated expansion of the tegument; the seed itself is reduced, oblong, and finely papillose. *Preussiella* differs from *Amphiblemma* by the following characters: epiphytic (sometimes epilithic) shrubs more or less glandular (vs mostly terrestrial perennial herbs and shrubs with glandular hairs frequent on the floral organs); calyx lobes conspicuous or minute (vs calyx lobes conspicuous); ovary adnate to the calyx at the apex, with no crown produced (vs ovary adnate to the calyx at the apex with a crown produced); capsule oblong-ellipsoid, weakly pentagonal, 5 (-10)-ribbed, dehiscence loculicidal or septicidal (vs capsule obconical, crateriform, campanulate, dehiscence valvate). See also Figs. 3L–3O.

Accepted taxa: *Preussiella kamerunensis* Gilg, *Preussiella gabonensis* Jacq.-Fél.

Note: Gilg (1898) described *Preussiella kamerunensis* and designated a specimen from Cameroon, Barombi-station collected by Preuss 442 as the type. This collection was housed in Berlin and destroyed during WW II. There is no trace of this specimen with no known duplicates. We thus designate a neotype, collected in Cameroon and housed in WAG together with two isoneotypes in WAG and BR, respectively.

Preussiella kamerunensis Gilg in Monogr. Afrik. Pflanzen-Fam. [Engler] 2: 36. 1898—**Neotype (designated here):** Cameroon, Forêt de Bakaka, 3 km E of Eboné, a village on Km 11 of Nkongsamba-Loum Road, A.J.M. Leeuwenberg 8329 (WAG barcode WAG.1094956!; isoneotypes: BR0000016974524!, WAG.1094957!).

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Author contributions

M.C.V.-L. and G.K. designed the study and acquired funding; M.C.V.-L. and H.M. performed the laboratory work, edited and aligned the sequences. M.C.V.-L. performed all the analyses and prepared a draft manuscript. L.C. assisted in preparing the figures. All authors, M.C.V.-L., H.M., L.C., G.K., R.D.S., X.v.d.B., S.T., and F.A. worked on the first draft and provided valuable comments to improve the manuscript.

Conflict of Interest

All authors declare that they have no conflicts of interest.

References

- Bacci LF, Amorim AM, Michelangeli FA, Goldenberg R. 2020. Flower morphology is correlated with distribution and phylogeny in *Bertolonia* (Melastomataceae), an herbaceous genus endemic to the Atlantic Forest. *Molecular Phylogenetics and Evolution* 149: 106844.
- Bacci LF, Michelangeli FA, Goldenberg R. 2019. Revisiting the classification of Melastomataceae: Implications for habit and fruit evolution. *Botanical Journal of the Linnean Society* 190: 1–24.
- Baillon H. 1877. Monographie des Mélastomacées. *Histoire des plantes* 7: 1–65.
- Bánki O, Roskov Y, Vandeputte L, DeWalt RE, Remsen D, Schalk P, Orrell T, Keping M, Miller J, Aalbu R, Adlard R, Adriaenssens E, Aedo C, Aesch E, Akkari N, Alonso-Zarazaga MA, Alvarez B, Alvarez F, Anderson G et al. 2021. Catalogue of Life Checklist (version 2021-08-25). Catalogue of Life [online]. Available from <https://doi.org/10.48580/d4sg> [accessed 15 January 2022].
- Bochorn T, Michelangeli FA, Almeda F, Goldenberg R. 2019. Phylogenetics, morphology and circumscription of Cambessedeeiae: A new Neotropical tribe of Melastomataceae. *Botanical Journal of The Linnean Society* 190: 281–302.
- Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fournier M, Gavryushkina A, Heled J, Jones G, Kühnert D, De Maio N, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, Du Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu CH, Xie D, Zhang C, Stadler T, Drummond AJ. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15: 1–28.
- Brenan JPM. 1953. Tropical African plants: XXIII: Melastomataceae. *Kew Bulletin* 8: 85–88.
- Burgt XM, van der Haba PM, Magassouba S, Verano-Libalah MC. 2022. *Benna alternifolia* (Melastomataceae: Sonerileae), a new herbaceous genus and species from Guinea, West Africa. *Willdenowia* 52: 25–37.
- Chevalier A. 1932. Sur quelques Mélastomacées nouvelles ou peu connues. *Bulletin du Museum national d'Histoire naturelle (Paris)* 2: 678–687.
- Clausing G, Renner SS. 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. *American Journal of Botany* 88: 486–498.
- Cogniaux A. 1891. Melastomaceae. In: de Candolle A, de Candolle C eds. *Monographiae Phanerogamarum*. Parisii: vol. 1–8, G. Masson; vol. 9, Masson & Cie. 1256.
- Engler A. 1921. Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete: Grundzüge der Pflanzenverbreitung in Afrika und die Charakterpflanzen Afrikas, vol. 3(2), Charakterpflanzen Afrikas (insbesondere des tropischen): Die Familien der afrikanischen Pflanzen. In: Engler A, Drude O eds. *Die Vegetation der Erde*. Leipzig: Verlag von Wilhelm Engelmann. 739–769.
- Farron C, Favarger C. 1983. Contribution à la Cytotaxonomie des Mélastomacées africaines. *Garcia de Orta: Série de Botânica* 6: 83–88.
- Favarger C. 1952. Recherches sur quelques Mélastomacées d'Afrique occidentale. *Berichte der Schweizerischen Botanischen Gesellschaft* 62: 5–65.
- Favarger C. 1962. Nouvelles recherches cytologiques sur les Mélastomacées. *Berichte der Schweizerischen Botanischen Gesellschaft* 72: 290–305.
- Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.

- Fernandes A, Fernandes R. 1956. Le genre *Gravesia* Naud. au Continent africain. *Boletim da Sociedade Broteriana* 2: 111–116.
- Fernandes A, Fernandes R. 1960. Melastomataceae africanae novae vel minus cognitae—IV. *Boletim da Sociedade Broteriana* Sér 2(34): 59–92(+26 plates).
- Fernandes A, Fernandes R. 1972. Melastomataceae Africanae novae vel minus cognitae—VI. *Boletim da Sociedade Broteriana* Sér 2(46): 63–71(+6 plates).
- Figueiredo E. 2001. A revision of *Calvoa* Hook. f. (Melastomataceae). *Botanical Journal of the Linnean Society* 136: 179–205.
- Fritsch PW, Almeda F, Renner SS, Martins AB, Cruz BC. 2004. Phylogeny and circumscription of the near-endemic Brazilian tribe *Microlicieae* (Melastomataceae). *American Journal of Botany* 91: 1105–1114.
- Gilg E. 1904. Drei interessante Melastomataceae aus Deutsch-Ostafrika. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 34: 99–102.
- Gilg E. 1898. Melastomataceae. In: Engler A ed. *Monographien Afrikanischer Pflanzen-Familien und -Gattungen*. Leipzig: Englemann, Wilhelm. 1–79.
- Guimarães PJF, Michelangeli FA, Sosa K, de Santiago Gómez JR. 2019. Systematics of *Tibouchina* and allies (Melastomataceae: Melastomataceae): A new taxonomic classification. *Taxon* 68: 937–1002.
- Hooker JD. 1867. Melastomataceae. In: Bentham G, Hooker JD eds. *Genera Plantarum*. Londini [London]: venit apud Reeve & Co. 726–773.
- Hooker JD. 1871. Melastomataceae. In: Oliver D ed. *Flora of Tropical Africa, Volume II*. London: Reeve & Co. 439–463.
- Hutchinson J, Dalziel JM. 1927. *Flora of West Tropical Africa*. London: The Crown Agents for the Colonies.
- Jacques-Félix H. 1952. Les recherches cytologiques de M. Favarger sur les Mélastomacées d'Afrique tropicale. *Revue internationale de botanique appliquée et d'agriculture tropicale* 32: 391–393.
- Jacques-Félix H. 1955. Introduction. *Institut français d'Afrique noire. Icones plantarum africanarum* 3: 1–2.
- Jacques-Félix H. 1973. Le genre *Amphiblemma* Naud. (Mélastomacées). *Adansonia* ser 2(13): 429–459.
- Jacques-Félix H. 1974a. Le genre *Dicellandra* Hook. f. (Mélastomacées). *Adansonia* 14: 77–98.
- Jacques-Félix H. 1974b. Complément au genre *Amphiblemma* (Mélastomacées): Description d'une espèce nouvelle. *Adansonia* ser 2(14): 467–472.
- Jacques-Félix H. 1976. Les genre *Cincinnobotrys* Gilg (Mélastomacées). *Adansonia* ser 2(16): 355–377.
- Jacques-Félix H. 1977. Le genre *Preussiella* Gilg (Mélastomacées). *Adansonia* ser 2(16): 405–414.
- Jacques-Félix H. 1981. Révision du genre *Calvoa* (Melastomataceae). *Bulletin du Muséum national d'Histoire naturelle (Paris)*, 4e sér., section B (*Adansonia*) 3: 123–143.
- Jacques-Félix H. 1983a. 25. Mélastomatacées. In: Leroy J-F ed. *Flore du Gabon*. Paris: Museum National d'Histoire Naturelle. 166.
- Jacques-Félix H. 1983b. 24. Mélastomatacées. In: Satabié B, Leroy J-F eds. *Flore du Cameroun*. Yaoundé: Délégation Générale à la Recherche Scientifique et Technique. 1–192.
- Jacques-Félix H. 1987. Un *Amphiblemma* (Melastomataceae) nouveau du Cameroun. *Bulletin du Muséum National d'Histoire Naturelle Section B, Adansonia, botanique, phytotaxonomie* 9: 125–127.
- Jacques-Félix H. 1995. Histoire des Melastomataceae d'Afrique. *Bulletin du Muséum national d'Histoire naturelle (Paris)*, section B (*Adansonia*) 16: 235–311.
- Jumelle H, Perrier de la Bâthie H. 1914. Le genre *Gravesia*. *Revue générale de Botanique* 25: 391–403.
- Kartonegoro A, Verano-Libalah MC, Kadereit G, Frenger A, Penneys DS, Mota de Oliveira S, Van Welzen PC. 2021. Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe *Dissochaetaceae*. *Taxon* 70: 793–825.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
- Keay RWJ. 1954. *Flora of West Tropical Africa*, vol. (1)1. London: Crown Agents for Overseas Governments and Administrations.
- Krasser F. 1893. Melastomataceae. In: Engler A, Prantl K eds. *Die natürlichen Pflanzenfamilien*. Leipzig: Engelmann. 3(7): 130–199.
- Kriebel R, Michelangeli FA, Kelly LM. 2015. Discovery of unusual anatomical and continuous characters in the evolutionary history of *Conostegia* (Miconiae: Melastomataceae). *Molecular Phylogenetics and Evolution* 82: 289–313.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701.
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2017. Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773.
- Leal ME. 2008. Novitates Gabonenses 65. A new rare endemic *Amphiblemma* (Melastomataceae) from Mve Lakene, Gabon. *Blumea—Biodiversity, Evolution and Biogeography of Plants* 53: 459–461.
- Liu Y, Verano-Libalah MC, Kadereit G, Zhou R, Quakenbush JP, Lin C, Wai JS. 2022. Systematics of the tribe Sonerileae. In: Goldenberg R, Michelangeli FA, Almeda F eds. *Systematics, evolution, and ecology of Melastomataceae*. Cham: Springer. 321–343.
- Maddison WP, Maddison DR. 2016. Mesquite: A modular system for evolutionary analysis, Version 3: 10 [online]. Available from <http://mesquiteproject.org> [accessed June 2017].
- Maurin O, Anest A, Bellot S, Biffin E, Brewer G, Charles-Dominique T, Cowan RS, Dodsworth S, Epitawalage N, Gallego B, Giaretta A, Goldenberg R, Gonçalves DJP, Graham S, Hoch P, Mazine F, Low YW, McGinnie C, Michelangeli FA, Morris S, Penneys DS, Pérez Escobar OA, Pillon Y, Pokorny L, Shimizu G, Staggemeier VG, Thornhill AH, Tomlinson KW, Turner IM, Vasconcelos T, Wilson PG, Zuntini AR, Baker WJ, Forest F, Lucas E. 2021. A nuclear phylogenomic study of the angiosperm order Myrales, exploring the potential and limitations of the universal Angiosperms353 probe set. *American Journal of Botany* 108: 1087–1111.
- Michelangeli FA, Almeda F, Goldenberg R, Penneys DS. 2020. Guide to curating New World Melastomataceae collections with a linear generic sequence to world-wide Melastomataceae. *Preprints 2020*: 2020100203.
- Michelangeli FA, Guimaraes PJF, Penneys DS, Almeda F, Kriebel R. 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Botanical Journal of the Linnean Society* 171: 38–60.
- Michelangeli FA, Judd WS, Penneys DS, Skean JD, Bécquer-Granados ER, Goldenberg R, Martin CV. 2008. Multiple events of dispersal and radiation of the Tribe Miconiae (Melastomataceae) in the Caribbean. *The Botanical Review* 74: 53–77.
- Michelangeli FA, Nicolas A, Morales-P ME, David H. 2011. Phylogenetic relationships of *Allomaieta*, *Alloneuron*, *Cyphostyla*, and *Wurdastrom* (Melastomataceae) and the resurrection of the

- tribe Cyphostyleae. *International Journal of Plant Sciences* 172: 1165–1178.
- Michelangeli FA, Penneys DS, Giza J, Soltis D, Hils MH, Skean JD. 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. *Taxon* 53: 279–290.
- Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, LA, November 1: 1–8.
- Naudin CV. 1851. Melastomacearum monographiae descriptionis. *Annales des Sciences Naturelles Botanique* Sér 3(15): 43–79.
- Penneys DS, Almeda F, Reginato M, Michelangeli FA, Goldenberg R, Fritsch PW, Stone RD. 2022. A new Melastomataceae classification informed by molecular phylogenetics and morphology. In: Goldenberg R, Michelangeli FA, Almeda F eds. *Systematics, evolution, and ecology of Melastomataceae*. Cham: Springer. 109–165.
- Penneys DS, Judd WS. 2013. Combined molecular and morphological phylogenetic analyses of the Blakeeae (Melastomataceae). *International Journal of Plant Sciences* 174: 802–817.
- Penneys DS, Michelangeli FA, Judd WS, Almeda F. 2010. Henrieteeae: A new neotropical tribe of berry-fruited Melastomataceae. *Systematic Botany* 35: 783–800.
- Perrier de la Bâthie H. 1951. 153. Mélastomatacées. In: Humbert H ed. *Flore de Madagascar et des Comores*. Paris: Firmin-Didot et Cie. 1–326.
- Rambaut A, Drummond AJ. 2013. Tracer v1.6 [online]. Available from <http://tree.bio.ed.ac.uk/software/tracer/> [accessed 30 June 2015].
- Regalado JC. 1990. Revision of *Medinilla* (Melastomataceae) of Borneo. *Blumea* 35: 5–70.
- Regalado JC. 1995. Revision of Philippine *Medinilla* (Melastomataceae). *Blumea* 40: 113–193.
- Reginato M, Michelangeli FA. 2016. Untangling the phylogeny of Leandra s.str. (Melastomataceae, Miconieae). *Molecular Phylogenetics and Evolution* 96: 17–32.
- Renner SS. 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic Journal of Botany* 13: 519–540.
- Rocha MJR, Batista JAN, Guimarães PJF, Michelangeli FA. 2016. Phylogenetic relationships in the Marctetia alliance (Melastomeae, Melastomataceae) and implications for generic circumscription. *Botanical Journal of the Linnean Society* 181: 585–609.
- Solt ML, Wurdack JJ. 1980. Chromosome numbers in the Melastomataceae. *Phytologia* 47: 199–220.
- Stamatakis A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- Stone RD. 2006. Phylogeny of major lineages in Melastomataceae, subfamily Olibeoideae: Utility of nuclear glyceraldehyde 3-phosphate dehydrogenase (GapC) gene sequences. *Systematic Botany* 31: 107–121.
- Stone RD. 2014. The species-rich, paleotropical genus *Memecylon* (Melastomataceae): Molecular phylogenetics and revised infrageneric classification of the African species. *Taxon* 63: 539–561.
- Stone RD, Andreasen K. 2010. The Afro-Madagascan genus *Warneckea* (Melastomataceae): Molecular systematics and revised infrageneric classification. *Taxon* 59: 83–92.
- Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution* 38(7): 3022–3027.
- Triana JJ. 1866. Dispositio Melastomacearum. *Bulletin du Congrès International de Botanique et d'Horticulture réuni à Amsterdam 1865*: 457–461.
- Triana JJ. 1872. Les Mélastomatacées. *Transactions of the Linnean Society of London* 28(1): 1–188.
- Ulloa Ulloa C, Almeda F, Goldenberg R, Kadereit G, Michelangeli FA, Penneys DS, Stone RD, Verano-Libalah MC. 2022. Melastomataceae: Global diversity, distribution, and endemism. In: Goldenberg R, Michelangeli FA, Almeda F eds. *Systematics, Evolution, and Ecology of Melastomataceae*. Cham: Springer. 3–28.
- Verano-Libalah MC, Kadereit G, Stone RD, Couvreur TLP. 2018. Multiple shifts to open habitats in Melastomataceae (Melastomataceae) congruent with the increase of African Neogene climatic aridity. *Journal of Biogeography* 45: 1420–1431.
- Verano-Libalah MC, Stone RD, Fongod AGN, Couvreur TLP, Kadereit G. 2017. Phylogeny and systematics of African Melastomataceae (Melastomataceae). *Taxon* 66: 584–614.
- Verano-Libalah MC, Stone RD, Kadereit G. 2020. Towards a complete phylogeny of African Melastomataceae: Systematics of Dissotis and allies (Melastomataceae). *Taxon* 69: 946–991.
- Van Vliet GJMC. 1981. Wood anatomy of the palaeotropical Melastomataceae. *Biodiversity, Evolution and Biogeography of Plants* 27: 395–462.
- Van Vliet GJMC, Koek-Noorman J, ter Welle BJH. 1981. Wood anatomy, classification and phylogeny of Melastomataceae. *Biodiversity, Evolution and Biogeography of Plants* 27: 463–473.
- Wickens GE. 1975. Melastomataceae. In: Polhill RM ed. *Flora of Tropical East Africa*. London: Crown Agents for Overseas Governments and Administrations. 1–73.
- Wildeman Ede. 1908. Études de systématique et de géographie botaniques sur la flore du Bas- et du Moyen-Congo. *Études de systématique et de géographie botaniques sur la flore du Bas- et du Moyen-Congo* 2: 327–334.
- Zhou Q, Dai J, Lin C, Ng W, Van Do T, Sae Wai J, Michelangeli FA, Reginato M, Zhou R-C, Liu Y. 2022. Out of chaos: Phylogenomics of Asian Sonerileae. *Molecular Phylogenetics and Evolution* 175: 107581.
- Zhou Q, Lin C, Ng WL, Dai J, Denda T, Zhou R, Liu Y. 2019. Analyses of plastome sequences improve phylogenetic resolution and provide new insight into the evolutionary history of Asian Sonerileae/Dissochaeteae. *Frontiers in Plant Science* 10: 1–16.

Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12921/supplinfo>:

Fig. S1. Bayesian inference phylogeny of African Sonerileae based on the nuclear matrix (nrITS, nrETS). Values at the nodes refer to posterior probabilities.

Fig. S2. Bayesian inference phylogeny of African Sonerileae based on the plastid matrix (accD-psal, ndhF, psbK-psbL). Values at the nodes refer to posterior probabilities.

Fig. S3. Maximum likelihood phylogeny of African Sonerileae based on the plastid matrix (accD-psal, ndhF, psbK-psbL). Values at the nodes refer to posterior probabilities.

Fig. S4. Maximum likelihood phylogeny of African Sonerileae based on the nuclear matrix (nrITS, nrETS). Values at the nodes refer to posterior probabilities.

Table S1. Voucher information for all the sequences generated in Burgt et al. (2022).

Appendix I. GenBank accession numbers for sequences used in the phylogenetic placement of African Sonerileae. GenBank accession numbers with an asterisk (*) are newly sequenced by Burgt et al. (2022). –, missing data.

Names	nrITS	accD-psal	psbK-psbL	nrETS	ndhF
<i>Acanthella sprucei</i>	JQ730036	JQ730247	JQ730456	KF462811	–
<i>Aciotis paludosa</i>	JQ730040	JQ730251	JQ730460	KF462814	–
<i>Aciotis purpurascens</i>	JQ730041	JQ730252	JQ730461	KF462815	AF215561
<i>Acisanthera hedyotoidea</i>	JQ730044	JQ730255	JQ730464	KU501001	–
<i>Adelobotrys subsessilis</i>	AY966407	–	MH781651	MH781591	MH760283
<i>Allomorphia balansae</i>	MG644470	MK994792	MK994792	–	MK994792
<i>Amphiblemma ciliatum</i> 2444	OL414843*	OL744332*	OL698719*	OK667182*	OL365035*
<i>Amphiblemma ciliatum</i> 4262	OL414844*	OL744333*	OL698720	OK667183*	OL365036*
<i>Amphiblemma ciliatum</i> BGD	OL414845*	OL744334*	–	OK667184*	OL365037*
<i>Amphiblemma cuneatum</i>	OL414846*	–	OL698721*	–	–
<i>Amphiblemma cymosum</i>	OL414847*	OL744335*	–	OK667185*	OL365034*
<i>Amphiblemma gossweileri</i> 455	OL414848*	OL744336*	OL698722*	–	OL365038*
<i>Amphiblemma gossweileri</i> 857	OL414849*	OL744337*	OL698723*	OK667186*	OL365039*
<i>Amphiblemma hallei</i>	OL414850*	–	OL698724*	–	–
<i>Amphiblemma heterophyllum</i>	OL414851*	OL744338*	OL698725*	OK667187*	OL365040*
<i>Amphiblemma lanceatum</i>	OL414852*	–	OL698726*	OK667188*	–
<i>Amphiblemma mildbraedii</i> 220	OL414853*	–	OL698727*	OK667189*	–
<i>Amphiblemma mildbraedii</i> 3767	OL414854*	OL744339*	OL698728*	–	OL365041*
<i>Amphiblemma molle</i> 2011	OL414855*	–	OL698729*	–	–
<i>Amphiblemma molle</i> 12836	OL414856*	–	OL698730*	–	–
<i>Amphiblemma mvensis</i>	OL414857*	–	–	–	–
<i>Amphiblemma setosum</i> 829	OL414858*	–	OL698731*	OK667190*	–
<i>Amphiblemma setosum</i> 1404	OL414859*	–	OL698732*	–	–
<i>Amphiblemma soyauxii</i>	OL414860*	–	OL698733*	–	–
<i>Amphiblemma</i> sp. 1059	OL414861*	OL744331*	OL698734*	OK667191*	OL365042*
<i>Amphiblemma</i> sp. 1279	OL414862*	OL744340*	OL698735*	OK667192*	OL365043*
<i>Amphiblemma</i> sp. 1506	OL414863*	OL744341*	OL698736*	OK667193*	OL365044*
<i>Amphiblemma</i> sp. 3440	OL414864*	–	OL698737*	OK667194*	–
<i>Amphorocalyx rupestris</i>	JQ730046	JQ730257	JQ730466	–	–
<i>Anerinicleistus macrophyllus</i>	MN031184	MK994887	MK994887	–	KF462820
<i>Appendicularia thymifolia</i>	JQ730049	JQ730260	JQ730468	KF462820	–
<i>Arthrostemma primaevum</i>	JQ730050	JQ730261	JQ730469	–	JF831972
<i>Barthea barthei</i>	MG644388	KY873324	KY873324	–	KY873324
<i>Benna alternifolia</i> 2323	OL414908*	–	OL698783*	–	–
<i>Benna alternifolia</i> 2274	OL414909*	–	OL698784*	OK667214*	–
<i>Bertolonia acuminata</i>	MK258150	KX826820	KX826820	MK296603	KX826820
<i>Bertolonia alternifolia</i>	MH708155	–	MK296663	MH722270	MH729204
<i>Bertolonia angustipetala</i>	MK258151	–	MK296664	MK296604	–
<i>Bertolonia bullata</i>	MH708154	–	–	MH722271	MH729205
<i>Bertolonia mosenii</i>	MH708156	–	MK296678	MK296614	JF831973
<i>Bertolonia paranaensis</i>	MH708157	–	MK296681	MH722277	MH729208
<i>Bertolonia reginatoi</i>	MK258160	–	MK296682	MK296615	–
<i>Blakea chlorantha</i>	GU968789	–	–	–	GU968806
<i>Blakea gracilis</i>	AY460445	–	–	–	GU968807
<i>Blakea schlimii</i>	AY460441	KX826821	KX826821	–	KX826821
<i>Blastus boreensis</i>	OL414865*	OL744342*	OL698738*	–	OL365045*
<i>Blastus ernaee</i>	MN382045	MK994800	–	–	MK994800
<i>Blastus mollissimus</i>	MN382046	MK994863	–	–	MK994863
<i>Boyania colombiana</i>	–	–	MK296693	MK296625	–
<i>Brachyotum incrassatum</i>	JQ730056	JQ730267	JQ730475	KF462826	–
<i>Bredia hirsuta</i>	MN031213	–	MK994872	–	MK994872
<i>Bredia repens</i>	MF952713	MK994832	–	–	MK994832
<i>Calvoa crassinoda</i>	OL414866*	–	OL698739*	–	–
<i>Calvoa hirsuta</i> 144	OL414867*	–	–	–	OL365027*
<i>Calvoa hirsuta</i> 1502	OL414868*	–	OL698740*	–	OL365028*

Continued

Names	nrITS	accD-psal	psbK-psbL	nrETS	ndhF
<i>Calvoa hirsuta</i> 4055	OL414869*	OL744343*	OL698741*	—	OL365029*
<i>Calvoa jacques-felixii</i>	OL414870*	—	OL698742*	—	OL365046*
<i>Calvoa maculata</i> 2006	OL414871*	—	—	—	OL365030*
<i>Calvoa monticola</i> 2323	OL414872*	—	OL698743*	—	OL365048*
<i>Calvoa monticola</i> 3246	OL414873*	—	OL698744*	—	OL365049*
<i>Calvoa orientalis</i> 2902	OL414874*	—	OL698745*	—	OL365050*
<i>Calvoa orientalis</i> 4122	OL414875*	OL744344*	OL698746*	OK667195*	OL365051*
<i>Calvoa pulcherrima</i> 1278	OL414876*	OL744345*	OL698747*	—	OL365052*
<i>Calvoa pulcherrima</i> 2018	OL414877*	OL744346*	OL698748*	—	OL365053*
<i>Calvoa pulcherrima</i> 2124	OL414866*	MG702538	—	—	MG702549
<i>Calvoa seretii</i> BGD	OL414865*	OL744347*	OL698749*	—	OL365054*
<i>Calvoa seretii</i> BGD	OL414878*	OL744348*	OL698750*	—	OL365055*
<i>Calvoa seretii</i> 1750	OL414879*	OL744349*	OL698751*	OK667196*	OL365056*
<i>Calvoa seretii</i> 1773	OL414880*	OL744350*	OL698752*	—	OL365057*
<i>Calvoa seretii</i> 1930	OL414881*	MG702539	MG518555	OK667197*	MG702550
<i>Calvoa seretii</i> 1930	MG518540	OL744349*	—	OK667198*	—
<i>Calvoa zenkeri</i>	OL414882*	—	OL698753*	—	OL365047*
<i>Cambessedesia espora</i>	—	JQ730273	JQ730481	KF462834	JQ899114
<i>Castratella piloselloides</i>	JQ730064	JQ730275	JQ730483	—	AY553783
<i>Centradenia inaequilateralis</i>	JQ730066	JQ730277	JQ730484	—	AF215563
<i>Chaetolepis cufodontisii</i>	JQ730067	JQ730278	JQ730485	—	—
<i>Chaetostoma armatum</i>	JQ730069	JQ730280	JQ730487	—	—
<i>Cincinnobotrys acaulis</i> 2861	OL414883*	—	OL414883*	—	—
<i>Cincinnobotrys acaulis</i> 8019	OL414884*	—	OL414884*	—	—
<i>Cincinnobotrys felicis</i> 438	OL414885*	—	OL414885*	—	OL365031*
<i>Cincinnobotrys felicis</i> 608	OL414886*	—	OL414886*	—	OL365032*
<i>Cincinnobotrys oreophila</i>	OL414887*	—	OL414887*	—	—
<i>Cincinnobotrys ranarum</i>	OL414888*	—	OL414888*	OK667200*	OL365033*
<i>Clidemia umbellata</i>	EU055674	—	KF821911	KF820711	EU055929
<i>Comolia microphylla</i>	JQ730070	JQ730281	JQ730488	KF462841	JF831975
<i>Creochiton roseus</i>	MW462482	—	MW462244	MW462332	MW462401
<i>Cyphotheca montana</i>	MG644447	MK994852	MK994852	—	MK994852
<i>Desmoscelis villosa</i>	JQ730073	JQ730284	JQ730491	KF462844	—
<i>Dicellandra barteri</i> 3524	MG518542	MG702537	MG518557	MG518532	MG702552
<i>Dicellandra barteri</i> 2087	OL414889*	OL744350*	OL414890*	OK667201*	OL365058*
<i>Dicellandra barteri</i> 266	OL414890*	OL744351*	OL414899*	OK667202*	OL365059*
<i>Dicellandra descoingsii</i> 189	OL414891*	OL744353*	OL414891*	OK667203*	OL365060*
<i>Dicellandra descoingsii</i> 1886	MG518541	—	MG518556	MG518531	MG702551
<i>Dicellandra</i> sp. 128	OL414892*	—	OL414892*	—	OL365061*
<i>Dichaetanthera arborea</i>	KX889223	—	KY284742	MF397948	MF398043
<i>Dinophora spenneroides</i>	KX889227	—	KY284746	MF397951	MF398047
<i>Dalenia beccariana</i>	MW462519	MK994889	MW462297	—	MW462442
<i>Dissochaeta griffithii</i>	MW462510	—	MW462278	MW462359	MW462433
<i>Dissochaeta rostrata</i>	MW462523	OL744354*	MW462293	OK667204*	OL365062*
<i>Dissochaeta stipularis</i>	—	OL744355*	—	OK667205*	OL365063*
<i>Driessnia glanduligera</i>	MN031197	MK994879	MK994879	—	MK994879
<i>Eriocnema fulva</i>	EF418811	KX826822	KX826822	KX826822	KX826822
<i>Ernestia glandulosa</i>	JQ730080	JQ730293	JQ730499	KF462847	—
<i>Fordiophyton cordifolium</i>	MN031160	MK994784	—	—	MK994784
<i>Fordiophyton strictum</i>	MN031161	MK994816	—	—	MK994816
<i>Fritzschia erecta</i>	JQ730083	JQ730296	JQ730502	KF462849	—
<i>Graffenrieda moritziana</i>	AY460451	JQ730298	JQ730504	KF820749	EU055944
<i>Gravesia aff. scripta</i> 1886	OL414893*	—	OL414893*	—	OL365021*
<i>Gravesia aff. scripta</i> 3983	OL414894*	—	OL414894*	—	OL365015*
<i>Gravesia barbata</i>	OL414895*	—	OL414895*	OK667206*	—
<i>Gravesia biauriculata</i>	OL414896*	—	OL414896*	—	OL365016*
<i>Gravesia serratifolia</i>	—	—	—	—	OL365018*
<i>Gravesia erecta</i>	OL414897*	—	OL414897*	—	OL365017*

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Names	nrITS	accD-psal	psbK-psbL	nrETS	ndhF
<i>Gravesia guttata</i>	—	MG702540	MG518558)	MG518533	MG702553
<i>Gravesia laxiflora</i>	—	MG702540	MG518558	MG518533	MG702553
<i>Gravesia nigrescens</i>	MG518543	MG702541	MG518559	—	MG702554
<i>Gravesia pterocaulon</i>	MG518544	MG702542	MG518560	MG518534	MG702555
<i>Gravesia pulchra</i>	OL414899*	—	OL414899*	—	—
<i>Gravesia pusilla</i>	—	OL744356*	—	—	OL365022*
<i>Gravesia riparia</i>	OL414900*	—	OL414900*	—	—
<i>Gravesia setifera</i> 9974	—	MG702543	MG518561	MG518535	MG702556
<i>Gravesia setifera</i> 302	—	OL744357*	OL414901*	OK667209*	OL365023*
<i>Gravesia</i> sp. 2651	OL414901*	OL744359*	OL414902*	OK667210*	OL365019*
<i>Gravesia</i> sp. 9924	OL414902*	OL744358*	OL414903*	OK667207*	—
<i>Gravesia</i> sp. 10071	—	—	OL414904*	OK667208*	OL365020*
<i>Gravesia</i> sp. 2652	OL414904*	OL744361*	OL414901*	—	—
<i>Gravesia</i> sp. 9923	OL414905*	OL744362*	—	—	OL365024*
<i>Gravesia</i> sp. 2660	OL414903*	OL744360*	—	—	—
<i>Gravesia tanalaensis</i>	MG518546	MG702544	MG518562	—	—
<i>Gravesia vestita</i>	OL414906*	OL744364*	OL414906*	OK667211*	OL365025*
<i>Gravesia viguieri</i>	—	OL744365*	—	—	OL365026*
<i>Henriettea barkeri</i>	KJ933957	—	KX826824	KX826824	KX826824
<i>Heteroblemma serpens</i>	MN031200	MK994886	MK994886	MK994886	MK994886
<i>Heterocentron muricatum</i>	JQ730086	JQ730300	JQ730507	KF462851	—
<i>Heterotis prostrata</i>	KX889287	KY284713	KY284812	MF398013	MF398111
<i>Itatiaia cleistopetala</i>	JQ730090	JQ730303	JQ730510	KF462854	—
<i>Lavoisiera phyllocalyicina</i>	KF463034	KF407960	KF463001	KF462856	—
<i>Leandra salicina</i>	EU055703	GQ139261	GQ139346	KR062444	EU055960
<i>Macairea thyrsiflora</i>	JQ730096	JQ730308	JQ730515	KF462860	—
<i>Macrocentrum anfractum</i>	KF821521	—	KF822037	KF820851	MH729210
<i>Macrocentrum brevipedicellatum</i>	MH819881	—	MH781674	MH781610	MH760311
<i>Macrocentrum cristatum</i>	MF785406	—	MF105286	MH781611	AM235412
<i>Macrocentrum droseroides</i>	KF821523	—	MK296696	KF820852	MH729211
<i>Macrocentrum neblinae</i>	KF821527	—	MH781675	KF820855	MH729212
<i>Macrocentrum parvulum</i>	MH819882	—	MH781676	MH781612	MH760315
<i>Macrocentrum repens</i>	KF821528	—	KF822043	KF820856	AF215551
<i>Macrolenes horrida</i>	MW462512	—	MW462280	MW462361	MW462435
<i>Macrolenes pachygyna</i>	MW462543	MK994894	—	—	MK994894
<i>Maguireanthus ayangannae</i>	MH819884	—	MH781677	MH781613	MH760317
<i>Marcteria taxifolia</i>	JQ730102	JQ730311	JQ730521	KU501041	GU968825
<i>Medinilla amplexens</i>	MN031219	MK994882	MK994882	—	MK994882
<i>Medinilla beamanii</i>	MN031220	MK994880	MK994880	—	MK994880
<i>Medinilla chermezonii</i>	—	MG702545	MG518563	MG518536	MG702557
<i>Medinilla fengii</i>	MG644482	MK994809	—	—	MK994809
<i>Medinilla humbertiana</i>	—	—	AF215517	—	AF215557
<i>Medinilla intermedia</i>	—	—	MW462318	—	MW462468
<i>Medinilla lophocladia</i>	—	MG702546	MG518564	MG518537	MG702558
<i>Medinilla mannii</i> 473	—	—	OK667212*	—	—
<i>Medinilla mannii</i> 3434	—	OL744366*	—	OK667213*	OL365064*
<i>Medinilla micrantha</i>	—	MG702547	MG518565	MG518538	MG702559
<i>Medinilla myrtiformis</i>	—	—	MW462319	—	MW462469
<i>Medinilla petelotii</i>	MN031218	MK994847	—	—	MK994847
<i>Medinilla rubicunda</i>	—	—	MW462320	—	MW462470
<i>Medinilla speciosa</i>	MN031221	MK994885	MK994885	MK994885	MK994885
<i>Medinilla squillula</i>	MG518547	MG702548	MG518566	MG518539	MG702560
<i>Medinilla teysmannii</i>	—	—	MW462322	MW462394	MW462471
<i>Melastoma sanguineum</i>	JQ730106	JQ730315	JQ730525	—	AF270754
<i>Melastomastrum afzelii</i>	KX889290	KY284715	KY284815	MF398015	MF398113
<i>Melastomastrum theifolium</i> 2052	OL414907*	OL744368*	—	—	—
<i>Melastomastrum theifolium</i>	KX889296	KY284720	KY284822	MF398021	MF398119
<i>Meriania calophylla</i>	EU055707	—	KF822062	KF820876	EU055969

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Names	nrITS	accD-psal	psbK-psbL	nrETS	ndhf
<i>Miconia dodecandra</i>	AY460506	JQ730317	JQ730527	KF821020	—
<i>Microlepis oleifolia</i>	JQ730107	JQ730319	JQ730529	KU501051	AF272815
<i>Microlicia fulva</i>	KU501105	KU501205	KF463004	KU501051	—
<i>Monochaetum discolor</i>	JQ730109	JQ730321	JQ730531	KF462863	—
<i>Monolena primuliflora</i>	—	—	MK164942	MK296626	AF215552
<i>Ochthocharis borneensis</i>	—	—	MK994895	—	MK994895
<i>Ochthocharis dicellandroides</i>	—	—	MG518550	MG518526	MG702562
<i>Ochthocharis dicellandroides</i>	—	—	MG518550	MG518526	MG702562
<i>Osbeckia nepalensis</i>	JQ730118	JQ730329	JQ730539	—	AF272817
<i>Ossaea angustifolia</i>	GQ139309	—	GQ139352	—	—
<i>Oxyspora paniculata</i>	MN031212	MK994816	MK994816	—	MK994816
<i>Oxyspora teretipetiolata</i>	MG644476	MK994853	—	—	MK994853
<i>Pachycentria constricta</i>	MW462548	—	MW462326	MW462397	MW462474
<i>Pachycentria microsperma</i>	—	OL744367*	631 (234 indels)	—	OL365065*
<i>Pachyloma huberioides</i>	JQ730120	JQ730331	JQ730541	KF821339	—
<i>Phainantha shuariorum</i>	—	—	—	—	JF831981
<i>Phyllagathis erecta</i>	MG644442	MK994811	—	—	MK994811
<i>Phyllagathis gracilis</i>	MG644403	MK994796	—	—	MK994796
<i>Phyllagathis hispida</i>	MG644435	MK994783	—	—	MK994783
<i>Phyllagathis stenophylla</i>	MG644427	MK994793	—	—	MK994793
<i>Phyllagathis tetrandra</i>	MG64443	MK994817	—	—	MK994817
<i>Plagiopetalum esquirolii</i>	MN031202	MK994851	—	—	MK994851
<i>Plagiopetalum serratum</i>	MN031170	MK994902	MK994902	—	MK994902
<i>Preussiella kamerunensis</i> 1886	OL414910*	—	OL414910*	—	—
<i>Preussiella kamerunensis</i> 4594	OL414911*	—	OL414911*	OK667215*	—
<i>Preussiella kamerunensis</i> 2303	OL414912*	—	OL414912*	—	—
<i>Pseudodissochaeta septentrionalis</i>	MN031231	MK994778	—	—	MK994778
<i>Pseudodissochaeta assamica</i>	MG644480	MK994848	MK994848	—	MK994848
<i>Pseudodissochaeta lanceata</i>	MN031232	MK994850	MK994850	—	MK994850
<i>Pseudosbeckia sywnertonii</i>	KX889302	KY284722	KY284828	MF398024	MF398125
<i>Pterogastra divaricata</i>	JQ730126	KX826829	KX826829	KX826829	—
<i>Pterolepis glomerata</i>	JQ730126	JQ730337	JQ730547	KF462875	—
<i>Rhexia aristosa</i>	JQ730129	JQ730340	JQ730550	KF462876	AF215571
<i>Rhexia virginica</i>	JQ730134	JQ730345	JQ730555	KF462878	—
<i>Rhynchanthera bracteata</i>	JQ730136	JQ730346	JQ730557	KF462879	AF215587
<i>Rhynchanthera grandiflora</i>	JQ730137	JQ730347	JQ730558	KF462880	—
<i>Rosettea elliotii</i>	JQ730138	JQ730348	JQ730559	KF462881	AF215584
<i>Rousseauxia andringitrensis</i>	JQ730139	JQ730350	JQ730561	—	—
<i>Salpinga glandulosa</i>	MH819927	—	MH781717	MH781649	—
<i>Salpinga maranonensis</i>	KY991873	KX826832	KX826832	—	KX826832
<i>Salpinga peruviana</i>	MH819928	—	MH781718	MH781650	MH760363
<i>Salpinga secunda</i>	KY991815	—	MF105092	—	—
<i>Sandemania hoehnei</i>	JQ730141	JQ730352	—	KF462882	—
<i>Scorpiothyrsus shangszeensis</i>	MN031186	MK994866	MK994866	—	MK994866
<i>Sonerila borneensis</i>	MN031190	MK994893	MK994893	—	MK994893
<i>Sonerila celebica</i>	MW462552	—	MW462331	MW462398	MW462479
<i>Sonerila parviflora</i>	MN031223	MK994900	MK994900	—	MK994900
<i>Sonerila pulchella</i>	MN031193	MK994884	MK994884	—	MK994884
<i>Sonerila velutina</i>	MN031224	MK994892	MK994892	—	MK994892
<i>Sonerila yunnanensis</i>	—	MK994862	MK994862	—	MK994862
<i>Sporoxeia clavicalcarata</i>	MN031192	MK994901	MK994901	—	MK994901
<i>Styrophyton caudatum</i>	MN031176	MK994860	MK994860	—	MK994860
<i>Svitramia pulchra</i>	JQ730145	JQ730356	JQ730567	KF462888	—
<i>Tashiroea okinawensis</i>	MN031204	MK994803	MK994803	—	MK994803
<i>Tetrazygia urbanii</i>	—	—	KF822547	—	AF270753
<i>Tibouchina arborea</i>	JQ730152	JQ730363	JQ730575	KF462893	—
<i>Tibouchina dubia</i>	JQ730179	JQ730388	JQ730599	KF462923	—
<i>Tibouchina gracilis</i>	JQ730190	JQ730398	JQ730610	KF462933	—

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Names	nrITS	accD-psal	psbK-psbL	nrETS	ndhF
<i>Tibouchina granulosa</i>	JQ730191	JQ730399	JQ730611	KF462934	—
<i>Tibouchina grossa</i>	JQ730192	JQ730400	JQ730612	KF462935	JF831983
<i>Tibouchina longifolia</i>	JQ730204	KY821071	JQ730624	—	AF215572
<i>Tibouchina ramboi</i>	JQ730224	JQ730432	JQ730644	KF462966	—
<i>Tibouchina saxosa</i>	KF463048	KF407981	KF463021	KF462968	—
<i>Tibouchina ursina</i>	JQ730237	JQ730446	JQ730658	KF462982	—
<i>Tibouchinopsis mirabilis</i>	JQ730241	JQ730450	JQ730662	KF462986	—
<i>Tigridiopalma magnifica</i>	MG644449	MF663760	MF663760	—	MF663760
<i>Tococa spadiciflora</i>	EU055897	—	KF822568	—	EU056139
<i>Trembleya parviflora</i>	JQ730242	JQ730451	JQ730663	KF462987	—
<i>Triolena amazonica</i>	—	KX826834	KX826834	KX826834	KX826834
<i>Triolena spicata</i>	KY782508	—	MK296701	MK296627	—
<i>Trysophyton merumense</i>	MF785430	—	—	—	MK284234