

SYSTEMATICS AND PHYLOGENY

Indo-Asian *Eriolaena* expanded to include two Malagasy genera, and other generic realignments based on molecular phylogenetics of Dombeyoideae (Malvaceae)

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Abstract Molecular phylogenetic analyses of Malvaceae subfamily Dombeyoideae based on a 6-marker dataset sampling all 21 currently accepted genera (including extinct *Astyria*) yielded improved resolution and evidence for multiple generic circumscription problems. The taxonomy of the subfamily is adjusted with the synonymization of 10 genera (eight in current use) and the description of one new one, for a revised Dombeyoideae comprised of 14 genera and supported by morphological, anatomical, and/or palynological evidence. *Eriolaena* is expanded from a narrow Indo-Asian group to include the Malagasy endemic genera *Helmiopsis* and *Helmiopsiella*, and a recently described species from continental Africa. A conspectus is presented of the new broadly circumscribed *Eriolaena* with 27 species (28 taxa, including 3 new Malagasy species and 16 new combinations) and defined by a unique winged-seed morphology. A new monotypic Malagasy genus (*Hafotra*), resolved as sister to *Eriolaena*, is described. A conspectus is presented of a broadly circumscribed Mascarene-Malagasy *Ruizia* (+ *Astyria* and *Trochetia*, with 13 new combinations). Two other genera are expanded and recircumscribed: *Melhania* (+ *Trochetiopsis* and *Paramelhania*, with one new name and two new combinations) and *Corchoropsis* (+ *Paradombeya*, with two new combinations). Additionally, two genera are typified, and 21 names are lectotypified.

Keywords *Eriolaena*; *Hafotra*; *Helmiopsiella*; *Helmiopsis*; Madagascar; molecular phylogenetics; *Ruizia*

■ INTRODUCTION

Our understanding of relationships, and generic and subfamily circumscriptions in Malvaceae is surprisingly incomplete despite the economic importance of the family (see Bayer & Kubitzki, 2003). For example, recent molecular phylogenetic studies (e.g., Le Péchon & al., 2010; Skema, 2012) in subfamily Dombeyoideae have challenged traditional generic circumscriptions and indicated the need to reevaluate the morphological bases for some of its constituent genera. Dombeyoideae (sometimes recognized as Dombeyaceae or Pentapetaceae, see Cheek, 2007; Doweld & Reveal, 2007) was most recently circumscribed as having 21 genera (reduced here to 14) and over 350 (probably 380+) species distributed across the Old World tropics (Bayer & Kubitzki, 2003; Skema, 2012). Dombeyoideae appear to be sister to Brownlowioideae (Hernández-Gutiérrez & Magallón, 2019), although relationships among major clades of Malvaceae have been difficult to establish and need a well-sampled phylogenomic perspective (Conover & al., 2019). While broader intergeneric relationships within the subfamily have yet to be comprehensively presented (see Won, 2009), over half of the species richness is contained in the relatively well-studied *Dombeya* clade (Le Péchon & al., 2010, 2015; Skema, 2012), which is a promising group for investigating breeding system evolution and endemism in the islands of the southwestern Indian Ocean.

Dombeya Cav. s.l. was found to be polyphyletic with a core *Dombeya* s.str. group containing the majority of the species and four early-diverging clades that also included five other related small genera. Nomenclatural adjustments such as the description of *Andringitra* Skema (Skema, 2012) have improved the morphological circumscription of *Dombeya*, but have not fully rectified these taxonomic problems. Further progress on the phylogenetics and classification of species excluded from *Dombeya* s.str. has been hampered by limited phylogenetic resolution and the need to reevaluate the morphological evidence used to define sections and genera. The principal focus of our study is the winged-seed clade (Skema, 2012), one of the four early-diverging groups excluded from *Dombeya* s.str., which consists of *Eriolaena* DC., *Helmiopsiella* Arènes, *Helmiopsis* H.Perrier, and *Dombeya* subsect. *Rigidae* Arènes.

Taxonomic history of the winged-seed clade. — When Candolle (1823) described *Eriolaena*, he compared it to *Wallichia* DC., nom. illeg. (= *Eriolaena*), also described in the same paper. Sepal and androecial characters convinced him that the two genera were distinct from other genera in the Byttneriaceae (i.e., Malvaceae) as both of his new genera each had two glandular spots on the interior surface of the sepals and androecia comprised of monadelphous stamens with extrorse 2-locular anthers. Fruit were not available to Candolle (1823) and thus he was unaware of seed morphology, which subsequently also provided important characters.

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Arnott in Wight & Arnott (1834) created the tribe Eriolaeneae to accommodate *Eriolaena* and *Microchlaena* Wall. ex Wight & Arn., nom. nov. ($\equiv$ *Wallichia* DC., nom. illeg.). His diagnosis of the tribe focused on androecial characters (i.e., stamens in “a multiple series” and an absence of staminodes), and although winged seeds are mentioned in the descriptions of both genera, the significance of this character was overlooked. Bentham in Bentham & Hooker (1862) and later Schumann (1890) both overlooked seed characters and adopted Arnott’s circumscription of the tribe, which became monotypic because *Microchlaena* was placed in synonymy. Nothing in any of these descriptions of Eriolaeneae, however, would differentiate it from Dombeyeae.

When Perrier de la Bâthie (1944) described *Helmiopsis* he allied it with *Nesogordonia* Baill. and argued that the sole character distinguishing the two genera was the complete inversion of the ovary, fruit, and seed in the former genus. He also compared these Afro-Malagasy genera to Indo-Asian *Pterospermum* Schreb. and *Eriolaena*, both of which also have winged seeds. A close relationship with *Pterospermum* was discounted when Perrier de la Bâthie (1944) noted that of the four genera only *Pterospermum* had a gynophore. He concluded that both *Helmiopsis* and *Nesogordonia* belonged in the Sterculiaceae (i.e., Malvaceae) but did not assign either genus to a tribe. Capuron (1953) observed that Perrier de la Bâthie (1944) misinterpreted the ovules and seed of *Nesogordonia*, but *Helmiopsis* nonetheless could be distinguished from the former by the presence of an apical (versus basal) wing on the seed (see Fig. 1C,D). Capuron (1953) provided little insight into the relationships of these two genera apart from noting that Burret (1926) had placed *Nesogordonia* (as *Cistanthera* K.Schum.) near *Dombeya*.

Perrier de la Bâthie (1944) and Capuron (1953) evidently intended to expand *Helmiopsis*, but their omissions of either Latin diagnoses or descriptions prevented the names they proposed from being valid until Arènes (1956a,d) reviewed the genus. Arènes’s (1956a,d, 1959) circumscription of *Helmiopsis* coincides with an idea first suggested by Baillon (1885a) that three species of Dombeyoideae, *Trochetia richardii* Baill., *T. boivinii* Baill., and “*Dombeya pseudopopulus*” Baill. (ined.), formed a natural group that he named *D. sect. Trochetiella* Baill. The species of the section (Baillon, 1885a) have many-flowered cymes, 10–25 fertile stamens, 2-ovulate locules, and calyces and ovaries with lepidote scales. Subsequently, Baillon (1885c) also described *D. pseudopopulus* Baill. and *D. bernieri* Baill., adding the last-named species to his *D. sect. Trochetiella* even though it had solitary flowers as well as few-flowered cymes. In a revision of the Malagasy species of *Dombeya*, Hochreutiner (1926) maintained *D. sect. Trochetiella* with the four species placed there by Baillon (1885a,b,c).

Arènes (1956b) also recognized a relationship between *Nesogordonia* and *Helmiopsis*, but thought their caducous petals and conduplicately folded and deeply indented cotyledons set them apart from other Dombeyeae. Consequently, Arènes (1956b) proposed a new tribe, Helmiopsidae. Shortly

thereafter, Arènes (1956c) created the genus *Helmiopsiella* to accommodate a single species, *Helmiopsiella madagascariensis* Arènes, found in the south of Madagascar, and he allied this new genus with *Helmiopsis* and *Nesogordonia*. Arènes (1956c) thought *Helmiopsiella* differed from *Helmiopsis* in having staminodes opposite the sepals (versus opposite the petals), 7–8-loculed ovaries (versus 5-loculed), and villous pubescence within the ovary (versus scaly).

Barnett (1987, 1988b) used morphology, anatomy, and palynology to establish that *Eriolaena*, *Helmiopsis*, and *Helmiopsiella* were closely related to each other and distinct from *Nesogordonia*. The capsules of *Eriolaena*, *Helmiopsis*, and *Helmiopsiella* are remarkably similar: all are woody, conical or globose in shape, loculicidally dehiscent, and possess basal placentae. The seeds of all three genera have apical or dorsal wings originating anatomically by extension of an umbonate projection of the chalazal region of the ovule (Fig. 1). Moreover, the wing is vascularized by the funiculus, which runs through the body of the seed wing. The superficially similar seed wings of *Pterospermum* and *Nesogordonia* are different anatomically.

The morphology of the androecium of *Eriolaena* s.str. is often used as a character to set it apart from other Dombeyoideae. It is monadelphous with numerous stamens (25–60 per flower) diverging at different levels along the column (Candolle, 1823; Gazet du Chatelier, 1940). This structure, however, is similar to *Helmiopsiella leandrii* (Hochr.) L.C. Barnett and species of *Dombeya* that have many stamens (Van Heel, 1966; pers. obs.); presumably, this “pseudowhorl” morphology is a result of developmental constraints caused by the congestion of numerous stamens in a single staminal column (Barnett, 1988b). In addition, the stamens of *Eriolaena*

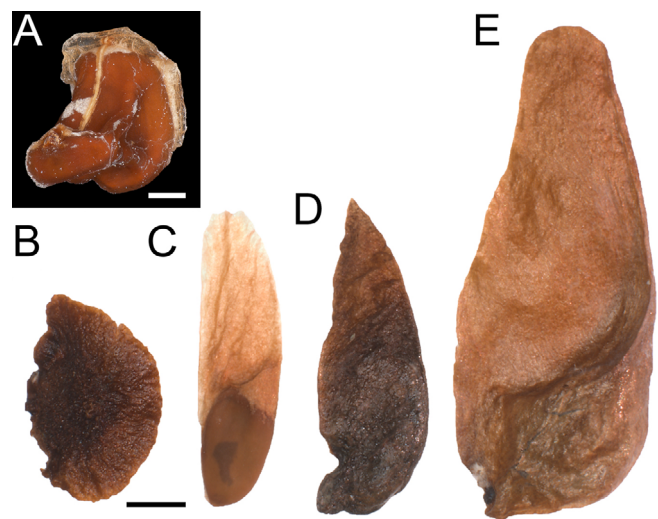


Fig. 1. Seed morphology with wing-like annulus of *Hafotra* gen. nov. and laterally compressed, dorsally or apically winged seeds of *Eriolaena* s.l. **A**, *H. superba* comb. nov. (Bussmann & al. 15245 [MO]); **B**, *E. rigida* comb. nov. (Perrier de la Bâthie 5535 [K]); **C**, *E. boivinii* comb. nov. (Randrianaivo & al. 399 [US]); **D**, *E. pseudopopulus* comb. nov. (Meyers & Boltz 167 [US]); **E**, *E. candollei* (Rock 1663 [US]). — Scale bars A = 0.5 mm, B–E = 2 mm.

s.str., *Astyria* Lindl., and *Ruizia* Cav. are all fertile (i.e., their androecia lack staminodes) and arise from two anatomically differentiated whorls as is typical of other Dombeyoideae (Gazet du Chatelier, 1940; Barnett, 1988b).

Barnett (1988b) also used pollen morphology to ally *Eriolaena* s.str. with *Helmiopsis* and *Helmiopsiella*, while differentiating all three genera from *Nesogordonia*. Dombeyoideae pollen is almost exclusively porate and echinate (Venkata Rao, 1950; Erdtman, 1952; Chaudhuri, 1969; Sharma, 1970; Presting & al., 1983) except for *Nesogordonia* (Presting & al., 1983; Barnett, 1988b), several *Burretiodendron* Rehder species (Tang & Gao, 1993), and one species of *Schoutenia* Korth. (Erdtman, 1952; Nyffeler & al., 2005, both as *Sicrea* (Baill.) Hallier f.), which lack spines and in the case of *Nesogordonia* are shaped differently (triangulate and oblately flattened to spheroid versus spherical). The pollen grains of the few species of *Eriolaena* s.str. examined are panporate with 12 pores (Sharma, 1970) or oligoporate with 8–9(?) pores (Erdtman, 1952; Chaudhuri, 1969). Otherwise, the pollen grains of *E. rulkensii* Dorr, *Helmiopsis*, and *Helmiopsiella* are 3(4)-colporate and remarkably uniform in shape and size (Fig. 2; see also Presting & al., 1983; Barnett, 1988b; Dorr, unpub.).

Despite marshalling evidence regarding the close relationship between *Eriolaena*, *Helmiopsis*, and *Helmiopsiella*, Barnett (1988b) treated them as distinct genera. She considered *Helmiopsiella* to be most closely related to *Helmiopsis*: the two genera sharing caducous epicalyx bracts, fusion of stamens and staminodes into a short column or annulus, a single style, loculicidal, $\pm$ woody capsules, and apically winged seeds. In addition to the characters Arènes (1956c) used to distinguish *Helmiopsiella* from *Helmiopsis*, Barnett (1988a) added that in the former there was an absence of nectariferous tissue on the calyx or corolla.

Dorr (2001) recognized that the seed wings of *Dombeya rigida* Baill. were anomalous within the genus *Dombeya*, and he transferred the species to *Helmiopsis*. Applequist (2009)

revised a narrowly conceived *Helmiopsis* excluding *H. rigida* (Baill.) Dorr and later (Applequist, 2011) argued for retaining *D.* subsect. *Rigidae* within *Dombeya* even though the characters defining the subsection were aberrant within the larger genus.

Skema (2012) provided molecular evidence to align *Dombeya* subsect. *Rigidae* with *Helmiopsis* and expressed doubt about a critical morphological character (i.e., the position of the staminodes relative to the sepals and petals) used to distinguish *Helmiopsis* and *Helmiopsiella*. Skema (2012) observed staminodes in different species of *Helmiopsiella* (and *Dombeya*) occupying positions from one extreme (opposite petals) to the other (opposite sepals). Similarly, Applequist (2009) observed variation of this character even within individuals of *Helmiopsis*. Thus, this character is not as constant as had been represented by Arènes (1956c, 1959) or Barnett (1988a).

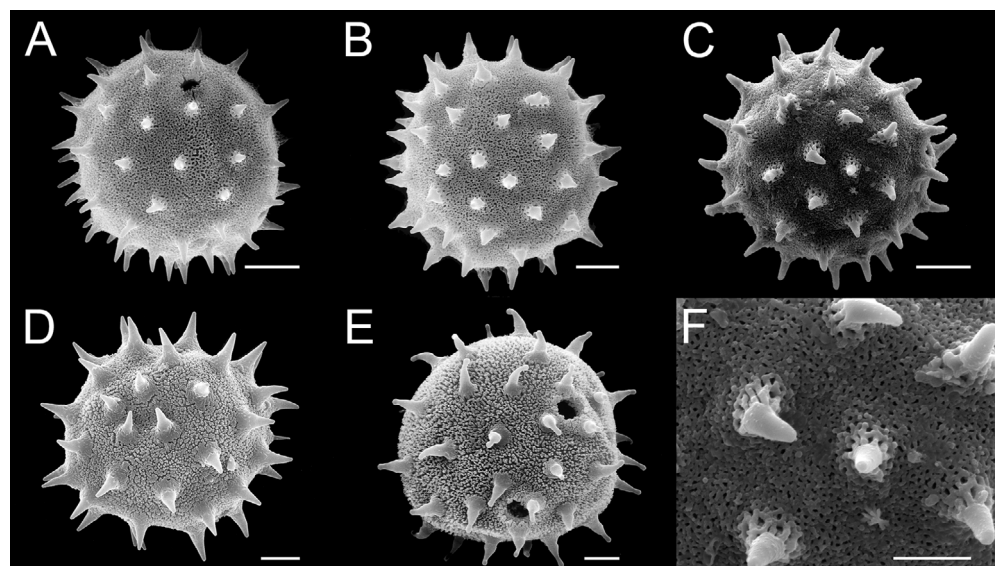
Our molecular study was initiated in an effort to unequivocally place *Eriolaena rulkensii*, recently discovered in coastal northeastern Mozambique (Dorr & Wurdack, 2018), which shared morphological features with the Malagasy endemics *Helmiopsis* and *Helmiopsiella*. We have expanded this phylogenetic perspective broadly across Dombeyoideae to enable a reevaluation of the morphological characters used to define many of its constituent genera. A better understanding of relationships and well delimited genera are critical steps toward a full reclassification of the subfamily and for further evolutionary studies.

■ MATERIALS AND METHODS

Molecular methods. — Our sampling included 96 taxa based on a subset of Le Péchon & al. (2010) and Skema (2012), other data from GenBank, and 41 newly sequenced accessions (totaling 114 tips). Appendix 1 provides details of data sources, including for the 176 newly generated sequences.

Fig. 2. Pollen of *Eriolaena* s.l.

A, *E. ctenostegia* comb. nov. (*Service Forestier 15850-SF* [P]); B, *E. madagascariensis* comb. nov. (*Humbert & Capuron 28830* [P]); C, *E. rulkensii* (*Rulkens 1* [US]); D, *E. leandrii* comb. nov. (*Randriamiera 8634-RN* [P]); E, *E. poissonii* comb. nov. (*Capuron 20105-SF* [P]); F, *E. rulkensii*, spine detail (*Rulkens 1* [US]). — Scale bars A–E = 10 μ m, F = 5 μ m.



For *Eriolaena* s.l., our taxon sampling included 21 of 28 taxa (missing *Helmiopsis calcicola*, *H. glaberrima*, *H. hily* subsp. *boinensis*, and four Indian species of *Eriolaena* s.str. including the generic type, *E. wallichii*). While *Nesogordonia* may be the first-diverging lineage of the Dombeyoideae (see Won, 2009; somewhat equivocal in Hernández-Gutiérrez & Magallón, 2019), we wanted a more distant root and chose representatives of other Malvaceae subfamilies including Byttnerioideae (*Theobroma* L.), Malvoideae (*Gossypium* L.), and Tilioideae (*Tilia* L.) that had full chloroplast genomes and ITS (internal transcribed spacer) in GenBank. Our six genetic markers followed Skema (2012) and included nuclear ribosomal ITS and plastid *trnC*^{GCA}-*ycf6-psbM-trnD*^{GUC} gene cluster (divided following Skema, 2012, along its three constituent intergenic spacers), *petL-psbE*, and *ndhA* intron. Much of the phylogenetic resolution of the winged-seed clade in Skema (2012) is derived from ITS variation, while the plastid markers have very low sequence variation. Given this low variation coupled with DNA degradation in our herbarium samples, our focus for new data was ITS and easily recoverable shorter plastid fragments rather than striving for matrix completeness, and we did not generate new data for *ycf6-psbM*.

General molecular methods for DNA extractions and amplifications followed Dorr & al. (2018). The extractions were as a series of small sets grouped by preservation level, which reduced cross-contamination risk. The old (1863) collection of *Astyria* was extracted and amplified separately from all other Malvales under conditions employed for “antique” DNA lab work. The DNA yield was high, and amplification products were consistent with its degraded quality (i.e., ITS only amplified as two fragments). Authenticity of those data are also indicated by the unique sequences, appropriate phylogenetic resolution of *Astyria*, and no evidence of laboratory contamination in negative controls. Amplifications used the indicated primer combinations and BIOLASE DNA Polymerase (Meridian Life Science, Memphis, Tennessee, U.S.A.) with generic thermocycling conditions (95°C for 30 s, 55°C for 1 min, 72°C for 1 min, ×35 cycles) for ITS (ITS5a + ITS4 or U4; partial with ITS5a + U2, 1m + P2, P3 + U4; White & al., 1990; Stanford & al., 2000; Cheng & al., 2016; Dorr & al., 2018), *trnC-ycf6* (*trnC*^{GCA}F + *ycf6*R; Shaw & al., 2005), *psbM-trnD* (*psbM*F + *trnD*^{GUC}R; Shaw & al., 2005), *petL-psbE* (*petL* + *psbE*; Shaw & al., 2007), and *ndhA* intron (*ndhA*x1 + *ndhA*x2 or *ndhA*x.intR1; Shaw & al., 2007; Skema, 2012). Sequencing used the respective amplification primers and ABI BigDye Terminator v.3.1 chemistry on ABI 3730xl DNA Analyzers (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.).

Sequence and phylogenetic analyses. — Contigs were assembled and edited with Sequencher v.5.2.4 (Gene Codes, Ann Arbor, Michigan, U.S.A.). Our sequence additions to the existing Skema (2012) plastid matrix were straightforward by eye using Se-Al v.2.0a11 (Rambaut, 1996–2002) and for the more variable ITS using MAFFT v.7.272 (Katoh & Standley, 2013) under the L-INS-i refinement method for a *de novo* multiple sequence alignment (MSA), followed by minor

manual alignment refinements based on similarity criteria. The MSAs for each marker are all relatively compact, although for ITS the early-diverging lineages present the highest sequence divergence and homology uncertainties in some segments. For *Theobroma*, ITS was not included due to high sequence divergence and uncertainty as to origin of most GenBank data. The rDNA assemblies of *Theobroma* in Kane & al. (2012) have 3' ends of 18S that are non-canonical relative to other Malvales, and BLAST searches yield fungal annotations. Searches using other relevant portions (i.e., ITS1, 5.8S, ITS2) also do not yield any Malvales as close matches (Wurdack, unpub.). Notable short inversions in the plastid markers were coded as missing data for *Cheirolaena* Benth., *Corchoropsis* Siebold & Zucc., *Nesogordonia tricarpellata* Skema & Dorr, and *Schoutenia* (MSA positions 3445–3453 for *trnC-ycf6* and 5259–5279 for *ycf6-psbM*). Sensitivity analyses to examine the impact of ambiguously aligned regions included: (1) all data (MSA length 6065 nucleotides [nt], 44.6% missing data), (2) a strict set excluding 1338 nt that removed positions with >50% missing data (MSA length 4727 nt, 33.3% missing data), and (3) a relaxed set excluding 613 nt that removed a subset (i.e., ITS hotspots and ragged ends) of the strict set (MSA length 5452 nt, 39.6% missing data). All three sensitivity analyses yielded similar topologies and support values, and the strict set (excluding 1338 nt) was selected for final analyses. Indels were not coded as had been done in Skema (2012). The MSA with exclusion sets is archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.76hdr7sv1>). We conducted a preliminary parsimony analysis with PAUP* v.4.0a167 (Swofford, 2002) on a global 167-tip dataset derived from Skema (2012) combined with our new data and ITS + *psbM-trnD* from Le Péchon & al. (2010). This analysis mostly confirmed concordance of data from the different sources and helped to optimize a reduced taxon sampling that maximized diversity from early-diverging clades while greatly reducing poorly resolved *Dombeya* s.str. clades that had no bearing on our study objectives and that decreased resolution. Substitution models were GTR+I+G4 for ITS, TPM1uf+I+G4 for *ndhA*, and TVM+I+G4 for each of the remaining four plastid markers based on AIC (Akaike information criterion; Akaike, 1974) using ModelTest-NG v.0.1.5. We employed maximum likelihood (ML) and Bayesian inference (BI) methods to the concatenated 6-marker dataset. The ML analyses were performed with RAxML v.8.2.12 (Stamatakis, 2014) as implemented on CIPRES XSEDE under GTR+I+Γ, and clade support estimated by 1000 rapid bootstrap replicates, and with IQ-TREE v.1.6.11 under GTR+F+I+G4 (Trifinopoulos & al., 2016). Each marker and a combined-plastid partition were also analyzed with RAxML to determine any strongly supported topological differences that could indicate incongruence; resolution is poor in *Eriolaena* and *Dombeya* s.str. within individual plastid markers. BI under the GTR+I+Γ model was performed using MrBayes v.3.2.7a (Ronquist & al., 2012) with two concurrent runs, each with four Markov chains (three cold and one heated), a 0.2 temperature coefficient, and sampling every 1000 generations over 50 million generations. A conservative

25% burn-in was implemented and an effective sample size (ESS) >200 verified with Tracer v.1.6.0 (Rambaut & al., 2013).

Morphological methods. — Herbarium specimens or their images (indicated by an identifier in brackets) were examined from the following herbaria: A, B, BM, BNRH, BR, C, CGE, CQNM, E, G, GH, H, IBSC, JE, K, L, LINN, M, MA, MO, MPU, NAS, NY, P, PE, TAN, TEF, US, W, and WAG. Additional specimens deposited in the following herbaria also are cited: CNARP, GZU, LMA, LU, MARS, MAU, NCU, SING, and WIS. Pollen grains were removed from herbarium specimens and acetolyzed following Erdtman (1960). For scanning electron microscopy, the acetolyzed grains were sputter-coated with gold-palladium or gold and examined with either a Philips 515 Scanning Electron Microscope at 25–30 kV (University of Texas, Austin, Texas, U.S.A.) or a Philips XL-30 Environmental Scanning Electron Microscope with LaB6 at 10 kV (Smithsonian Institution). For light microscopy seeds were imaged with an Olympus DSX100 (Olympus, Tokyo, Japan).

■ RESULTS

The results of our combined 114-tip, 6-marker phylogenetic analyses are shown in Fig. 3. A comparison of ML to BI results showed only a handful of poorly supported (bootstrap percentage, BP < 50) topological differences. RAxML and IQ-TREE yielded very similar results, and the former is used for the purposes of discussion. No differences with BP > 70 were found when comparing ML analyses of each individual marker or combined plastid versus ribosomal. The monophyly of Dombeyoideae (although outgroups are very limited) and its early-diverging branches are mostly strongly supported (posterior probability, PP 1.0, BP 99–100, except PP 0.60 at the divergence of the Schoutenia + Pterospermum clade), including *Nesogordonia* as the sister group to the rest of the subfamily. *Dombeya*, *Eriolaena* s.str., *Helmiopsiella*, *Helmiopsis*, and *Melhanian* Forssk. are not monophyletic. The winged-seed clade encompassing *Eriolaena* s.l. (including *Helmiopsiella* and *Helmiopsis*) is strongly supported (PP 1.0, BP 98) and reveals a distinct geographic structure: notably the Asian taxa form a clade within Malagasy + African groups. *Andringitra* and *Dombeya superba* (herein described as a new genus) are successive sisters to *Eriolaena* s.l., with mixed (PP 0.99–1.0, BP < 80) support.

Within the *Eriolaena* s.l. clade, three of the four species of *Helmiopsiella* are in a clade with *Eriolaena* s.str. while the fourth is in a clade of Malagasy species of *Helmiopsis*, including taxa formerly included in *Dombeya* subsect. *Rigidae*. The strongly supported *Eriolaena* s.l. clade forces a reinterpretation of the boundaries of several genera of Dombeyoideae that have been recognized as distinct despite morphological, anatomical, and palynological evidence of their close relationship. Paraphyletic *Melhanian* also shows geographic structure with the Malagasy taxa (*M. tulearensis* Arènes, *Paramelhanian decaryana* Arènes) separate from our limited sampling of

continental African *Melhanian* plus St. Helena endemic *Trochetiopsis* Marais.

■ DISCUSSION

Our phylogeny of Dombeyoideae is the most comprehensive to date, with all genera sampled (including four with no prior sequence data in GenBank). Skema (2012) focused on *Dombeya* s.str. and near allies, and that portion of our phylogeny resembles those results, which is expected given our subsampling of those data. We have fleshed out the taxon sampling for the winged-seed clade, including taxa such as *Helmiopsiella poissonii* (Arènes) Capuron ex L.C. Barnett and *Eriolaena rulkensii* that have combinations of morphological characters that blur the distinction between *Helmiopsis* and *Helmiopsiella*.

***Eriolaena* clade.** — The winged-seed clade of Skema (2012: fig. 1) is strongly supported (PP 1.0, BP 98) in our combined analyses (Fig. 3), which incorporate a greatly expanded taxon sampling including the types of all the genera that had been thought to be allied to *Eriolaena* (except for *Eriolanea* itself) as well as eight of eleven species of *Helmiopsis* and all four species of *Helmiopsiella*. Seed morphology, wood anatomy, and pollen had earlier established a close relationship between the three genera (Barnett, 1987, 1988b). Within our winged-seed clade, there are clades that show, in part, relationships to other previously proposed taxonomic groupings, but we still fail to find unique morphological (or anatomical) characters to define these clades. Morphological characters previously used to justify the recognition (and separation) of *Helmiopsis* and *Helmiopsiella* are of little value, and their pollen is uniform and of no value at the generic level. Based on the available evidence and renewed emphasis on shared characters (stamen vasculature, echinate pollen, woody capsules, and apically or dorsally winged seeds), with a concomitant deemphasis on the apparent dichotomy presented by the presence or absence of staminodes and relatively minor characters such as locule number and indumenta, we conclude that the winged-seed clade should be united under *Eriolaena*, which is the oldest generic name.

Our *Eriolaena* s.l. phylogeny shows one major dichotomy, each part of which is divided into either two or three well-supported (PP 0.98–1.0; BP 84–100, except 73 for clade BC) monophyletic groups of taxa (Fig. 3, clades A, AA, AB, B, BA, BB, BC). Clade AA contains the “rigida complex”, which Arènes (1958) first formally recognized as *Dombeya* subsect. *Rigidae* when he united two species (*D. linearifolia* Hochr., *D. rigida*) that had densely papillate glandular petals below. Subsequently, these taxa have been treated as either *Dombeya* (Arènes, 1959; Applequist, 2011) or, following the discovery of winged seeds in *D. rigida*, as *Helmiopsis* (Dorr, 2001; Skema, 2012). The winged seeds clearly argue for their separation from *Dombeya* s.str. and support their inclusion in *Eriolaena*. Although the “rigida complex” generally has been considered to consist of two species with varying numbers of

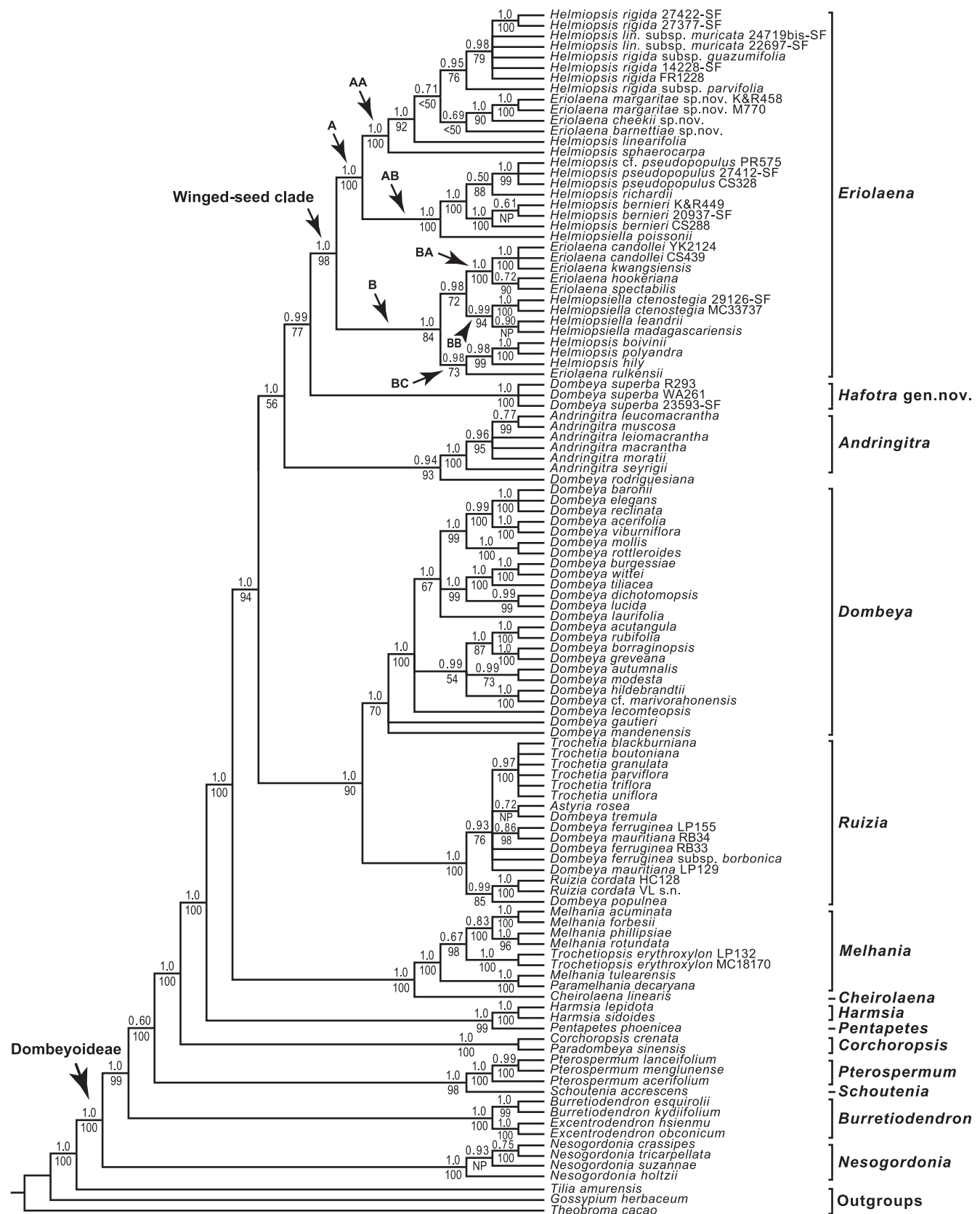


Fig. 3. Phylogenetic relationships of Dombeyoideae. Bayesian 50% majority-rule consensus tree based on the combined 6-marker, 114-tip dataset with posterior probability and ML (RAxML) bootstrap values indicated above and below branches, respectively. NP = an edge not present with ML. Species are listed with existing taxonomy, with newly recognized generic circumscriptions indicated at brackets.

intraspecific taxa, our data suggest that there are at least seven species in this complex: *H. linearifolia*, *H. rigida*, three herein newly described species (see below), *H. rigida* subsp. *parvifolia* ($\equiv$ *E. parvifolia*), and *H. sphaerocarpa*. The last species is an unexpected addition to the “*rigida* complex”. Barnett (1988a), who described *H. sphaerocarpa*, noted its glandular petals and many-flowered inflorescence and thought therefore that it might be allied to *H. pseudopopulus* (Baill.) Capuron. Applequist (2011) formalized this postulated relationship by including *H. sphaerocarpa* in *H. sect. Glandulipetalae* Arènes, which also includes *H. pseudopopulus*. Our analyses indicate those two species are not closely related.

The boundaries between *Helmiopsis rigida* and *H. linearifolia* have been confused by an overemphasis on leaf width (see, e.g., Arènes, 1958, 1959; Applequist, 2011, all as *Dombeya*). Although the type specimens underpinning both names lack fruit, it appears that *H. rigida* has muricate fruit (Dorr, 2001: fig. 1) and *H. linearifolia* has smooth, $\pm$ apocarpous fruit (Applequist, 2011: fig. 2F, as *D. linearifolia* subsp. *linearifolia*). This leads us to a different conclusion about the taxonomy of the group than that proposed by Applequist (2011) or implied by Skema (2012).

Clade AB contains the three species, *Helmiopsis bernieri* (Baill.) Arènes, *H. richardii* (Baill.) Capuron, and *H. pseudopopulus* (Baill.) Capuron, which Arènes (1956d, 1959) included in *Helmiopsis* sect. *Glandulipetalae* Arènes. Applequist (2011) selected *H. pseudopopulus* as the type of this sectional name and argued that *H. sphaerocarpa* also should be included (see above). Sister to this section, however, is *Helmiopsiella poissonii*, which does not have glandular petals, nor does it have lepidote sepals.

Clade B includes all of the species that typify genera that have been closely associated with *Eriolaena*: *Helmiopsis boivinii* (Baill.) Arènes (type of *Helmiopsis*), *Helmiopsiella leandrii* (type of *Dendroleandria*), and *Helmiopsiella madagascariensis* (type of *Helmiopsiella*). All of the taxa of *Eriolaena* s.str. that we sampled cluster as clade BA, which is not surprising given their shared androecial structure and Indo-Asian distribution. These species are also sister to most species of *Helmiopsiella* (Barnett, 1988a) (clade BB), all of which are endemic to Madagascar. Surprisingly, the close relationship of these Malagasy species eluded Arènes (1959), who placed them in three different genera in two different tribes.

Clade BC contains most of the Malagasy species of *Helmiopsis* that were classified by Applequist (2009) in *Helmiopsis* sect. *Helmiopsis* except for *H. glaberrima* Arènes, which we were unable to sample and which is known only from the type collection. This clade also includes the sole continental African species of the winged-seed clade, *E. rulkensii*. *Eriolaena rulkensii* is one of a handful of examples of a species belonging to an Asian/Malagasy genus that occurs in Mozambique but is otherwise absent from continental Africa (Dorr & Wurdack, 2018).

Although there is a natural tendency to emphasize the endemic aspect of the Malagasy flora, this can obfuscate the relationships of this flora to other geographic regions. There

are numerous other examples of genera, both plant and animal, found in Asia, Madagascar, and continental Africa (Schatz, 1996; Renner, 2004; Warren & al., 2010).

***Dombeya superba* clade.** — In our analyses, *Dombeya superba* Arènes forms a separate clade (Fig. 3) sister to *Eriolaena* s.l., and we propose to recognize it as *Hafotra* gen. nov. (see below). Prior phylogenies (Le Péchon & al., 2010, 2015; Skema, 2012) had recovered its exclusion from *Dombeya* s.str., but a taxonomic treatment was left unresolved. Although our support values are mixed (PP 0.99, BP 77; better than in Skema, 2012), the species is manifestly different than the strongly supported related genera *Eriolaena* and *Andringitra*.

Dombeya superba is morphologically distinct from *Eriolaena* s.l. in having large hyaline, stinging or irritating stellate hairs; an epicalyx that encloses the flower in bud; red petals; calyx and corolla persistent in fruit; 5 petaloid staminodes terminating the apical rim of the staminal tube; chartaceous capsules; and $\pm$ turbinate-angular seeds that have a wing-like apical annulus (Fig. 1A). The species superficially resembles *Andringitra*, and both taxa have large, mostly solitary flowers on long, articulated peduncles; pink or red petals; persistent perianth parts; and large capsular fruits with many seeds. However, in contrast to *Andringitra*, the epicalyx of *D. superba* is entire (versus dissected) and caducous (versus persistent) in fruit; the capsules are relatively thin walled (versus woody) and lack (versus sometimes possess) pubescence in the central axis; and the seeds have a wing-like annular appendage (versus being wingless). Additionally, the unusual hyaline, irritating hairs of *D. superba* are not found in *Andringitra*, nor are they common in other Malvaceae. Stinging or irritating hairs have only been reported to occur on capsules of *Fremontodendron* Coville (Bombacoideae), fruit valves of *Neesia* Blume (Helicterioideae), and the interior surface of follicles of *Sterculia* L. (Sterculioideae) (see Bayer & Kubitzki, 2003; Cheek & Dorr, 2007).

***Andringitra* clade.** — Skema (2012) described *Andringitra* for a monophyletic clade of large-flowered species formerly assigned to *Dombeya* and consisting of *D.* subsect. *Macranthae* Arènes plus *D. moratii* L.C. Barnett & Dorr. These species form a strongly supported (PP 1.0, BP 100), morphologically cohesive group, with relatively large, pink or red flowers, persistent perianth parts, fascicular stamens, linear staminodes, palmately or pinnately divided to dissected epicalyx bracts that are persistent into the fruiting stage along with the perianth, and large capsular fruits with many seeds and occasionally tomentose centralseptal pubescence. Highly dissected epicalyx bracts are not otherwise known in *Dombeya*, but are seen in species of *Eriolaena* and *Pterospermum* and may be a synapomorphy for the former. The six species of *Andringitra* (all sampled here) are endemic to Madagascar where they are found in the central highlands, and in the south and southeastern part of the island especially in the Andringitra Massif and nearby inselbergs. Our analyses place *Dombeya rodriguesiana* sister to *Andringitra* (PP 0.94, BP 93), which differs from relationships recovered under sparser taxon sampling (i.e., Le Péchon & al., 2010, 2015). Morphology suggests that *D. rodriguesiana*

belongs in the *Ruizia* clade (see also Le Péchon & al., 2009) and it is scarcely distinguishable from *D. ferruginea* Cav. (= *Ruizia ferruginea* comb. nov.) or *D. mauritiana* F. Friedmann (= *R. mauritiana* comb. nov.). Additional data are needed to test this further, and we have refrained from making taxonomic changes for this species.

Dombeya s.str. clade. — *Dombeya* s.str. is comprised of ca. 200 species, which occur in continental Africa, the Arabian Peninsula, the Comoro Islands, Madagascar, and the Mascarene Islands. The vast majority of species are endemic to Madagascar (ca. 175) and the Mascarene Islands (ca. 15, or fewer), and while Arènes (1958, 1959, 1960) constructed an infrageneric scheme for his treatment of the non-African species that relied on carpel number and inflorescence type, the scheme is mostly artificial. Resolution of the infrageneric relationships of *Dombeya* s.str. is beyond the scope of the present study. However, we can infer that carpel number only loosely corresponds with some of the larger clades recovered (Fig. 3) (Skema, 2012: fig. 1) and none of the inflorescence types recognized by Arènes (1959, 1960) defines monophyletic groups although those species with scorpioid cymes more or less correspond to two clades recovered by Skema (2012: fig. 1) (see also Fig. 3). Le Péchon & al. (2010) recovered a sparsely sampled clade (“clade E”) that included two subspecies of *D. acutangula* Cav. from the Mascarene Islands and one accession of the same species from Madagascar, all of which possess scorpioid cymes. Skema (2014) did not resolve *D. sect. Hilsenbergia* (Bojer) Baker, which Arènes (1959, as *D. sect. Astrapaea* (Lindl.) Baill. ex M. Gómez) recognized based on its constituent species having distinctive inflorescences as well as long tubular staminal columns. Additional sampling could not only resolve phylogenetic relationships, but also be used to infer aspects of the geographic origin of the genus (Le Péchon & al., 2010, 2015) and the evolution of its complicated breeding systems (Gigord & al., 1998; Humeau & al., 1999a,b, 2000; Humeau & Thompson, 2001; Le Péchon & al., 2010, 2013, 2015).

Ruizia clade. — *Ruizia*, *Trochetia* DC., *Astyria* (usually incorrectly spelled as *Astiria*), and several species of *Dombeya* form a distinct, strongly supported (PP 1.0, BP 100) *Ruizia* clade (Fig. 3). All the species of this clade are endemic to the Mascarene Islands, except for *D. tremula* Hochr., which is known only from southernmost Madagascar. Molecular phylogenetic research on Mascarene Dombeyoideae has consistently shown these taxa to be related (herein; see also clade D of Cao & al., 2008: fig. 3; clade D' of Cao & al., 2008: fig. 5; clade C of Le Péchon & al., 2010; clade A of Boura & al., 2011; major Mascarene clade of Skema, 2012; clade A of Le Péchon & al., 2015). Our data (Fig. 3) resolve several monophyletic lineages within the *Ruizia* clade: one group includes *R. cordata* Cav. and *D. populnea* (Cav.) Baill., and the other includes *Trochetia*, *Dombeya* spp., and *Astyria*. The species of *Trochetia*, resolved as a strongly supported group (PP 0.97, BP 100), are notable for their large, showy flowers (perhaps a response to vertebrate pollinators) and they have several characters that set them apart from the remaining

taxa in this clade (i.e., spathiform epicalyx bracts and well-developed styles).

The multiple accessions for *Dombeya mauritiana* and *D. ferruginea* are each not resolved as monophyletic, and we are not confident that all the voucher specimens are correctly identified. While one specimen that vouchers *D. mauritiana* is a garden accession stated to be from the type locality (*Bone 34*, MAU), the other one (*Le Péchon 129*, P barcode P00915316 [image!]) is from a Mauritian plant cultivated in France and presents pubescence differences with specimens that typify the name *D. mauritiana* (see below). Likewise, both vouchers for *D. ferruginea* are from cultivated plants: *Bone 33* (MAU) and *Le Péchon & Sevathian 155* (P barcode P00915339 [image!]). The former is stated to be from the type locality.

Monotypic *Astyria* is assumed to be extinct (Friedmann, 1987; Lesouef, 1988; Bayer & Kubitzki, 2003; Le Péchon & Gigord, 2014) and is known from less than 20 collections all made in the 19th century (Dorr, unpub.). *Astyria* generally has been allied with *Ruizia* s.str. (Lindley, 1844b; Benthams & Hooker, 1862; Friedmann, 1987; Bayer & Kubitzki, 2003), from which it differs in having a 5 (versus 10)-locular ovary. Arènes (1960), however, subsumed *Astyria* under a broadly construed *Dombeya*.

Le Péchon & Gigord (2014) already discussed the possible taxonomic solutions for dealing with the polyphyly uncovered in the present taxonomic classification of “Mascarene Dombeyoideae” (Friedmann, 1987), which recognizes four genera: *Astyria*, *Dombeya*, *Ruizia*, and *Trochetia*. One could recognize two or three genera in the Mascarene Islands (Le Péchon & Gigord, 2014: fig. 3D, 3C); the former is the solution adopted here, where we accept *Dombeya* s.str. and an expanded *Ruizia*. An expanded *Ruizia* includes a heterogeneous group of species that appears to be united based on epicalyx and seed characters. Their epicalyces tend to be fused, cupuliform or spathiform, and the seeds are wingless. Although not found in all *Ruizia* taxa, there also is a remarkable tendency toward unisexual flowers and heterophylly, which are uncommon in the other clades of Dombeyoideae. Heterophylly, however, is widespread among woody taxa native to the Mascarene Islands (Hansen & al., 2003).

Cheirolaena. — When Benthams in Benthams & Hooker (1862) described the monotypic Malagasy endemic *Cheirolaena*, he speculated that it might be related to *Eriolaena*. Our molecular data, however, show *Cheirolaena* to be sister to *Melhaniania*. *Cheirolaena* can be distinguished from *Melhaniania* by its petals that are adnate below to the staminal column and caducous with it, and by having 10(15) stamens that are inserted in two series outside and below the five staminodes.

Melhaniania clade. — *Melhaniania*, *Paramelhaniania* Arènes, and *Trochetiopsis* form a strongly supported (PP 1.0, BP 100) distinct clade (Fig. 3). Prior studies (Skema, 2008, 2010; Won, 2009) have recovered a close relationship between *Paramelhaniania* and *Trochetiopsis* but did not sample *Melhaniania*, which provides critical context. *Melhaniania* s.str., thought to be restricted to continental Africa, the Arabian Peninsula, Madagascar, southern Asia (China, India, Myanmar), and

Australia, is the most widespread genus in the subfamily and contains 50+ morphologically diverse species.

The relationships of the species of Dombeyoideae endemic to St. Helena have long been the subject of speculation. The first Dombeyoideae species described from that isolated island was *Pentapetes erythroxylon* G.Forst., which Brown (1812) transferred to *Melhanian* when he described a second endemic species, *M. melanoxydon* R.Br. (The name of the latter species, an inadvertent renaming of *P. melanoxydon* Sol. ex Sims, is the correct name for the species in *Melhanian*). Subsequently, Benth (1862) transferred both species to *Trochetia*, a genus previously considered endemic to the Mascarene Islands. Benth emphasized stamen number as a key-distinguishing character: *Melhanian* with 5 and *Trochetia* with 10 stamens. Marais (1981), citing other morphological differences, recognized that the St. Helena and Mascarene taxa were distinct, and he proposed the genus *Trochetiopsis* to accommodate the former. Cronk (1995, 2000), accepting Marais's circumscription, expanded *Trochetiopsis* to three species and one hybrid, all restricted to St. Helena, albeit one of the species now extinct.

Although Marais (1981; see also Cronk, 1990; Skema, 2010) argued that “sepals appressed sericeous inside” helped define *Trochetiopsis*, the inner surfaces of the sepals of *T. melanoxydon* (Sol. ex Sims) Marais, at least, are glabrous (Cronk, 2000). In any case, sepal pubescence is a weak generic character, and there is nothing else to support recognizing *Trochetiopsis* as distinct from *Melhanian* (as opposed to *Trochetia*). The statement made by Marais (1981) that *Trochetiopsis* has “5 or 10” stamens alternating with 5 staminodes evidently is incorrect. Descriptions of species of *Trochetiopsis* all mention only 5, not 10, stamens (see, e.g., Cronk, 2000). The inclusion of *Trochetiopsis* as a synonym of *Melhanian* extends the range of the latter genus to St. Helena in the South Atlantic Ocean.

When Arènes (1949) described the monotypic genus *Paramelhanian*, he contrasted it with *Melhanian* and enumerated what he considered to be distinguishing morphological characters. Among them were epicalyx bracts connate at the base; a biseriate androecium (5 stamens inserted on the apex of the staminal column alternating with 5 staminodes inserted internally and below the apex of the staminal column); capsules villous basally at the interior juncture of the locules; and the presence of sessile, lepidote scales. None of these characters fundamentally differs from those of *Melhanian*, and a generic-level distinction between taxa with stellate versus lepidote vestiture has already been shown to be untenable (Jenny & al., 1999).

Our expanded *Melhanian* includes species with the following characters: hermaphroditic flowers solitary or borne in few-flowered axillary cymes; epicalyx bracts 3, free or sometimes fused at the base; anthers 5 alternating with 5 staminodes; carpels 5(6); styles simple, 5-branched or 5-lobed; capsules relatively thin-walled with 1–6(–12) seeds per locule; and seeds without wings. Previously, *Melhanian* consisted solely of yellow-flowered species, but as with *Eriolaena* the expanded genus now has both yellow- and white-flowered species.

Tang (1992b) reported a diploid chromosome number of $2n = 60$ for one Asian species of *Melhanian*, while Bates (1967)

reported a haploid number of $n = 30$ for one African species. Cronk (1995) reported a diploid chromosome number of $2n = 40$ for two species of *Trochetiopsis* and the hybrid that he described.

Harmsia. — The two species of *Harmsia* K.Schum., which are restricted to northeastern Africa (Ethiopia, Kenya, Somalia), form a monophyletic group (PP 1.0, BP 100) that further supports the reduction of monotypic *Aethiocarpa* Vollesen proposed by Jenny & al. (1999) based on morphology. Both species have biovulate unilocular ovaries (Jenny & al., 1999; Cheek & Dorr, 2007), a character unique within the Dombeyoideae.

Pentapetes. — Although presumably native to south Asia, northern Australia, and New Guinea, the weedy habit of monotypic *Pentapetes* L. makes fixing its exact place of origin difficult. Our phylogenetic results resolve it sister to African *Harmsia* (PP 1.0, BP 99). Both *Pentapetes* and *Harmsia* usually have three stamens per bundle alternating with a petaloid staminode. Nonetheless, the 5-locular ovary of *Pentapetes* immediately separates it from *Harmsia*. Huang & al. (1988) reported a diploid chromosome number of $2n = 76$ for *Pentapetes*. Although there are no cytological data for the closely related *Harmsia*, the diploid number for *Pentapetes* is distinct from that of *Corchoropsis* (see below).

Corchoropsis clade. — Won (2009) found that *Corchoropsis*, originally described in Tiliaceae (Siebold & Zuccarini, 1843), was well-resolved within Dombeyoideae and supported by morphological and palynological data (Takeda, 1912; Tang, 1990, 1992a, 1994; Bayer & Kubitzki, 2003). Our phylogenetic results are consistent with Won (2009), and additional taxon sampling indicates that *Paradombeya* Stapf also belongs to this clade (Fig. 3). *Corchoropsis* and *Paradombeya* are morphologically similar Asian genera with 2 or 3 epicalyx bracts that are distant from the calyx; sepals fused at the base; petals asymmetric to strongly asymmetric; stamens shortly connate; staminodes petaloid; style simple; stigma slightly 3–5-grooved; and capsules loculicidally dehiscent. Petals in *Corchoropsis* s.l. are either yellow (*Corchoropsis*) or white (*Paradombeya*), a color dichotomy also seen in *Eriolaena* s.l. and *Melhanian* s.l. The differences in stamen number are not discrete as suggested by Stapf (1902): Bayer & Kubitzki (2003) reported (5–)10–15 stamens for *Corchoropsis* and (5–)15(–25) for *Paradombeya*. *Corchoropsis* and *Paradombeya* also have the same diploid chromosome number ($2n = 20$) (Huang & al., 1986, 1989; Ge & al., 1989; Tang, 1992a, 1993).

Pterospermum clade. — This Asian clade unites *Pterospermum* and *Schoutenia* with strong support (PP 1.0, BP 98). *Pterospermum* contains 18–40 species (Bayer & Kubitzki, 2003; Tang & al., 2007; Ganesan & al., 2020) that are found from the Himalayas across Southeast Asia and southern China to Malesia. The species are also winged-seeded, and the wings appear to arise from the sarcotesta in the region of the chalaza (Venkata Rao, 1949, 1953; Corner, 1976; Barnett, 1988b). The funiculus, however, runs along the margin of the seed wing (Venkata Rao, 1953) unlike the funiculus of *Eriolaena* that runs through the body of the seed wing (Barnett, 1988b). *Schoutenia* (including *Sicrea*) contains 10 species that are

found in Southeast Asia and portions of Malesia. The species lack seed wings.

Burretiodendron clade. — The *Burretiodendron* clade is an early-diverging lineage of *Dombeyoideae* that contains 5–6 species distributed in southwestern China and adjacent Myanmar, Thailand, and Vietnam. Whether or not *Excentrodendron* Hung T.Chang & R.H.Miao should be recognized as a genus distinct from *Burretiodendron* is problematic. Pollen (Tang & Gao, 1993), wood anatomy (Tang & al., 2005), fruit and leaf morphology (Lebreton Anberrée & al., 2015), and limited molecular data (Li & al., 2004) suggest that they are distinct but closely related (sister groups). Nonetheless, both genera have the same floral and fruit morphology: 5-locular ovaries with 2 ovules per locule and winged fruit separating septically into 1-seeded mericarps. Consequently, we follow Zhuge (1990), who only recognizes the genus *Burretiodendron*.

Nesogordonia clade. — *Nesogordonia* contains ca. 20 species that are largely endemic to Madagascar, and a few in Mayotte and continental Africa. Our resolution of *Nesogordonia* spp. as the first-diverging clade of *Dombeyoideae* differs from the family-wide sampling of Hernández-Gutiérrez & Magallón (2019: fig. 1) that weakly grouped *Nesogordonia*, *Schoutenia*, and *Burretiodendron*. Even though the seeds of *Nesogordonia* are usually winged, their wing is not homologous with the wing on seeds of *Eriolaena* s.l. The seed wings of *Eriolaena* arise from the chalaza, while those of *Nesogordonia* arise from sarcotestal tissue in the region of the micropyle. In addition, the androecium of *Nesogordonia* is polydelphous (versus monadelphous), its cotyledons are entire (versus bifid), and its pollen exine is reticulate (versus echinate) (Barnett, 1988b; Nyffeler & al., 2005).

■ TAXONOMY

Key to genera of *Dombeyoideae*

1. Seeds laterally compressed, winged or keeled2
1. Seeds rounded, trigonal, angular-turbinate or subreniform, not laterally compressed, winged or keeled4
2. Androgynophore present; Asia.....*Pterospermum*
2. Androgynophore absent3
3. Androecium monadelphous, stamens and staminodes or only stamens (staminodes lacking) forming a tube; fruit ovoid to cylindrical, never truncate; seed wings apical, dorsal or sometimes reduced and keel-like; pollen echinate; continental Africa, Madagascar, Asia *Eriolaena*
3. Androecium polydelphous, stamens in separate fascicles, not fused with staminodes (staminodes rarely absent); fruit obconical-truncate (often bell-shaped); seed wings basal; pollen reticulate (not echinate); continental Africa, Mayotte, Madagascar.....*Nesogordonia*
4. Ovary 1-locular; fruit covered with bristles or prickles; continental Africa *Harmsia*
4. Ovary 2–5(–10)-locular; fruit not covered with bristles or prickles5
5. Fruit winged; Asia.....*Burretiodendron*
5. Fruit not winged6
6. Epicalyx bracts divided, persistent7
6. Epicalyx bracts entire (rarely fused and cupuliform or spatheous), persistent or caducous8
7. Epicalyx bracts palmately or pinnately divided to dissected; flowers large (2–6 cm); petals pink or red; Madagascar.....*Andringitra*
7. Epicalyx bracts digitately divided into 3 lobes; flowers small (to 1 cm); petals yellow; Madagascar *Cheiolaena*
8. Calyx and capsule covered with large hyaline, irritating or stinging hairs; androecium with 15 stamens borne on the inner surface of the androecial tube and 5 staminodes borne on the apex; seeds turbinate-angular with a wing-like apical annulus; Madagascar.....*Hafotra*
8. Without the above combination of characters9
9. Staminodes absent10
9. Staminodes present (sometimes rudimentary in *Dombeya* and *Ruizia*).....11
10. Sepals ± petaloid; stamens free or nearly free; Asia, Australia *Schoutenia*
10. Sepals not petaloid; stamens forming a short to long staminal tube; Mascarene Islands *Ruizia*
11. Stamens 5, not in fascicles, alternating with 5 staminodes; calyx persistent; St. Helena, continental Africa, Arabian Peninsula, Madagascar, Asia, and Australia *Melhanina*
11. Stamens (5–)10–50, in fascicles of 2–10 (rarely stamens solitary), alternating with 5 staminodes; calyx persistent or caducous12
12. Herbs13
12. Trees or shrubs14
13. Flowers yellow or white; ovary 2–5-locular; Asia..... *Corchoropsis*
13. Flowers red; ovary 5-locular; Asia, New Guinea, Australia *Pentapetes*
14. Epicalyx bracts free, often caducous; corolla usually persistent or marcescent; ovary 2–5(–6)-locular; continental Africa, Arabian Peninsula, Comoro Islands, Madagascar, Mascarene Islands *Dombeya*
14. Epicalyx bracts fused, cupuliform and persistent or spatheous and caducous, rarely free (then 3 minute bracts); ovary 5-locular; Madagascar, Mascarene Islands*Ruizia*

A conspectus of *Eriolaena*

Eriolaena DC. in Mém. Mus. Hist. Nat. 10: 102. 1823 – Type: *Eriolaena wallichii* DC.

= *Wallichia* DC. in Mém. Mus. Hist. Nat. 10: 104. 1823, non Roxb., Pl. Coromandel 3: 91. 1819 ≡ *Jackia* Spreng., Syst. Veg. 3: 10, 85. 1826, nom. nov., non Wall. in Roxburgh, Fl. Indica 2: 321. 1824, nec Blume, Bijdr.: 60. 1825 ≡ *Schillera* Rchb., Consp. Regn. Veg.: 204. 1828 [1829?], nom. nov. ≡ *Microchlaena* Wall. ex Wight & Arn., Cat. Ind. Pl.: 16. 1833 (“*Microchlaena*”), nom. nov.

– Type: *Wallichia spectabilis* DC. (= *Eriolaena spectabilis* (DC.) Planch. ex Mast.).

= *Helmiopsis* H.Perrier in Bull. Soc. Bot. France 91: 230. 1944 – Type: *Helmiopsis inversa* H.Perrier (= *Eriolaena boivinii* (Baill.) Dorr), **syn. nov.**

= *Helmiopsiella* Arènes in Bull. Mus. Natl. Hist. Nat., sér. 2, 28: 150. 11 May 1956 – Type: *Helmiopsiella madagascariensis* Arènes (= *Eriolaena madagascariensis* (Arènes) Dorr), **syn. nov.**

= *Dendroleandria* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 7: 66. Oct–Dec 1956 – Type: *Dendroleandria leandrii* (Hochr.) Arènes. (= *Eriolaena leandrii* (Hochr.) Dorr), **syn. nov.**

Large shrubs or trees; young stems and leaves with stellate hairs or lepidote scales, glabrescent in age. Leaves simple, entire, palmately 3–7(–9)-veined at base, margin entire, weakly undulate, crenate, crenulate or serrulate; petiolate; stipulate. Inflorescences terminal, pseudoterminal or axillary, few- to many-flowered cymes or flowers solitary; peduncles glabrescent or with stellate hairs or lepidote scales. Flowers hermaphroditic. Epicalyx bracts 3(–5), free or briefly fused, entire, apically toothed, fimbriate or pinnatilobed, in a single whorl immediately below the flower or dispersed along the length of the pedicel, caducous. Sepals (4)5, fused at base or almost free, equal, sometimes reflexed at anthesis, glandular or eglandular, adaxial surface pubescent or glabrous, caducous or sometimes marcescent. Petals (4)5, symmetric or asymmetric, unguiculate, sometimes reflexed at anthesis, glandular or eglandular, white, creamy, yellowish or bright yellow, usually caducous. Stamens (5)–10–60, fused basally at least; anthers 2-locular, linear or linear-oblong, dorsifixed, connective broad, sometimes prolonged apically; filaments partly free, unequal; staminodes (0)5, when present ligulate to spatulate. Ovary 3–10-locular; ovules 2–6 or numerous per locule, anatropous, ascending; style simple; stigma 3–10-lobed or grooved. Fruit a capsule, ovoid, conical or pyriform, woody, 3–10-valved, loculicidally dehiscent; seeds 1–3 or many per locule, usually laterally compressed, winged or keeled, wings apical, dorsal or reduced and keel-like; cotyledons bifid, foliose, plicate. $2n = 120$.

Distribution. – Twenty-seven species (28 taxa) found in continental Africa (coastal Mozambique), Madagascar, and Asia.

1. *Eriolaena barnettiae* Dorr, **sp. nov.** – Holotype: Madagascar. Diego-Suarez/Antsiranana: Sous-préfecture de Vohe-mar, commune rurale de Daraina, Daraina, forêt d’Antsaharaingy (12°54.25’S, 049°39.43’E), 55 m, 27 Feb 2005 (fl), L. Nusbaumer & P. Ranirison LN 1496 (US barcode 00976611!; isotype: G barcode G00019517 n.v.).

Shrubs, 3–3.5 m tall, 5 cm d.b.h.; stems dark reddish-brown, glabrous. Leaves broadly ovate or slightly obovate to ± pentagonal, 2.3–6 × 2.4–6 cm, 5–7-nerved from the base, glabrous above and below, 1° and 2° veins and veinlets dark and visible below, domatia lacking, margin crenate throughout or sometimes entire for lower third and then crenate above to

apex, base broadly cuneate to truncate or imperceptibly cordate, apex abruptly acuminate, acumen deltoid, ca. 3–4 × 4–7 mm; petioles 1.5–5.5 cm long, slender, glabrous; stipules fugacious, not seen. Inflorescences clustered at apices of branchlets, 2(–4)-flowered; peduncles stout, to 5 mm long, densely lepidote. Epicalyx bracts 3, deltoid, ca. 3 × 1 mm, densely lepidote, inserted just below the flower, caducous. Calyx 5-parted, fused for ca. 1 mm, lobes narrowly lanceolate, ca. 2–3 × 8–9 mm, densely lepidote abaxially, glabrous adaxially except for small patches of glandular tissue at base. Petals 5, obovate, strongly asymmetric, ca. 1.5 × 1.1 cm, glabrous, yellow or bright yellow. Androecium fused ca. 0.5 mm; stamens 15, in 5 fascicles of 3, yellow; anthers unequal, 6–7 mm long; filaments unequal, 2–2.5 mm long; staminodes 5, linear, ca. 8 × 1 mm. Gynoecium 5-carpellate; ovary ca. 2 × 3 mm, 5-lobed, lepidote; ovules with a narrow margin (= incipient wing?); style ca. 7 mm long; stigma 5-fid. Fruit and seed unknown.

Distribution. – Endemic to northeastern Madagascar.

Additional specimens examined. – Madagascar. Diego-Suarez/Antsiranana: Sous-préfecture de Vohe-mar, commune rurale de Daraina, Daraina, forêt d’Antsaharaingy (12°53.925’ S, 049°39.823’E), 90 m, 4 Mar 2005 (fl), P. Ranirison & L. Nusbaumer PR 956 (G barcode G00019683 n.v., US barcode 00976612!).

Etymology. – Named for Lisa C. Barnett.

Note. – The broadly ovate or slightly obovate to ± pentagonal leaf blades with abruptly acuminate apices set this species apart from the other members of the “rigida complex”, which have ovate to narrowly ovate leaf blades and acute to short-acuminate apices. In addition, *Eriolaena barnettiae* has bright yellow flowers as opposed to the white, creamy or yellowish flowers typical of the complex.

2. *Eriolaena bernieri* (Baill.) Dorr, **comb. nov.** ≡ *Dombeya bernieri* Baill. in Bull. Mens. Soc. Linn. Paris. 1: 500. 1885 (“Bernieri”) ≡ *Assonia bernieri* (Baill.) Kuntze, Revis. Gen. Pl. 1: 76. 1891 (“Bernieri”) ≡ *Helmiopsis bernieri* (Baill.) Arènes in Bull. Mus. Natl. Hist. Nat., sér. 2, 28: 416. 1956 (“Bernieri”) – **Lectotype (designated here):** Madagascar. Antsiranana: Lingvatou, 1835 (fl), A.C.J. Bernier 338 (2° envoi) (P barcode P00037202 [image!]; isolectotypes: BM barcode BM000797645!, G barcode G00015570!, P barcode P00037203 [image!]).

Distribution. – Endemic to Madagascar.

3. *Eriolaena boivinii* (Baill.) Dorr, **comb. nov.** ≡ *Trochetia boivinii* Baill. in Adansonia 10: 109. 1871 (“Boivini”) ≡ *Dombeya boivinii* (Baill.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 496. 1885 (“Boivini”) ≡ *Assonia boivinii* (Baill.) Kuntze, Revis. Gen. Pl. 1: 76. 1891 (“Boivini”) ≡ *Helmiopsis boivinii* (Baill.) Arènes in Bull. Mus. Natl. Hist. Nat., sér. 2, 28: 418. 1956 (“Boivini”) – Holotype: Madagascar. Mahajanga: Ambongo, 16 Feb 1841 (fl), A. Per-villé 642 [Bernier comm., 1846] (P barcode P00037205 [image!]; isotypes: G barcode G00015569!, K barcode

- K001040397 [image!], P barcodes P00037204 [image!], P00547776 [image!] & P00547777 [image!]).
 = *Helmiopsis inversa* H.Perrier in Bull. Soc. Bot. France 91: 230. 1944 – Lectotype (designated by Applequist in Ann. Missouri Bot. Gard. 96: 527. 2009): Madagascar. Mahajanga: Ampasimarina au N de Majunga, May 1927 (fl, fr), *H. Perrier de la Bâthie* 17986 (P barcode P00037206 [image!]; isolectotypes: P barcode P00037207 [image!], TAN barcode TAN000723 [image!]).
 – “*Helmiopsis inversa* var. *arenicola*” H.Perrier in Bull. Soc. Bot. France 91: 231. 1944, nom. nud.
 See Fig. 1C.
Distribution. – Endemic to northwestern Madagascar.

4. *Eriolaena calcicola* (Arènes) Dorr, **comb. nov.** ≡ *Helmiopsis calcicola* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 7: 55. 1956 – **Lectotype (designated here)**: Madagascar. Antsiranana: Kama-Kama, sur le plateau d’Ankara (Boina), ca. 100 m, Jan 1900 (fl), *H. Perrier de la Bâthie* 1018 (P barcode P00037212 [image!]; isolectotypes: P barcodes P00037213 [image!] & P00037214 [image!]).
 – “*Helmiopsis inversa* var. *calcicola*” H.Perrier in Bull. Soc. Bot. France 91: 231. 1944, nom. nud.
Distribution. – Endemic to the Ankara region (Boina) of northwestern Madagascar.

5. *Eriolaena candollei* Wall., Pl. Asiat. Rar. 1: 51, t. 64. 1830 (“*Eriolaena Candollii*”) – **Lectotype (designated here)**: Myanmar. “Legi in montibus Prome ripae Irawaddi”, 1826 (fl), *N. Wallich* 1175 (K barcode K00112311!; isolectotypes: G barcodes G00358601 [image!] & G00358602 [image!], K barcodes K000380325! & K000380326!).
 = *Eriolaena affinis* Pierre, Fl. Forest. Cochinch. 2(11): t. 176, A, 1–10, A¹. 1888 – **Lectotype (designated here)**: Cambodia. in prov. Tpong ad montem Pang Chahk, May 1870 (fl), *L. Pierre* 808 (P barcode P06625559!; isolectotypes: C n.v., K barcode K000380323 [image!], MO n.v., P barcodes P04457578!, P06625556!, P06625557!, P06625558! & P06772050!, SING n.v.), **syn. nov.**
 = *Eriolaena glabrescens* Aug.DC. in Bull. Herb. Boissier, sér. 2, 3: 370. 1903 (“*Eriolaena*”) – Holotype: Vietnam. Tonkin, environs de Phuon-Lam, Jan 1887 (fr), *B. Balansa* 3710 (G barcode G00358603 [image!]; isotypes: K barcode K001045628!, P barcodes P04694781!, P06625538!, P06625539!, P06738647! & P06738648!), **syn. nov.**
 = *Eriolaena glabrescens* Hu in J. Arnold Arbor. 5: 231. 1924, nom. illeg. – Holotype: China. Yunnan: Szemao, southern mountains, 4000 ft, s.d. (fl), *A. Henry* 12343 (A barcode 00062819!; isotypes: K barcode K000380331!, NY barcode 00222236!).
 = *Eriolaena kwangsiensis* Hand.-Mazz. in Sinensia 3: 193. 1933 – **Lectotype (designated here)**: China. Guangxi: Tung Loo, E. Tang Lan, 1800 ft, 23 Jul 1928 (fl), *R.C. Ching* 6525 (W No. 1940-0008076!; isolectotypes: A barcode 00062820!, CQNM barcode 0010680 [image!], IBSC barcode 0004161 [image!], LU n.v., NAS barcodes

NAS00071632 [image!] & NAS00071633 [image!], NY barcode 00222237 [image!], PE barcodes 00024222 [image!], 00024223 [image!]), **syn. nov.**
 See Fig. 1E.

Distribution. – Bangladesh, Bhutan, Cambodia, China, India, Laos, Myanmar, Thailand, and Vietnam.

Note. – The attempt by Chandramohan & al. (2020) to lectotypify *Eriolaena candollei* failed because the phrase “designated here” or an equivalent (Turland & al., 2018, Art. 7.11) was omitted.

The protologue of *Eriolaena affinis* cites “*Herb Pierre*, N° 38240”, but the only material of this taxon collected by Pierre is labeled and numbered “*Herb. L. Pierre*” and “No 808”. The locality data on labels of *Pierre* 808 are abbreviated from a statement made in the protologue, viz. “Habite la plaine s’entendant entre les monts Pano [sic] Chahk et Knang Repœu dans la province cambodgienne de Tpong.” Curiously, *Grewia polygama* Roxb., illustrated in the same fascicle of the *Flore forestière de la Cochinchine* by Pierre (1888: t. 166), is stated also to be based on “*Herb Pierre*, N° 3824” for which a different locality is given. We can only assume that the collection number cited in the protologue of *E. affinis* is a mistake. Further support for this conclusion is the presence of a pencilled sketch attached to the lectotype that appears to be a study for part of the illustration (t. 176, fig. 9) accompanying the description of *E. affinis*.

6. *Eriolaena cheekii* Dorr, **sp. nov.** – Holotype: Madagascar. Antsiranana: Diana region, Ankarongana, Analafandro, 12°37’38”S, 049°31’37”E, 71 m, 25 Feb 2006 (fl), *N.M. Andrianjafy* 1632 (US barcode 01183505!; isotypes: CNARP n.v., MO barcode MO-2990358!, P n.v., TAN n.v.).
Trees, 4 m tall; bark fibrous; stems dark reddish-brown to black with scattered light-colored lenticels. *Leaves* borne on short brachyblasts; leaf blades broadly ovate, 3–5 × 1.7–3.6 cm, 5-nerved from the base, young leaves with scattered stellate hairs, soon glabrous above and below, 1°, 2°, and 3° veins dark and visible below, domatia of simple hairs in axils of 1° and 2° veins below, margins crenate throughout, base cordate, apex long acuminate; petioles of young leaves stellate pubescent, soon glabrate and dark reddish brown, 1.5–3 cm long; stipules subulate, ca. 1–2 mm long, caducous. *Inflorescences* lateral and pseudoterminal, cymose, scorpioid when young, peduncles and pedicels stellate pubescent. *Epicalyx* bracts 3, rhombic, unequal in size and shape, 3–4 × 1–2 mm, densely stellate-pubescent, borne immediately beneath buds, caducous. *Calyx* 3-parted, fused basally, lobes ovate, almost cucullate, unequal, 7–8 × 4 mm, pubescent, green. *Petals* 5, obovate, strongly asymmetric, ca. 1 × 0.8 cm, base above claw with a 3 mm wide band of papillae adaxially, white. *Androecium* very briefly fused at base; stamens 10, in 5 fascicles of 2, pale yellowish-white; anthers unequal, ca. 3 mm long; filaments unequal, ca. 1 mm long; staminodes 5, narrowly ligulate, ca. 6 × 1 mm, white. *Gynoecium* 5-carpellate; ovary spherical, unlobed, 2 × 2 mm, stellate; ovules 2 per locule; style ca. 2–2.5 mm long, appearing clavate;

stigma imperceptibly 5-fid. *Fruit* and seed unknown. — See Fig. 4C.

Distribution. — Restricted to northeastern Madagascar.

Etymology. — Named for Martin R. Cheek.

Note. — Applequist (2011) had trouble placing collections of this species and speculated they might be a hybrid involving *Dombeya rigida* ($\equiv$ *Eriolaena rigida*) and a species of *D.* subg. *Dombeya*. There is no evidence to support this hypothesis, with no ITS polymorphisms and congruent phylogenetic placement between nuclear (ITS) and plastid data. The new species is sister to *E. margaritae* in our analysis (Fig. 3) but is readily distinguished morphologically by its leaves borne on short brachyblasts and its 3- versus 5-parted calyx.

7. *Eriolaena ctenostegia* (Hochr.) Dorr, **comb. nov.** $\equiv$ *Dombeya ctenostegia* Hochr. in Candollea 3: 26, 98. 1926 $\equiv$ *Helmiopsiella ctenostegia* (Hochr.) L.C.Barnett in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 10: 71. 1988 — Lectotype (designated by Barnett in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 10: 71. 1988): Madagascar. Mahajanga: Bord de la rivière Iopy [sic] entre Andranomavo et Itampitso (Ambongo), May 1902 (fl), *H. Perrier de la Bâthie* 1425 (P barcode P00037197!; isoelectotypes: G barcode G00015174 [image!], P barcode P00037198!). See Fig. 2A.

Distribution. — Endemic to Madagascar.

8. *Eriolaena glaberrima* (Arènes) Dorr, **comb. nov.** $\equiv$ *Helmiopsis glaberrima* Arènes in Bull. Mus. Hist. Nat. (Paris),

sér. 2, 28: 417. 1956 — Holotype: Madagascar. Antsirana: Analamerana — Diégo-Suarez, 16 Mar 1954 (fl), *Service Forestier* 9423-SF (P barcode P00037215!; isotype: MO barcode MO-150804!).

Distribution. — Known from a single collection made in northernmost Madagascar.

9a. *Eriolaena hily* (Arènes) Dorr, **comb. nov.** $\equiv$ *Helmiopsis hily* Arènes in Bull. Mus. Natl. Hist. Nat., sér. 2, 28: 415. 1956 (“*Hily*”) — Holotype: Madagascar. Toliara: Betsipotika–Analaiwa–Morondava, 5 Mar 1953 (fl), *Service Forestier* [J.B. Rabarijaona] 7226-SF (P barcode P00037216!; isotypes: BR n.v., K barcode K001096885!, TEF barcode TEF000559!).

Distribution. — Endemic to Madagascar.

9b. *Eriolaena hily* subsp. *boinensis* (Appleq.) Dorr, **comb. nov.** $\equiv$ *Helmiopsis hily* subsp. *boinensis* Appleq. in Ann. Missouri Bot. Gard. 96: 531, fig. 2. 2009 — Holotype: Madagascar. Mahajanga: Forêt de Bekapika, sur le plateau Antanimena (Boina), 12 & 14 Nov 1957 (fr), *R. Capuron* 18423-SF (P barcode P00547694 [image!]; isotypes: A barcode 01154990!, K barcode K001096884!).

Distribution. — Known from a single collection made in the Boina region of northwestern Madagascar.

10. *Eriolaena hookeriana* Wight & Arn., Prodr. Fl. Ind. Orient.: 70. 1834 (“*Eriochlaena Hookeriana*”) $\equiv$ *Eriolaena candollei* var. *hookeriana* (Wight & Arn.) K.C.Mohan

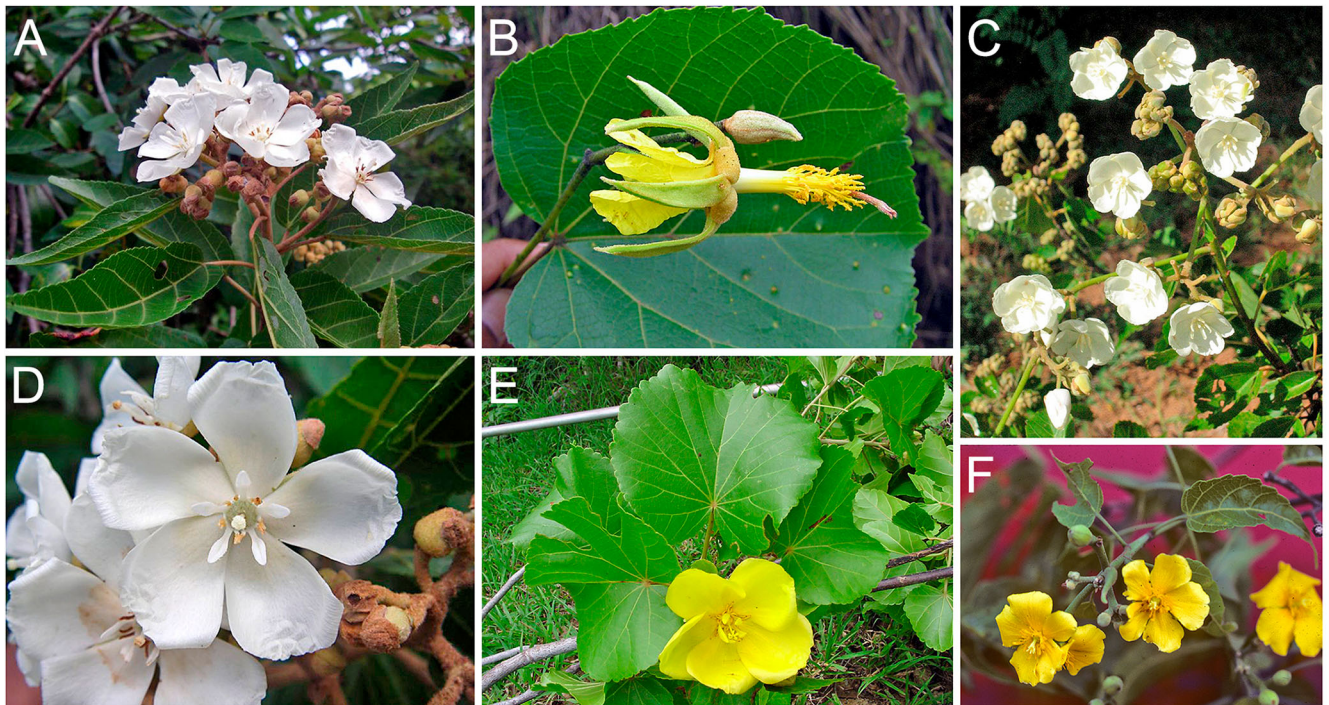


Fig. 4. Floral and/or inflorescence morphology of *Eriolaena* s.l. **A & D**, *E. rigida* (Ratovoson 1228 [MO]); **B**, *E. hookeriana* (V. Raman, unvouchered); **C**, *E. cheekii* (Andrianjafy 1632 [MO]); **E**, *E. poissonii* (Schatz 4325 [MO]); **F**, *E. madagascariensis* (L.C. Barnett, unvouchered). — Photos: A & D by F. Ratovoson; B by V. Raman; C by N.M. Andrianjafy; E by G.E. Schatz; F by L.C. Barnett.

in Ann. Pl. Sci. 9: 3684. 2020 – **Lectotype (designated here)**: India. Columala, s.d. (fl, fr), *R. Wight 956* (E barcode E00174186 [image!]; probable isoelectotypes: BR barcode 000005430628 [image!], GZU barcode GZU000259525 [image!], K barcode K000380340!, NY barcode 00222239!).

= *Eriolaena hookeriana* var. *viridis* Haines, Bot. Bihar Orissa 2: 81. 1921 – Type: Not designated.

See Fig. 4B.

Distribution. – India and Sri Lanka.

11. *Eriolaena leandrii* (Hochr.) Dorr, **comb. nov.** = *Ruizia leandrii* Hochr. in Arch. Sci. 1: 413. 1948 (“*Leandrii*”) = *Dendroleandria leandrii* (Hochr.) Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 7: 66. 1956 = *Helmiopsiella leandrii* (Hochr.) L.C.Barnett in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 10: 75. 1988 – Lectotype (designated by Barnett in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 10: 75. 1988): Madagascar. Mahajanga: Nord d’Antsalova, 1932–33 (fl), *J. Leandri 995* (K barcode K000241737!; isoelectotypes: G barcode G00015571!, P barcodes P00093410!, P00046583! & P00046584!).

See Fig. 2D.

Distribution. – Endemic to Madagascar.

Note. – Hochreutiner (1948) designated *Leandri 995* as type of this name without mentioning the herbarium where the type specimen was deposited. Barnett (1988a: 75) selected a lectotype from among the four duplicates of this collection that were deposited in Paris. She chose the one sheet of the four annotated by Hochreutiner (viz., “*Ruizia leandrii* Hochr. sp. nov. det. Hochreutiner 1948”). Subsequently, the lectotype designated by Barnett (1988a) was sent to Kew as exchange, presumably inadvertently.

12. *Eriolaena linearifolia* (Hochr.) Dorr, **comb. nov.** = *Dombeya linearifolia* Hochr. in Annuaire Conserv. Jard. Bot. Genève 11–12: 1. 1907 (“1908”) = *Helmiopsis linearifolia* (Hochr.) Skema in Taxon 61: 625. 2012 – Holotype: Madagascar. Antsiranana: Nord de Madagascar [“Sur les bords de la baie de Lingvatou”], 1835 (fl), *A.C.J. Bernier 340* (2° envoi) pro parte (G barcode G00015437!).

Distribution. – Endemic to northern Madagascar.

Note. – We have adopted a narrow interpretation of *Eriolaena linearifolia*. The species has very narrowly oblong leaves; flowers are relatively small; indumentum of the calyx is homotrichous; fruit is almost apocarpous, deeply lobed, and the walls are smooth; and seeds are flattened on one side with only the hint of a wing. Two other taxa were described as subspecies of *Dombeya linearifolia* (= *E. linearifolia*), but are here considered to be synonyms of *E. rigida* (see below).

13. *Eriolaena lushingtonii* Dunn in Bull. Misc. Inform. Kew 1915: 88. 1915 (“*Lushingtonii*”) – Holotype: India. Madras Presidency: Kurnool District: Cheloena, Nallamalais, 1902–03 (fl, fr), *A.W. Lushington s.n.* (K barcode K000380321!).

Distribution. – Restricted to the Eastern Ghats of India.

14. *Eriolaena madagascariensis* (Arènes) Dorr, **comb. nov.** = *Helmiopsiella madagascariensis* Arènes in Bull. Mus. Natl. Hist. Nat., sér. 2, 28: 150. 1956 – **Lectotype (designated here, as second step lectotypification)** based on Barnett in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 10: 73. 1988): Madagascar. Toliara: Ambovombe – Antanimora, 12 May 1925 (fl, fr), *R. Decary 3788* (P barcode P00037199!; isoelectotypes: P barcodes P00367981! & P00037200!).

See Figs. 2B and 4F.

Distribution. – Endemic to Madagascar.

Note. – Arènes (1956c) designated *Decary 3788* as the type of this name. Barnett (1988a: 73) wrote that there were four sheets of this collection deposited in Paris, and she selected “the sheet with the most ample material” as the lectotype. There now are three duplicates in Paris, and all are annotated “Typus” by Arènes: none of them annotated by Barnett. One of these three sheets in Paris is explicitly designated as the lectotype because it is not clear which of the three (or four) sheets examined by Barnett has the amplest material.

15. *Eriolaena margaritae* Dorr, **sp. nov.** – Holotype: Madagascar. Diego Suarez, Orangea, en route to military camp, 12°15'21"S, 049°23'01"E, ca. 32 m, 21 Mar 2007 (fl, fr), *M. Koopman & J. Razafitsalama 458* (US barcode 01183504!; isotype: WIS barcode v0260639WIS n.v.).

Shrubs, ca. 3 m tall; stems tan to dark brown, glabrous.

Leaves ovate to broadly ovate, 5.5–8 × 5–8.4 cm, decreasing in size toward inflorescence, 7-nerved from the base, thinly coriaceous, bright green and glabrous above, sparingly stellate pubescent below especially toward base, 1° and 2° veins and veinlets dark and visible below, domatia of hairs in axils of 1°, 2° and 3° veins below, margin crenate or crenulate throughout, base cordate, apex acute to acuminate; petioles 2.5–5.5 cm long, sparingly appressed pubescent, especially toward base and apex; stipules caducous, not seen, stipular scars conspicuous. *Inflorescences* axillary cymes, ± diffuse, scorpioid when immature. *Epicalyx* bracts 3, rhomboid, ca. 5 × 2 mm, pubescent, inserted below the flower, caducous. Flowers crateriform, unscented. *Calyx* 5-parted, briefly fused at base, lobes triangular, ca. 7 × 4 mm, glabrous adaxially, pubescent abaxially, pale brownish white, caducous. *Petals* 5, obovate, strongly asymmetric, ca. 1.8 × 1.5–1.7 cm, glabrous, white. *Androeium* fused ca. 2 mm; stamens 10, in 5 fascicles of 2; anthers unequal, 2.5–3 mm long; filaments unequal, 0.5–1 mm long; staminodes 5, ligulate, ca. 10 × 1.5–2 mm, white. *Gynoeium* 5-carpellate; ovary ca. 2 × 2.5 mm, 5-lobed, pubescent; ovules 2 per locule; style ca. 5 mm long, white; stigma 5-fid, white. *Fruit* deeply 5-lobed, almost apocarpous, densely villous, locules 2-seeded; seeds ca. 4 × 2.5 mm, glabrous, with a narrow distal wing.

Distribution. – Endemic to northeastern Madagascar, where it is found in scrubland on fine, white sand.

Additional specimens examined. – Madagascar. Antsiranana: NE of Antsiranana (Diego Suarez), forest of Orangea, N of the Baie des Sakalava, 12°16'00"S, 049°23'16"E, ca.

50 m, 1 Apr 1994 (fl), *D.J. Du Puy & J. Andriantiana M770* (K n.v., MO!, P barcode P00059511 [image!]).

Etymology. – Named for Margaret Hanes (née Koopman).

Note. – The ovate to broadly ovate leaf blades with cordate bases and crenate or crenulate leaf margin set this species apart from the other “rigida complex” taxa.

16. *Eriolaena parvifolia* (Appleg.) Dorr, **comb. & stat. nov.** ≡ *Dombeya rigida* subsp. *parvifolia* Appleg. in *Adansonia*, sér. 3, 33: 259, fig. 3. 2011 ≡ *Helmiopsis rigida* subsp. *parvifolia* (Appleg.) Skema in *Taxon* 61: 625. 2012 – Holotype: Madagascar. Toliara: près d’Ankazoabo, Feb 1963 (fl), *J.M. Bosser 17502* (P barcode P00552803 [image!]; isotypes: K barcode K001096886!, MO barcodes MO-3025805! & MO-2720896!, NY barcode 01404600!).

Distribution. – Endemic to southwestern and south-central Madagascar.

17. *Eriolaena poissonii* (Arènes) Dorr, **comb. nov.** ≡ *Dombeya poissonii* Arènes in *Candollea* 16: 284. 1958 ≡ *Helmiopsiella poissonii* (Arènes) Capuron ex L.C. Barnett in *Bull. Mus. Natl. Hist. Nat., B, Adansonia*, sér. 4, 10: 72. 1988 – Holotype: Madagascar. Antsiranana: Montagne des Français, 7 Jan 1917 (fl), *H. Poisson 88* (P barcode P00037201!). See Figs. 2E and 4E.

Distribution. – Endemic to northern Madagascar.

18. *Eriolaena polyandra* (Appleg.) Dorr, **comb. nov.** ≡ *Helmiopsis polyandra* Appleg. in *Ann. Missouri Bot. Gard.* 96: 531, fig. 3. 2009 – Holotype: Madagascar. Antsiranana: Forêt d’Analafiana, au N de la basse Manambery (au SW de Vohémar), 11 Mar 1967 (fl), *R. Capuron 27532-SF* (P barcode P000547700!; isotypes: K barcode K001096883!, MO barcode MO-2720950!, NY barcode 01404601!).

Distribution. – Endemic to northeastern Madagascar.

19. *Eriolaena pseudopopulus* (Baill.) Dorr, **comb. nov.** ≡ *Dombeya pseudopopulus* Baill. in *Bull. Mens. Soc. Linn. Paris* 1: 500. 1885 (“pseudo-*Populus*”) ≡ *Assonia pseudopopulus* (Baill.) Kuntze, *Revis. Gen. Pl.* 1: 76. 1891 (“*Pseudopopulus*”) ≡ *Helmiopsis pseudopopulus* (Baill.) Capuron ex Arènes in *Bull. Mus. Natl. Hist. Nat., sér. 2*, 28: 416. 1956 (“*Pseudo-Populus*”) – Holotype: Madagascar. Antsiranana: Lingvato, 1837 (fl), *A.C.J. Bernier 339* (2^e envoi) (P barcode P00037217!; isotypes: G barcode G00015564 [image!], P barcode P00037218 [image!]).

See Fig. 1D.

Distribution. – Endemic to northernmost Madagascar.

Note. – The label on the isotype at Geneva (G) lacks the locality data given on the holotype and states simply “Nord de Madagascar.”

20. *Eriolaena quinquelocularis* (Wight & Arn.) Drury, *Handb. Ind. Fl.* 1: 99. 1864 (“*Eriochlaena*”) ≡ *Microchlaena*

quinquelocularis Wight & Arn., *Prodr. Fl. Ind. Orient.* 1: 71. 1834 ≡ *Wallichia quinquelocularis* (Wight & Arn.) Steud., *Nomencl. Bot.*, ed. 2, 783. 1841 – Lectotype (designated by Dorr in *Taxon* 63: 1341. 2014): India. [Nilgiri Hills], s.d. (fl), *R. Wight 253* (K barcode K000380342!; probable isoelectotype: E barcode E00174187 [image!]).

– “*Microchlaena flavescens*” Garcke ex Mast. in Hooker, *Fl. Brit. India* 1(2): 371. 1874 (“*Microchlaena*”), nom. nud., pro syn.

Distribution. – China and India.

Note. – Chandramohan & al. (2020) failed to include the phrase “designated here” or an equivalent (Turland & al., 2018, Art. 7.11) when they attempted to designate a lectotype for *Eriolaena quinquelocularis*, a name already lectotypified by Dorr (2014).

21. *Eriolaena richardii* (Baill.) Dorr, **comb. nov.** ≡ *Trochetia richardii* Baill. in *Adansonia* 10: 108. 1871 (“*Richardii*”) ≡ *Dombeya richardii* (Baill.) Baill. in *Bull. Mens. Soc. Linn. Paris* 1: 500. 1885 (“*Richardii*”) ≡ *Assonia richardii* (Baill.) Kuntze, *Revis. Gen. Pl.* 1: 76. 1891 (“*Richardii*”) ≡ *Helmiopsis richardii* (Baill.) Capuron ex Arènes in *Bull. Mus. Natl. Hist. Nat., sér. 2*, 28: 416. 1956 (“*Richardii*”) – Holotype: Madagascar. Antsiranana: Ile Nossi-Bé [= Nosy Be], 1840 (fl), *J.M.C. Richard 343* (P barcode P00037219 [image!]; isotype: P barcode P00037220 [image!]).

Distribution. – Endemic to northern Madagascar, including Nosy Be.

22. *Eriolaena rigida* (Baill.) Dorr, **comb. nov.** ≡ *Dombeya rigida* Baill. in *Bull. Mens. Soc. Linn. Paris* 1: 487. 1 Apr 1885 ≡ *Assonia rigida* (Baill.) Kuntze, *Revis. Gen. Pl.* 1: 76. 1891 ≡ *Helmiopsis rigida* (Baill.) Dorr in *Adansonia*, sér. 3, 23: 151. 2001 – Holotype: Madagascar. Mahajanga: pr. Trabonji [= Trabonjy], May 1880 (fl), *J.M. Hildebrandt 3442* (P barcode P00044942 [image!]; isotypes: BM barcode BM000797646!, G barcodes G00015381 [3 sheets!] & G00190629 [2 sheets!], JE barcodes JE00003427 [image!] & JE00003428 [image!], K barcode K000241166!, M barcode M-0109360 [image!], P barcode P00044943 [image!], US barcode 00102080!, W-Rchb. No. 1889-0020028!).

≡ *Dombeya guazumifolia* Baill. in *Bull. Mens. Soc. Linn. Paris* 1: 495. 6 May 1885 (“*guazumæfolia*”) ≡ *Assonia guazumifolia* (Baill.) Kuntze, *Revis. Gen. Pl.* 1: 76. 1891 ≡ *Dombeya rigida* subsp. *guazumifolia* (Baill.) Appleg. in *Adansonia*, sér. 3, 33: 258. 2011 ≡ *Helmiopsis rigida* subsp. *guazumifolia* (Baill.) Skema in *Taxon* 61: 625. 2012 – Lectotype (designated by Skema in *Taxon* 61: 625. 2012): Madagascar. Antsiranana: Sur les bords de la baie de Lingvato, 1835 (fl), *A.C.J. Bernier 340* (2^e envoi) pro parte (P barcode P00573597!; isoelectotypes: G barcode G00190633!, P barcodes P00573598! & P00573599!), **syn. nov.**

≡ *Dombeya linearifolia* subsp. *sely* Arènes in *Candollea* 16:

297. 1958 = *Helmiopsis linearifolia* subsp. *sely* (Arènes) Skema in Taxon 61: 625. 2012 – Lectotype (designated by Skema in Taxon 61: 625. 2012); Madagascar. Antsiranana: Montagne des Français – Diégo-Suarez, 4 Apr 1954 (fl), *Service Forestier 9734-SF* (P barcode P00044702!; isolectotypes: K barcode K000683022!, P barcode P00044703!, TEF barcode TEF000176 [image!]), **syn. nov.**

= *Dombeya linearifolia* subsp. *muricata* Appleq. in Adansonia, sér. 3, 33: 254, fig. 2A–E. 2011 = *Helmiopsis linearifolia* subsp. *muricata* (Appleq.) Skema in Taxon 61: 625. 2012 – Holotype: Madagascar. Antsiranana: Forêt d’Analafiana, au N de la basse Manambery (au SW de Vohémar), 11 Mar 1967 (fl), *R. Capuron 27502-SF* (P barcode P000547750!; isotypes: K barcode K001089058!, MO barcode MO-2723072!, NY barcode 01404599!, TAN n.v.), **syn. nov.** See Figs. 1B, 4A,D.

Distribution. – Endemic to Madagascar

Note. – The isolectotype of *Dombeya guazumifolia* at G (G barcode G00190633!) lacks an original label, and the locality given is simply “Nord de Madagascar.” Hochreutiner removed part of this collection and the material that he segregated became the type of *D. linearifolia* (= *Eriolaena linearifolia*).

Two paratypes (*Service Forestier 22697, 24719*) of *Dombeya linearifolia* subsp. *muricata* were sampled and are included in our analysis. As expected from fruit morphology, all three fall within the portion of the *Eriolaena* clade (Fig. 3) that includes samples of *E. rigida*. Similarly, a specimen (*Service Forestier 14228*) that Applequist (2011) speculated might be a hybrid between *D. rigida* and an unidentified species of *D.* subg. *Dombeya*, also falls in the same position and evidently is merely a robust *E. rigida*. Although Applequist (2011) stated no similar material existed, this last specimen (the putative hybrid) clearly matches *Bardot-Vaucolon & Véné 1777* (P barcode P00643328 [image!]), also from the Montagne des Français.

23. *Eriolaena rulkensis* Dorr in PhytoKeys 111: 12, figs. 1, 2. 2019 – Holotype: Mozambique. Cabo Delgado: Pemba, close to Pemba Bay, near Chibuaburare, 12°58'26"S, 040°30'10"E, 9 m, 23 Feb 2014 (fl, fr), *A.J.H. Rulkens 1* (US barcode 01184177!; isotypes BNRH Nos. BNRH0007110-1 [image!] & BNRH0007110-2 [image!], K barcodes K0001291030 n.v., K0001291031 n.v., LMA n.v., US barcode 01184178!).

See Fig. 2C,F.

Distribution. – Endemic to northeastern coastal Mozambique.

24. *Eriolaena spectabilis* (DC.) Planch. ex Mast. in Hooker, Fl. Brit. India 1(2): 371. 1874 = *Wallichia spectabilis* DC. in Mém. Mus. Hist. Nat. 10: 104, t. 6. 1823 = *Jackia spectabilis* (DC.) Spreng., Syst. Veg. 3: 85. 1826 = *Microchlaena spectabilis* (DC.) Endl. ex Walp., Repert. Bot. Syst. 1(2): 351. 1842 – Holotype: Nepal. [“Napaul”], 1821 (fl), *N. Wallich s.n.* (G barcode G00209063!;

isotype: K barcode K00112303!; possible isotypes: K-2!).

= *Sterculia malvacea* H.Lév. in Repert. Spec. Nov. Regni Veg. 12: 185. 1913 = *Eriolaena sterculiacea* H.Lév., Fl. Kouy-Tcheou: 405. 1915, nom. illeg. superfl. = *Eriolaena malvacea* (H.Lév.) Hand.-Mazz., Symb. Sin. 7(3): 613. 1933 – Holotype: China. Guizhou: Kouy-Tchéou, Kiaò-tâ, 750 m, Jun 1910 (fl), *J. Esquirol 2185* (E barcode E00284363 [image!]; isotypes: A barcode 01154992!, K barcode K000380335!, P barcode P04640392!).

= *Eriolaena szemaoensis* Hu in J. Arnold Arbor. 5: 230. 1924 – Holotype: China. Yunnan: Szemao, W. mts., s.d. (fl), *A. Henry 11873* (A barcode 00062821!; isotypes: K barcode K000380333!, NY barcode 00222238!).

= *Eriolaena ceratocarpa* Hu in Bull. Fan Mem. Inst. Biol. 10: 143. 1940 – **Lectotype (designated here)**: China. Yunnan: Lan-Tsang Hsien, 1500 m, May 1936 (fl), *C.W. Wang 73378* (PE barcode PE00024220 [image!]; isolectotypes: A barcode 00062818!, PE barcode PE00024221 [image!]). *Distribution.* – Bhutan, China, India, Myanmar, and Nepal.

Note. – The isotype of *Wallichia spectabilis* is labeled “mons Nag-Arjoon, May 1821”, which presumably is Nagarjun Hill in the Kathmandu Valley.

25. *Eriolaena sphaerocarpa* (L.C.Barnett) Dorr, **comb. nov.** = *Helmiopsis sphaerocarpa* L.C.Barnett in Ann. Missouri Bot. Gard. 74: 450, fig. 1. 1987 – Holotype: Madagascar. Antsiranana: Massif de la Montagne d’Ambre, crête entre les bassins de la rivière des Makis et de la rivière d’Ankazobe, 26–27 May 1970 (fl), *R. Capuron 29194-SF* (P barcode P00037221!; isotypes: K barcode K000241736!, MO barcode MO-150798!, P barcodes P00367982! & P00037222!, TEF!).

Distribution. – Endemic to Madagascar.

26. *Eriolaena stocksii* Hook.f. & Thomson ex Mast. in Hooker, Fl. Brit. India 1(2): 370. 1874 (“*Stocksii*”) = *Eriolaena candollei* var. *stocksii* (Hook.f. & Thomson ex Mast.) K.C.Mohan in Ann. Pl. Sci. 9: 3683. 2020 – **Lectotype (designated here)**: India. Konkan districts: Concan [Konkan], s.d. (fl), *J.E. Stocks s.n.* (K barcode K000380319 [image!]; isolectotypes: GH barcode GH00062822!, K barcode K000380320!, P barcode P06625574!).

Distribution. – Endemic to India.

Note. – Chandramohan & al. (2020) failed to include the phrase “designated here” or an equivalent (Turland & al., 2018, Art. 7.11) when they attempted to designate a lectotype for *Eriolaena stocksii*.

27. *Eriolaena wallichii* DC. in Mém. Mus. Hist. Nat. 10: 102, t. 5. 1823 (“*Eriolaena Wallichii*”) – Holotype: India. H.B. Calc. [= Hortus Botanicus Calcutta], 1818 (fl), *N. Wallich s.n.* (G barcode G00209064 [image!]).

Distribution. – India and Nepal.

Note. – The protologue states simply that this name is based on material cultivated in the Calcutta Botanical Garden

that Wallich sent to Candolle. The type consequently must be a specimen in the Candolle Herbarium (G-DC). No number was associated with this specimen or collection. However, Wallich (1829) assigned this species (collection?) number 1174 in his catalogue, and there are many duplicates with this number: E barcodes E00273757 [image!], E00273758 [image!] & E00273759 [image!], G barcode G00358605 [image!], GH barcode 00062823!, K barcodes K001112308! & K001112309!, and P barcode P06625565!. The numbered specimen in G is labeled “M. Wallich, 1829”, a date posterior to the description. There also is a Wallich collection of this species without number in Paris (P barcode P06625566!).

Hafotra, a new monotypic Malagasy genus

When Arènes (1958) described *Dombeya superba*, its distinctiveness was apparent. Neither it nor the simultaneously described *D. poissonii* Arènes (≡ *Eriolaena poissonii* (Arènes) Dorr), both with large solitary flowers and undissected epicalyces, fit well with the other species of *Dombeya* that have large solitary flowers and dissected epicalyces that Arènes (1958) grouped as *D. subsect. Macranthae* (= *Andringitra*). Arènes (1958) consequently created *D. subsect. Superbae* Arènes to accommodate these two species but failed to appreciate that not only did they differ from the species with dissected epicalyces but also from each other. *Dombeya superba* has a tubular staminal column with 15 stamens irregularly inserted near the apex inside and 5 staminodes borne on the apex of the column (see Arènes, 1958: fig. XLVI, 12). This is fundamentally different from *D. poissonii* with a short coriniform staminal column with 15 stamens in 5 fascicles of 3 alternating with 5 staminodes all of which are borne on the apex of the column (see Arènes, 1958: fig. XLVII, 6).

Hafotra Dorr, **gen. nov.** – Type: *Hafotra superba* (Arènes) Dorr.

Hafotra differs from other genera of Dombeyoideae in having hyaline, stinging or irritating stellate hairs; a tubular androecium with 15 stamens borne on the inner surface of the staminal tube and 5 staminodes borne on the apex; large ovoid-oblong to almost cylindrical, chartaceous capsules; and ± turbinate-angular seeds that have a wing-like apical annulus (Fig. 1A).

Shrubs or small trees; stems ± glaucescent. *Leaves* simple, entire, palmately 5-veined at base, margin irregularly crenate; petiolate; stipulate. *Flowers* hermaphroditic, solitary, long pedunculate; peduncles articulate immediately below the flowers, inserted in the axils of apical leaves. *Epicalyx* bracts 3, briefly fused at base, ovate, entire, initially completely enclosing flower buds, caducous. *Flowers* zygomorphic. *Calyx* deeply 5-lobed, glabrous adaxially except for glandular patch at base, persistent. Indument of peduncles and abaxial surface of calyx two layered: dense, very short stellate hairs intermixed with large, hyaline stinging or irritating stellate hairs. *Petals* 5, obovate, asymmetric, slightly attenuate below, eglandular, glabrous, red. *Perianth* persistent in fruit. *Stamens* 15, irregularly

inserted inside near the apex of a well-developed tubular staminal tube; anthers 2-locular, linear, loculicidally dehiscent; filaments partly free, unequal; staminodes 5, spatulate, terminating staminal tube. *Ovary* 5-locular, ovoid-oblong, densely and long hispid at base; ovules numerous per locule, anatropous; style simple, lower half pubescent, upper glabrous; stigma 5-lobed, branches arcuate-recurved. *Fruit* a capsule, ovoid-oblong to almost cylindrical, chartaceous, 5-lobed, loculicidally dehiscent (mature fruit not seen), densely hispid; seeds numerous per locule, ± turbinate-angular, smooth, with a wing-like apical annulus (Fig. 1A).

Distribution. – A single species endemic to southeastern Madagascar.

Etymology. – The generic name is derived from the common name of the type. In Malagasy, the word “hafotra” is applied to plants that yield fiber or bast.

Hafotra superba (Arènes) Dorr, **comb. nov.** ≡ *Dombeya superba* Arènes in Candollea 16: 285. 1958 – **Lectotype (designated here):** Madagascar. Fianarantsoa: Amboangibé-Farafangana, 28 Jul 1955 (fl), *Service Forestier 13944-SF* (P barcode P00044987 [image!]; isoelectotype: P barcode P00044988 [image!]).

Distribution. – Endemic to southeastern Madagascar.

A new synonym for Dombeya

Cavanilla J.F.Gmel. is generally considered a synonym of *Dombeya* (see, e.g., Seyani, 1991; Applequist, 2014), but the former genus name has not been typified, and among the 12 species cited in its protologue four now belong to genera other than *Dombeya*, including *Pentapetes*, *Pterospermum*, and *Ruizia*. Typification fixes current usage.

Dombeya Cav., Diss. 2, App.: [iv]. 1786, nom. cons. – Type: *Dombeya palmata* Cav. (= *Dombeya acutangula* Cav.). = *Cavanilla* J.F.Gmel., Syst. Nat. 2(2): 999, 1037. 1792 (“1791”) – **Type (designated here):** *Cavanilla acutangula* (Cav.) J.F.Gmel. (≡ *Dombeya acutangula* Cav.), **syn. nov.**

A conspectus of Ruizia

Ruizia Cav., Diss. 2, App.: [iv]. 1786 – **Type (designated here):** *Ruizia cordata* Cav.

= *Assonia* Cav., Diss. 2, App.: [v]. 1786 ≡ *Dombeya* sect. *Assonia* (Cav.) Cordem., Fl. Réunion: 309. 1895 – Type: *Assonia populnea* Cav. (≡ *Ruizia populnea* (Cav.) Dorr), **syn. nov.**

= *Vahlia* Dahl, Observ. Bot.: 21. 1787, non Thunb., Nov. Gen. Pl. 2: 36. 1782 – Type: *Vahlia fastuosa* Dahl (= *Ruizia populnea* (Cav.) Dorr), **syn. nov.**

= *Trochetia* DC. in Mém. Mus. Hist. Nat. 10: 106. 1823 – Type (designated by Hutchinson, Gen. Fl. Pl. 2: 504. 1967): *Trochetia uniflora* DC. (≡ *Ruizia uniflora* (DC.) Dorr), **syn. nov.**

= *Astyria* Lindl. in Edwards's Bot. Reg. 30 [Misc.]: 27. May 1844 & t. 49. 1 Sep 1844 (“*Astiria*”) – Type: *Astyria rosea* Lindl. (= *Ruizia rosea* (Lindl.) Dorr), **syn. nov.**
 – “*Koenigia*” Comm. ex Juss., Gen. Pl.: 275. 1789, nom. nud., pro syn.

Shrubs or small *trees*; stellate pubescent or lepidote; dioecious, monoecious or hermaphroditic; sometimes heterophyllous (and then juvenile leaf blades highly dissected or lobed). *Leaves* simple, entire or deeply dissected, palmately 3–9-veined at base, margin entire, irregularly lobed, crenate or crenulate; petiolate; stipulate. *Inflorescences* axillary, flowers solitary or in 2- or 3-flowered pseudo-cymes; peduncles bracteate, short or long (and then often pendent), stellate pubescent, lepidote or glabrescent. Single sex flowers male or female by abortion; male flowers larger than female. *Epicalyx* bracts fused, cupuliform with (0)3 teeth apically and persistent or spathiform and caducous, rarely bracts 3, free (then minute). *Sepals* 5, free or slightly to ± completely fused at base, valvate, adaxial surface usually glandular below. *Petals* 5, free, slightly to strongly asymmetric, white, pink or reddish, persistent or caducous. *Stamens* 15–40(–45), united in a tube (stamens sterile and indehiscent in female flowers); anthers 2-locular; staminodes (0)5. *Ovary* (reduced and non-functional in male flowers) 2–10-locular; ovules 2–15 per locule, anatropous, ± horizontal to ascending; style reduced or sometimes well-developed; stigmas weakly united at base or free, 5–10-branched. *Fruit* a capsule, globose or obovoid, tardily dehiscent or indehiscent, loculicidal when dehiscent; seeds 1–2(–many) per carpel, not winged; cotyledons bifid, not or ± plicate.

Distribution. – Fourteen species (15 taxa) found in southern Madagascar and the Mascarene Islands.

Note. – The generic name *Astyria* is usually misspelled as *Astiria*. A combined generic-specific description of *Astyria rosea* appeared as text-only in May 1844 (Lindley, 1844a). When the plate (t. 49) illustrating this new species with a more ample generic-specific description was published on 1 September 1844, the spelling of the genus name was altered to *Astiria* (Lindley, 1844b). According to the *ICN*, the original spelling is to be retained (Turland & al., 2018; Art. 60.1), and this is the spelling used by Friedmann (1987).

1. ***Ruizia blackburniana*** (Bojer ex Baker) Dorr, **comb. nov.** ≡ *Trochetia blackburniana* Bojer ex Baker, Fl. Mauritius: 29. 1877 (“*Blackburniana*”) – **Lectotype (designated here):** Mauritius. “in dense forests round Grand Bassin and Trois Mamelles”, s.d. [“Presented ... 17 July 1863”], [herb.] *Justice Blackburn s.n.* (K barcode K000241248 [image!]; isolectotype: K barcode K000241249 [image!]).
 – “*Trochetia blackburniana*” Bojer, Hortus Maurit.: 41. 1837 (“*Blackburniana*”), nom. nud.
 – “*Dombeya blackburniana*” Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 192. 1960 (“1959”), nom. nud.
Distribution. – Endemic to Mauritius.

2. ***Ruizia boutoniana*** (F.Friedmann) Dorr, **comb. nov.** ≡ *Trochetia boutoniana* F.Friedmann in Adansonia, n.s.,

20: 446. 1981 – **Lectotype (designated here):** Mauritius. Le Morne Brabant, 11 Aug 1976, F. Friedmann, J. Guého & Lecordier 2935 (P barcode P00046588 [image!]; isolectotypes: MAU n.v., P barcodes P00046587 [image!], P05350605 [image!] & P05350606 [image!]).

Distribution. – Endemic to Mauritius.

Note. – The lectotype is one of four specimens in Paris that has both the name of the new species and the collection number cited by Friedmann (1981: 446). A fifth specimen (P barcode P05350604 [image!]) has the name of the new species, but not the collection number even though it was collected on the same date as the type.

3. ***Ruizia cordata*** Cav., Diss. 3: 117, t. 36, fig. 2, x. 1787 – Lectotype (designated by Friedmann in Bosser & al., Fl. Mascareignes 53: 9. 1987, as “holotype”): La Réunion. “Habitat in Insula Bourbon prope vicum Sancti Dionysii”, [Ph. Commerson s.n.] (P-JU 12512 [microfiche!]; possible isolectotypes: MA barcode MA 476205 [image!], MPU barcode MPU016378 [image!], P barcode P06644145 [image!]).

= *Ruizia lobata* Cav., Diss. 3: 118, t. 36, fig. 1a–m. 1787 – **Lectotype (designated here, as second step lectotypification** based on Friedmann in Bosser & al., Fl. Mascareignes 53: 9. 1987): La Réunion. “Habitat in Insula Bourbon ad promontorium Sancti Bernardi circa vicum D. Dionysii, et alibi”, [Ph. Commerson s.n.] (P-JU 12513 pro parte [“B” as “*Ruizia lobata* C. n.º. 5”] [microfiche!]; possible isolectotypes: MA barcode MA 476207 [image!], MPU barcodes MPU016392 [image!], MPU016393 [image!], MPU016394 [image!], MPU016395 [image!] & MPU016396 [image!], P barcodes P06644216 [image!], P06644218 [image!] & P06644220 [image!], P-JU 12513 pro parte [“A” & “C”] [microfiche!], W [herb. Jacq. fil.] No. 0004798!).

= *Ruizia palmata* Cav., Diss. 3: 119, t. 37, fig. 1, f, g. 1787 – **Lectotype (designated here, as second step lectotypification** based on Friedmann in Bosser & al., Fl. Mascareignes 53: 9. 1987): La Réunion. “Habitat in Insula Bourbon prope vicum Sancti Dionysii”, [Ph. Commerson s.n.] (P-JU 12514 pro parte [“B” as “*Ruizia palmata* C. n.º. 3”] [microfiche!]; possible isolectotypes: LINN-HS No. 1149.15.2 pro parte [“1”] [image!], MA barcode MA 476208 [image!] pro parte, MPU barcodes MPU016374 [image!], MPU016375 [image!] & MPU016376 [image!], P-JU 12514 pro parte [“C”] [microfiche!]).

= *Ruizia laciniata* Cav., Diss. 3: 119, t. 37, fig. 2. 1787 – *Ruizia variabilis* var. *laciniata* (Cav.) G.Don, Gen. Hist. 1: 535. 1831 (“Var. β, *laciniata*”), comb. illeg. – **Lectotype (designated here, as second step lectotypification** based on Friedmann in Bosser & al., Fl. Mascareignes 53: 9. 1987): La Réunion. Habitat in Insula Bourbon prope vicum Sancti Pauli”, [Ph. Commerson s.n.] (P-JU 12514 pro parte [“A” as “*Ruizia laciniata* C. n.º. 4”] [microfiche!]; possible isolectotypes: LINN-HS No. 1149.15.2 pro parte [“2”] [image!], MA barcode MA 476206 [image!], MPU barcode MPU016377 [image!]).

= *Ruizia variabilis* Jacq., Pl. Hort. Schoenbr. 3: 24, t. 295 (“*Ruizia diversifolia*”). 1798, nom. superfl. & illeg.

Distribution. – Endemic to La Réunion.

Note. – Friedmann (1987) designated lectotypes (as “holotypes”) for the names of several species of *Ruizia* described by Cavanilles, and he identified these specimens in the Jussieu Herbarium (P-JU) by catalog number adding “pro parte” when there was more than one sheet with the same number. The multiple sheets are informally distinguished here as A, B, and C (from left to right on the microfiche) and second step lectotypifications are designated to obviate any ambiguity as to which one of these multiple sheets typifies a given name.

4a. *Ruizia ferruginea* (Cav.) Dorr, **comb. nov.** ≡ *Dombeya ferruginea* Cav., Diss. 3: 128, t. 42, fig. 2. 1787 ≡ *Cavanilla ferruginea* (Cav.) J.F.Gmel., Syst. Nat. 2(2): 1038. 1792 (“1791”) ≡ *Pentapetes ferruginea* (Cav.) Poir. in Lamarck, Encycl. 5: 159. 1804 ≡ *Assonia ferruginea* (Cav.) Kuntze, Revis. Gen. Pl. 1: 76. 1891 – Lectotype (designated by Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 201. 1960 [“1959”], as “type”): Mauritius. “in summo cacumine montis Trimamis [= Trois Mamelles Mountain]”, s.d., [*Ph. Commerson s.n.*] (P-JU 12506 [microfiche!]; possible isoelectotypes: C barcode C10001390 [image!], H barcode H1768855 [image!], MA barcode MA 475630 [image!], P barcode P00042005 [image!]).

= *Dombeya ovata* Cav., Diss. 3: 127, t. 41, fig. 2n–z, R. 1787 ≡ *Cavanilla ovata* (Cav.) J.F.Gmel., Syst. Nat. 2(2): 1038. 1792 (“1791”) ≡ *Pentapetes ovata* (Cav.) Poir. in Lamarck, Encycl. 5: 158. 1804 ≡ *Assonia ovata* (Cav.) Kuntze, Revis. Gen. Pl. 1: 76. 1891 – Lectotype (designated by Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 202. 1960 [“1959”], as “type”): Mauritius. “Habitat in Insula Bourbon [sic]”, s.d., [*Ph. Commerson s.n.*] (P-JU 12505 [microfiche!]; possible isoelectotypes: MA barcode MA 475631 [image!], P barcode P06700181 [image!]).

= *Assonia viburnoides* DC., Prodr. 1: 498. 1824 (“*viburnoides*”) ≡ *Dombeya viburnoides* (DC.) Cordem., Fl. Réunion: 309. 1895 (“*viburnoides*”) – Holotype: Mauritius. Ile de France ou de Bourbon, 1821, [*Ph. Commerson?*] (G barcode G00208844 [image!]).

Distribution. – Endemic to Mauritius.

4b. *Ruizia ferruginea* subsp. *borbonica* (F.Friedmann) Dorr, **comb. nov.** ≡ *Dombeya ferruginea* subsp. *borbonica* F.Friedmann in Adansonia, sér. 2, 20: 444. 1981 – Holotype: La Réunion. Bélouve, Rampart dominant, Hell-Bourg, 8 Feb 1968 (♂), *R. Capuron 28236-SF* (P barcode P00042006 [image!]; isotypes: K barcode K000241181 [image!], P barcode P00042007 [image!]).

= *Dombeya richardiana* Cordem., Fl. Réunion: 318. 1895 (“*Richardiana*”) – Lectotype (designated by Friedmann in Bosser & al., Fl. Mascareignes 53: 27. 1987, as “holotype”): La Réunion. Bois du Boucan Launay, s.d., *A. Richard s.n.* (MARS n.v.).

Distribution. – Endemic to La Réunion.

5. *Ruizia granulata* (Cordem.) Dorr, **comb. nov.** ≡ *Trochetia granulata* Cordem., Fl. Réunion: 319. 1895 – Holotype: La Réunion. “Cilaos, sur la rive droite du Bras des Étangs, près de la cascade”, 1100 m, s.d., *E.J. de Cordemoy s.n.* (MARS n.v.).

Distribution. – Endemic to La Réunion.

6. *Ruizia mauritiana* (F.Friedmann) Dorr, **comb. nov.** ≡ *Dombeya mauritiana* F.Friedmann in Adansonia, sér. 2, 20: 439, t. 1, fig. 1–7. 1981 – Holotype: Mauritius. Magenta, 5 Jun 1976, *F. Friedmann & T. Cadet 2854* (P barcode P00044756 [image!]; isotypes: K barcodes K000241179 [image!] & K000241180 [image!], MAU n.v., P barcodes P00044757 [image!], P06606586 [image!], P06606588 [image!] & P06606589 [image!]).

Distribution. – Endemic to Mauritius.

7. *Ruizia parviflora* (Bojer ex Baker) Dorr, **comb. nov.** ≡ *Trochetia parviflora* Bojer ex Baker, Fl. Mauritius: 30. 1877 – Lectotype (designated by Friedmann in Bosser & al., Fl. Mascareignes 53: 17. 1987, as “holotype”): Mauritius. “in high woods of the Pouce”, s.d., *W. Bojer s.n.* (MAU n.v.; possible isoelectotype: K barcode K000241247 [image!]).

– “*Trochetia parviflora*” Bojer, Hortus Maurit.: 41. 1837, nom. nud.

– “*Dombeya parviflora*” Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 193. 1960 (“1959”), nom. nud.

Distribution. – Endemic to Mauritius, where it is known from a single population (Florens & al., 2001).

8. *Ruizia populnea* (Cav.) Dorr, **comb. nov.** ≡ *Assonia populnea* Cav., Diss. 3: 120, t. 42, fig. 1a–j, k–m, nn. Feb 1787 ≡ *Pentapetes populnea* (Cav.) Poir. in Lamarck, Encycl. 5: 154. 1804 ≡ *Dombeya populnea* (Cav.) Baill., Hist. Pl. 4: 67. 1872 – Lectotype (designated by Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 194. 1960 [“1959”], as “holotype”): La Réunion. “in sylvis montosis Divi Pauli pago imminentibus”, s.d., [*Ph. Commerson s.n.*] (P-JU 12511 [microfiche!]; possible isoelectotypes: B barcode B-W 12614 -01 0 [image!], C barcode C10001395 [image!], LINN-HS No. 1149.1 [image!], MA barcode MA 475338 [image!], MPU barcodes MPU016694 [image!], MPU016695 [image!], MPU016696 [image!], MPU016697 [image!] & MPU016698 [image!]).

= *Vahlia fastuosa* Dahl, Observ. Bot.: 22. Oct 1787 (“*Tastuosa*”) – Type: Not located.

– “*Dombeya globosa*” Bojer ex Baker, Fl. Mauritius: 28. 1877, nom. nud., pro syn.

Distribution. – La Réunion and Mauritius; possibly extirpated on the latter island.

Note. – Friedmann (1987) observed that specimens of this species from Mauritius and La Réunion are distinct morphologically. Le Péchon & al. (2015: fig. 2, clade A) found that the populations of this species from Mauritius are sister to *Dombeya mauritiana* (≡ *Ruizia mauritiana*) and not populations of *D. populnea* (≡ *R. populnea*) from La Réunion. The

taxonomic implications of these relationships need to be investigated further.

9. *Ruizia rosea* (Lindl.) Dorr, **comb. nov.** $\equiv$ *Astyria rosea* Lindl. in Edwards's Bot. Reg. 30 [Misc.]: 27. May 1844 & t. 49. 1 Sep 1844 ("*Astiria*") – Lectotype (designated by Friedmann in Bosser & al., Fl. Mascareignes 53: 5. 1987): [illustration in] Edwards's Bot. Reg. 30: t. 49. 1844.

= *Dombeya boutonii* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 193, t. 7. 1960 ("1959") ("*Boutonii*") – Holotype: Mauritius. "Île Maurice", sine loc., [1830] (♀), *L. Bouton* s.n. (P barcode P00093406 [image!]; isotype: P barcode P00093407 [image!]).

= *Dombeya astylosa* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 199. 1960 ("1959") – Holotype: Mauritius. Sine loc., s.d. (♂), [*L. Bouton*?] s.n. (P barcode P00093408 [image!]).

– "*Dombeya astrapaoides*" Bojer ex Baker, Hortus Maurit.: 40. 1837 ("*astrapaoides*"), nom. nud.
Distribution. – Endemic to Mauritius, possibly extinct.

10. *Ruizia sevathianii* (Le Péchon & Baider) Dorr, **comb. nov.** $\equiv$ *Dombeya sevathianii* Le Péchon & Baider in Phytotaxa 24: 2, fig. 1, 2, 41 A₂, B₂, C₂. 2011 – Holotype: Mauritius. Black River Gorges National Park, 595 m, 20°23'01.8"S, 057°27'04.9"E, 12 May 2004, J.C. Sevathian s.n. (MAU 23856 n.v.).
Distribution. – Endemic to Mauritius.

11. *Ruizia tremula* (Hochr.) Dorr, **comb. nov.** $\equiv$ *Dombeya tremula* Hochr. in Candollea 3: 71. 1926 – Holotype: Madagascar. Toliara: Ambovombe, 1 May 1925, R. Decary 3726 (P barcode P00044992 [image!]; isotype: P barcode P00044993 [image!]).
Distribution. – Endemic to southernmost Madagascar.

12. *Ruizia triflora* (DC.) Dorr, **comb. nov.** $\equiv$ *Trochetia triflora* DC. in Mém. Mus. Hist. Nat. 10: 109, t. 8 ["4"]. 1823 $\equiv$ *Dombeya triflora* (DC.) Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 193. 1960 ("1959") – Lectotype (designated by Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 193. 1960 ["1959"]); Mauritius. Sine loc., s.d., *Hb. de Jussieu* (P-JU n.v.; isoelectotype: G barcode G00208856 [image!]).

= *Trochetia grandiflora* Bojer ex Lindl. in Edwards's Bot. Reg. 30: ad t. 21. 1844 – Lectotype (designated by Friedmann in Bosser & al., Fl. Mascareignes 53: 17. 1987): [illustration in] Edwards's Bot. Reg. 30: t. 21. 1844.

– "*Trochetia grandiflora*" Bojer, Hortus Maurit.: 41. 1837, nom. nud.

– "*Trochetia serrata*" Bojer, Hortus Maurit.: 41. 1837, nom. nud.

– "*Dombeya serrata*" Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 194. 1960 ("1959"), nom. nud.
Distribution. – Endemic to Mauritius.

13. *Ruizia uniflora* (DC.) Dorr, **comb. nov.** $\equiv$ *Trochetia uniflora* DC. in Mém. Mus. Hist. Nat. 10: 107, t. 7. 1823 $\equiv$ *Dombeya uniflora* (DC.) Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 192. 1960 ("1959") – Lectotype (designated by Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 9: 193. 1960 ["1959"]); Mauritius. Sine loc., 1810, [herb.] B. Delessert s.n. (G barcode G00208859 [image!]).

= *Trochetia candolleana* Bojer, Hortus Maurit.: 41. 1837 ("*Candolleana*"), nom. superfl. & illeg.

Distribution. – Endemic to Mauritius.

A new name and two new combinations in *Melhanina*

Melhanina Forssk., Fl. Aegypt.-Arab.: cviii, 64. 1775 – Type: *Melhanina velutina* Forssk.

= *Brotera* Cav., Icon. 5: 19. 1799 – Type: *Brotera ovata* Cav. ($\equiv$ *Melhanina ovata* (Cav.) Spreng.).

= *Sprengelia* Schult., Observ. Bot.: 134. 1809, non Sm. in Kongl. Vetensk. Acad. Nya Handl. 15: 261. 1794 – Type: *Sprengelia modesta* Schult. (= *Melhanina ovata* (Cav.) Spreng.).

= *Vialia* Vis. in Index Seminum (Padova [Pataviae]) 1840: 9. 1840 – Type: *Vialia macrophylla* Vis. (= *Melhanina didyma* Eckl. & Zeyh.).

= *Cardiostegia* C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 609 ["960"]. 1851 & Epimel. Bot.: 249. 1851 ("1849") – Type: *Cardiostegia kotschyi* (Hochst.) C.Presl (= *Melhanina denhamii* R.Br.).

= *Sideria* Ewart & Petrie in Proc. Roy. Soc. Victoria, ser. 2, 38: 174. 1926 – Type: *Sideria reverta* Ewart & Petrie (= *Melhanina oblongifolia* F.Muell.).

= *Paramelhanina* Arènes in Mém. Inst. Sci. Madagascar, sér. B, Biol. Vég. 2: 24. 1949 – Type: *Paramelhanina decaryana* Arènes ($\equiv$ *Melhanina lisae* Dorr), **syn. nov.**

= *Trochetiopsis* Marais in Kew Bull. 36: 645. 1981 – Type: *Trochetiopsis erythroxydon* (G.Forst.) Marais ($\equiv$ *Melhanina erythroxydon* (G.Forst.) R.Br.), **syn. nov.**

Herbs, shrubs or small *trees*; stems and leaves with stellate hairs, sometimes with glandular hairs or lepidote. *Leaves* simple, entire, palmately 3–5-veined at base, margin crenate, crenulate, dentate or entire; petiolate; stipulate. *Inflorescences* axillary (often clustered toward the shoot apex), few-flowered cymes or flowers solitary. Flowers hermaphroditic, rarely polygamous. *Epicalyx* bracts 3, entire, sometimes fused at base, usually close to calyx, usually persistent. *Sepals* 5, free or almost free, persistent, sometimes accrescent. *Petals* 5, symmetric to strongly asymmetric, yellow, white or cream, caducous or marcescent, sometimes persistent on the fruit after falling. *Stamens* 5, forming a short staminal tube; anthers 2-locular, sometimes with an extension of the connective; staminalodes 5, lanceolate to spatulate, shortly fused with stamens. *Ovary* 5(6)-locular; ovules 1–12 per locule, ascending; style simple; stigma 5-branched or 5-lobed. *Fruit* a capsule, pericarp usually thin, loculicidally dehiscent, splitting into 5 valves; endocarp glabrous or pubescent at central part of

septae; locules 1-several seeded; seeds glabrous, not winged, elaisome present or not; cotyledons bifid, bipartite, plicate. $2n = 40, 60$.

Distribution. – Approximately 75 species found in St. Helena, continental Africa, the Arabian Peninsula, Madagascar, southern Asia, and Australia.

Note. – Although the petals of *Trochetiopsis* are white or creamy-white at anthesis, those of the extant species and hybrid have all been described as turning or “flushing” to pink when senescing (Brodie & al., 1998; Cronk, 2000).

Melhanian ×benjaminii (Cronk) Dorr, **comb. nov.** $\equiv$ *Trochetiopsis ×benjaminii* Cronk in Edinburgh J. Bot. 52: 211. 1995 (“*benjaminii*”) – **Lectotype (designated here):** St. Helena: Pounceys, 24 Aug 1986 (fl), *Q.C.B. Cronk 480* (E barcode E00841463 [image!]).

Distribution. – Described from cultivated material.

Note. – A lectotype is designated because the “holotype” was not deposited in CGE as stated in the protologue (Turland & al., 2018, Art. 9.2 & 40.7): the specimen was deposited in E (Cronk, in litt.).

Melhanian ebena (Cronk) Dorr, **comb. nov.** $\equiv$ *Trochetiopsis ebenus* Cronk in Edinburgh J. Bot. 52: 210. 1995 – Holotype: St. Helena: Near the Asses Ears, Nov 1980 (fl), *Q.C.B. Cronk & G. Benjamin s.n.* (CGE barcode 33418 [image!]). **Distribution.** – Endemic to St. Helena.

Melhanian lisae Dorr, **nom. nov.** $\equiv$ *Paramelhanian decaryana* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 2: 26, t. 4. 1949 (“*Decaryana*”), non *Melhanian decaryana* Arènes in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 7: 116. 1956 – **Lectotype (designated here):** Madagascar. Ambovombe, 11 Apr 1925 (fl, fr), *R. Decary 2522* (P barcode P00093409 [image!]; isolectotypes: P barcodes P00046623 [image!] & P00046662 [image!]). **Distribution.** – Endemic to southern Madagascar. **Etymology.** – Named for Lisa C. Barnett.

Two new combinations in *Corchoropsis*

Corchoropsis Siebold & Zucc. in Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3(3): 737. 1843 – Type: *Corchoropsis crenata* Sieb. & Zucc.

$\equiv$ *Paradombeya* Stapf in Hooker’s Icon. Pl. 28: t. 2743A. 1902 – Type: *Paradombeya burmanica* Stapf ($\equiv$ *Corchoropsis burmanica* (Stapf) Dorr), **syn. nov.**

Herbs, shrubs or small trees; stems with stellate, bifurcate or simple hairs. **Leaves** simple, palmately (3–)5–7-veined at base, margin crenate, dentate or serrulate; petiolate; stipulate. **Inflorescences** axillary, few- to many-flowered cymes or flowers solitary, cymes sometimes very dense; pedicels articulate. **Epicalyx** bracts 2–3, entire, distant from the calyx, free or shortly connate, caducous to persistent. **Sepals** 5, fused at base, persistent. **Petals** 5, asymmetric to strongly asymmetric, yellow or white, caducous or sometimes persistent.

Stamens (5)10–15(25), in fascicles of (1)2–3(5) alternating with staminodes, forming a short staminal tube; staminodes 5, linear to lanceolate, oblanceolate or spatulate. **Ovary** 2–5-locular, 2-many ovules per locule; style simple, swollen apically; stigma slightly 3–5-grooved. **Fruit** a capsule, loculicidally dehiscent or carpels freely separating into 1(2)-seeded mericarps, pericarp thin, pubescent, endocarp glabrous or central part of septae sometimes pubescent; seeds glabrous, not winged; cotyledons 2-lobed or bifid. $2n = 20$.

Distribution. – Four species restricted to eastern and southeastern Asia.

Note. – The rank of one of the four species is not settled and merits further study. It is treated as either *Corchoropsis psilocarpa* Harms & Loes. (Won, 2009) or *C. crenata* var. *hupehensis* Pamp. (Tang, 1994, as *C. tomentosa* var. *psilocarpa* (Harms & Loes.) C.Y. Wu & Tang; Tang & al., 2007).

Corchoropsis burmanica (Stapf) Dorr, **comb. nov.** $\equiv$ *Paradombeya burmanica* Stapf in Hooker’s Icon. Pl. 28: t. 2743A. 1902 – Holotype: Myanmar. “Upper Burma”, Upper Shan States at Supmut, 3500 ft, 1895 (fl), *H.H. Hildebrand s.n.* (K barcode K000671859!).

$\equiv$ *Paradombeya multiflora* Gamble in Bull. Misc. Inform. Kew 1912: 198. 1912 – **Lectotype (designated here):** Myanmar. “Southern Shan States” Loi Ai near Sukat Kyaukdwinn, 760 m, Dec 1909 (fl, fr), *W.A. Robertson 65* (K barcode K000671860!; isolectotype: K barcode K000875458!).

Distribution. – Myanmar and Thailand.

Corchoropsis sinensis (Dunn) Dorr, **comb. nov.** $\equiv$ *Paradombeya sinensis* Dunn in Hooker’s Icon. Pl. 28: t. 2743B. 1902 – Holotype: China. Yunnan: Yunnanfu, s.d. (fl), *Rev. Père F. Ducloux 480* (K barcode K000671861!).

$\equiv$ *Lysimachia mairei* H.Lév. in Bull. Acad. Int. Géogr. Bot. 25: 40. 1915 (“*Mairei*”) – **Lectotype (designated here):** China. Yunnan: rives du fleuve Bleu, à Kiang-pien, 350 m, Aug 1912 (fl), *E.E. Maire s.n.* (E barcode E00284365 [image!]; isolectotypes: A barcode 00247484!, E barcode E00284366 [image!]; possible isolectotype: E barcode E00284373 [image!]).

$\equiv$ *Paradombeya szechuenica* Hu in Bull. Fan Mem. Inst. Biol. 7: 215. 1936 – **Lectotype (designated here):** China. Szechuan: Ping-Shan Hsien, 280 m, 22 Oct 1934 (fl), *T.T. Yü 4152* (E barcode E00284364 [image!]; isolectotypes: A barcode 00247485!, PE barcodes PE00024230 [image!], PE01304667 [image!], PE01304668 [image!] & PE01304669 [image!]).

$\equiv$ *Paradombeya rehderiana* Hu in Bull. Fan Mem. Inst. Biol. 10: 145. 1940 (“*Rehderiana*”) – **Lectotype (designated here):** China. Yunnan: Lu-Shuei, 1500 m, 20 Sep 1933 (fl, fr), *H.T. Tsai 54547* (PE barcode PE00024227 [image!]; isolectotypes: A barcode 00247512!, IBSC barcode 0004163 [image!], PE barcodes PE00024228 [image!], PE00024229 [image!], PE01304670 [image!] & PE01304671 [image!]).

Distribution. – Endemic to southern China.

■ AUTHOR CONTRIBUTIONS

LD and KW designed the study. LD provided systematic and taxonomic data based on 35 years of field and herbarium observations, and KW performed the molecular labwork and data analyses. A first draft of the manuscript, except for molecular materials and methods provided by KW, was written by LD. Both LD and KW refined subsequent drafts, including the conclusions. — LD, <https://orcid.org/0000-0001-7157-363X>; KW, <https://orcid.org/0000-0003-0010-6932>

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Appendix 1. Sources of Malvaceae data used in the phylogenetic analyses.

Taxon, voucher information for newly reported data, and GenBank accession numbers (new data start with MT) ordered ITS, *trnC-ycf6*, *ycf6-psbM*, *psbM-trnD*, *petL-psbE*, *ndhA* intron. En-dashes (–) indicate missing sequences. Taxonomic and/or nomenclatural changes recognized here are provided, which include updates for data from Le Péchon & al. (2010) and Skema (2012).

Andringitra leiomacrantha (Hochr.) Skema [as *Dombeya leiomacrantha* Hochr.], JF939245, JF939589, JF939674, JF939504, JF939417, JF939332. *Andringitra leucomacrantha* (Hochr.) Skema [as *Dombeya leucomacrantha* Hochr.], JF939246, JF939590, JF939675, JF939505, JF939418, JF939333. *Andringitra macrantha* (Baker) Skema [as *Dombeya macrantha* Baker], JF939249, JF939593, JF939678, JF939508, JF939421, JF939336. *Andringitra moratii* (L.C.Barnett & Dorr) Skema [as *Dombeya moratii* L.C.Barnett & Dorr], JF939256, JF939600, JF939685, JF939515, JF939428, JF939342. *Andringitra muscosa* (Hochr.) Skema [as *Dombeya muscosa* Hochr.], JF939257, JF939601, JF939686, JF939516, JF939429, JF939343. *Andringitra seyrigii* (Arènes) Skema, Madagascar, Toliara, N. *Andrianjafy* & al. 634 (MO-5906128), MT625265, MT635190, –, MT625343, –, –, *Astytia rosea* Lindl. [= *Ruizia rosea* (Lindl.) Dorr], Mauritius, 17 Jul 1863, *J. Blackburn s.n.* (MO-5450333), MT625266, –, –, –, –, *Burretiodendron esquirolii* (H.Lév.) Rehder, AY629201, –, –, –, –, *Burretiodendron kydtifolium* Y.C.Hsu & R.Zhughe, AY629202, –, –, –, –, *Cheirolaena linearis* Benth., Madagascar, Mahajanga, L. *Ranaivoarisoa* & I. Luino LUR 038 (US 3667763), MT625267, MT625306, –, MT625344, MT625382, MT625410. *Corchoropsis crenata* Siebold & Zucc. [as misapplied *Corchoropsis tomentosa* (Thunb.) Makino], JF939206, JF939549, JF939634, JF939462, JF939375, JF939291. *Dombeya acerifolia* Baker, JF939210, JF939553, JF939638, JF939466, JF939379, JF939295. *Dombeya acutangula* Cav., DC, JF939212, JF939555, JF939640, JF939468, JF939381, JF939297. *Dombeya autumnalis* I.Verd., JF939223, JF939567, JF939652, JF939481, JF939394, JF939309. *Dombeya baronii* Baker, JF939218, JF939560, JF939645, JF939474, JF939387, JF939302. *Dombeya borraginopsis* Hochr., JF939267, JF939611, JF939696, JF939526, JF939439, JF939352. *Dombeya burgessiae* Gerr. ex Harv. & Sond., JF939226, JF939570, JF939655, JF939484, JF939397, JF939312. *Dombeya dichotomopsis* Hochr. [as *Dombeya angustipetala* Arènes], JF939214, JF939557, JF939642, JF939470, JF939383, JF939299. *Dombeya elegans* Cordem., JF939231, JF939575, JF939660, JF939489, JF939402, JF939317. *Dombeya ferruginea* Cav. [= *Ruizia ferruginea* (Cav.) Dorr], [RB33], JF939234, JF939578, JF939663, JF939492, JF939405, JF939320. *Dombeya ferruginea* subsp. *borbonica* F.Friedmann [= *Ruizia ferruginea* subsp. *borbonica* (F.Friedmann) Dorr], GU938053, –, –, GU937911, –, –, *Dombeya ferruginea* Cav. subsp. *ferruginea* (Cav.) Dorr subsp. *ferruginea*, [LP155], GU938054, –, –, GU937912, –, –, *Dombeya gautieri* Dorr & Skema, JF939235, JF939579, JF939664, JF939493, JF939406, JF939321. *Dombeya greveana* Baill., JF939236, JF939580, JF939665, JF939494, JF939407, JF939322. *Dombeya hildebrandtii* Baill. [as *Dombeya borraginea* Hochr.], JF939265, JF939609, JF939694, JF939524, JF939437, –, *Dombeya laurifolia* (Bojer) Baill., JF939243, JF939588, JF939673, JF939502, JF939415, JF939330. *Dombeya leconteopsis* Arènes, JF939244, –, –, JF939503, JF939416, JF939331. *Dombeya lucida* Baill., JF939248, JF939592, JF939677, JF939507, JF939420, JF939335. *Dombeya mandanensis* Arènes, JF939251, JF939595, JF939680, JF939510, JF939423, JF939337. *Dombeya* cf. *marivorahonensis* Arènes, JF939266, JF939610, JF939695, JF939525, JF939438, JF939351. *Dombeya mauritiana* F.Friedmann [= *Ruizia mauritiana* (F.Friedmann) Dorr], [RB34], JF939252, JF939596, JF939681, JF939511, JF939424, JF939338. *Dombeya mauritiana* F.Friedmann [= *Ruizia mauritiana* (F.Friedmann) Dorr], [LP129], GU938058, –, –, GU937916, –, –, *Dombeya modesta* Baker, JF939253, JF939597, JF939682, JF939512, JF939425, JF939339. *Dombeya mollis* Hook., JF939508, JF939683, JF939513, JF939426, JF939340. *Dombeya populnea* (Cav.) Baill. [= *Ruizia populnea* (Cav.) Dorr], JF939259, JF939603, JF939688, JF939518, JF939431, JF939345. *Dombeya reclinata* Cordem., JF939260, JF939604, JF939689, JF939519, JF939432, JF939346. *Dombeya rodriguesiana* F.Friedmann, GU938064, –, –, GU937922, –, –, *Dombeya rotleroides* Baill., JF939261, JF939605, JF939690, JF939520, JF939433, JF939347. *Dombeya rubifolia* Baill., JF939262, JF939606, JF939691, JF939521, JF939434, JF939348. *Dombeya superba* Arènes [= *Hafotra superba* (Arènes) Dorr], [WA261], JF939273, JF939618, JF939703, JF939533, JF939446, JF939359. *Dombeya superba* Arènes [= *Hafotra superba* (Arènes) Dorr], [23593-SF], JF939285, JF939617, JF939702, JF939532, JF939445, JF939358. *Dombeya superba* Arènes [= *Hafotra superba* (Arènes) Dorr], [R293], GU938070, –, –, GU937928, –, –, *Dombeya tiliacea* Planch., JF939277, JF939622, JF939707, JF939537, JF939450, JF939363. *Dombeya tremula* Hochr. [= *Ruizia tremula* (Hochr.) Dorr], GU938072, –, –, GU937930, –, –, *Dombeya viburniflora* Bojer, JF939280, JF939625, JF939710, JF939540, JF939453, JF939366. *Dombeya wittei* De Wild. & Staner, JF939209, JF939552, JF939637, JF939465, JF939378, JF939294. *Eriolaena barnettiae* Dorr, Madagascar, Antsiranana, L. Nusbauer & P. Ranirison LN 1496 (US 3490603, type), MT625268, MT625307, –, MT625345, MT625383, MT625411. *Eriolaena candollei* Wall., [CS439], JF939230, JF939574, JF939659, JF939488, JF939401, JF939316. *Eriolaena candollei* Wall., Myanmar, Mandalay, Y.Y. Kyi 2124 (US 3407158), MT625269, MT625308, –, MT625346, MT625384, MT625412. *Eriolaena cheekii* Dorr, Madagascar, Antsiranana, N.M. *Andrianjafy* 1632 (US 3653965, type), MT625270, MT625309, –, MT625347, MT625385, MT625413. *Eriolaena hookeriana* Wight & Arn., India, Tamil Nadu, W. *Bembower* 95 (N.Y.), MT625271, MT625310, –, –, *Eriolaena kwangsiensis* Hand.-Mazz. [= *Eriolaena candollei* Wall.], China, W. *Xingwei* 4767 (MO-4202048), MT625272, MT625311, –, MT625348, –, –, *Eriolaena margaritae* Dorr, Madagascar, Antsiranana, M. *Koopman* & J. *Razafitsalama* 458 (US 3592220, type), MT625273, –, –, MT625349, MT625386, MT625414. *Eriolaena margaritae* Dorr, Madagascar, Antsiranana, D. *DuPuy* & J. *Andrianiana* M770 (MO-5074509), MT625274, MT625312, –, MT625350, MT625387, MT625415. *Eriolaena rulkensis* Dorr, Mozambique, Cabo Delgado, A.J.H. *Rulkens* 1 (US 3687807, type), MT625275, MT625313, –, –, MT625351, MT625388, MT625416. *Eriolaena spectabilis* (DC.) Planch. ex Mast., China, Zhang Zhaoqian 10109 (MO-4129028), MT625276, MT625314, –, MT625352, –, –, *Excentrodendron hsienmu* (Chun & F.C.How) H.T.Chang & R.H.Miao [= *Burretiodendron hsienmu* Chun & F.C.How], AY629198, –, –, –, –, *Excentrodendron obconicum* (Chun & F.C.How) H.T.Chang & R.H.Miao [= *Burretiodendron obconicum* Chun & F.C.How], AY629197, –, –, –, –, *Gossypium herbaceum* L., GHU12713, plastid all NC_023215. *Harmsia lepidota* (Vollsen) M.Jenny, Somalia, Dangorayo Distr., *Lavranos* & *Carter* 24618 (MO-3780155), MT625277, MT625315, –, MT625353, MT625389, MT625417. *Harmsia sidoides* K.Schum., Ethiopia, Bale, M. *Gilbert* & al. 7857 (MO-3860348), MT625278, MT625316, –, MT625354, MT625390, MT625418. *Helmiopsiella ctenostegia* (Hochr.) L.C.Barnett [= *Eriolaena ctenostegia* (Hochr.) Dorr], [MC33737], JF939241,

Appendix 1. Continued.

JF939585, JF939670, JF939499, JF939412, JF939327. *Helmiopsiella ctenostegia* (Hochr.) L.C.Barnett [= *Eriolaena ctenostegia* (Hochr.) Dorr], Madagascar, Mahajanga, *R. Capuron 29126-SF* (NY), MT625279, MT625317, –, MT625355, –, –, *Helmiopsiella leandrii* (Hochr.) L.C.Barnett [= *Eriolaena leandrii* (Hochr.) Dorr], Madagascar, Mahajanga, *B.F.L. Rakotozafy BFL 050* (US 3662993), MT625280, MT625318, –, MT625356, MT625391, MT625419. *Helmiopsiella madagascariensis* Arènes [= *Eriolaena madagascariensis* (Arènes) Dorr], JF939242, JF939586, JF939671, JF939500, JF939413, JF939328. *Helmiopsiella poissonii* (Arènes) Capuron ex L.C.Barnett [= *Eriolaena poissonii* (Arènes) Dorr], Madagascar, Antsiranana, *M. Koopman & J. Razafitsalama 463* (US 3592222), MT625281, MT625319, –, MT625357, MT625392, MT625420. *Helmiopsis bernieri* (Baill.) Arènes [= *Eriolaena bernieri* (Baill.) Dorr], [CS288], JF939238, JF939582, JF939667, JF939496, JF939324. *Helmiopsis bernieri* (Baill.) Arènes [= *Eriolaena bernieri* (Baill.) Dorr], Madagascar, Antsiranana, *M. Koopman & J. Razafitsalama 449* (US 359221), MT625282, –, –, MT625358, –, –, *Helmiopsis bernieri* (Baill.) Arènes [= *Eriolaena bernieri* (Baill.) Dorr], [20937-SF], GU938075, –, –, GU937933, –, –, *Helmiopsis boivinii* (Baill.) Arènes [= *Eriolaena boivinii* (Baill.) Dorr], Madagascar, Mahajanga, *R.F. Bolliger & al. RFB 293* (US 3063109), MT625283, MT625320, –, MT625359, MT625393, MT625421. *Helmiopsis hily* Arènes [= *Eriolaena hily* (Arènes) Dorr], Madagascar, Toliara, *R. Capuron 22531-SF* (MO-3522151), MT625284, MT625321, –, MT625360, MT625394, MT625422. *Helmiopsis linearifolia* (Hochr.) Skema [= *Eriolaena linearifolia* (Hochr.) Dorr], Madagascar, Antsiranana, *R. Capuron 20920-SF* (NY), MT625285, MT625322, –, MT625361, –, –, *Helmiopsis linearifolia* subsp. *muricata* (Appelq.) Skema [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *R. Capuron 24719bis-SF* (NY), MT625286, MT625323, –, MT625362, –, –, *Helmiopsis linearifolia* subsp. *muricata* (Appelq.) Skema [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *R. Capuron 22697-SF* (NY), MT625287, MT625324, –, MT625363, –, –, *Helmiopsis polyandra* Appelq. [= *Eriolaena polyandra* (Appelq.) Dorr], Madagascar, Antsiranana, *L. Gautier & al. LG 4508* (US 3476384), MT625288, MT625325, –, MT625364, MT625395, MT625423. *Helmiopsis pseudopopulus* (Baill.) Capuron ex Arènes [= *Eriolaena pseudopopulus* (Baill.) Dorr], [CS328], JF939239, JF939583, JF939668, JF939497, JF939410, JF939325. *Helmiopsis pseudopopulus* (Baill.) Capuron ex Arènes [= *Eriolaena pseudopopulus* (Baill.) Dorr], [27412-SF], GU938076, –, –, GU937934, –, –, *Helmiopsis* cf. *pseudopopulus* (Baill.) Capuron ex Arènes [= *Eriolaena* cf. *pseudopopulus* (Baill.) Dorr], Madagascar, Antsiranana, *P. Ranirison PR 575* (US 3479806), MT625289, MT625326, –, MT625365, MT625396, MT625424. *Helmiopsis richardii* (Baill.) Capuron ex Arènes [= *Eriolaena richardii* (Baill.) Dorr], Madagascar, Antsiranana, *D.K. Harder & al. 1725* (US 3333718), MT625290, MT625327, –, MT625366, MT625397, MT625425. *Helmiopsis rigida* Baill. [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *R. Capuron 27422-SF* (MO-4318272), MT625291, MT625328, –, MT625367, MT625398, MT625426. *Helmiopsis rigida* Baill. [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *Service Forestier 14228-SF* (MO-3924448), MT625292, MT625329, –, MT625368, –, –, *Helmiopsis rigida* Baill. [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *R. Capuron 27377-SF* (MO-4318273), MT625293, MT625330, –, MT625369, MT625399, MT625427. *Helmiopsis rigida* Baill. [= *Eriolaena rigida* (Baill.) Dorr], misid. as *Dombeya linearifolia* subsp. *sely* Arènes], [FRI1228], JF939240, JF939584, JF939669, JF939498, JF939411, JF939326. *Helmiopsis rigida* subsp. *guazumifolia* (Baill.) Skema [= *Eriolaena rigida* (Baill.) Dorr], Madagascar, Antsiranana, *P. Ranirison & L. Nusbaumer PR447* (US 3479807), MT625294, MT625331, –, MT625370, MT625400, MT625428. *Helmiopsis rigida* subsp. *parvifolia* (Appelq.) Skema [= *Eriolaena parvifolia* (Appelq.) Dorr], Madagascar, Toliara, *J. Bossier 17502* (NY, type), MT625295, MT625332, –, MT625371, –, MT625429. *Helmiopsis sphaerocarpa* L.C.Barnett [= *Eriolaena sphaerocarpa* (L.C. Barnett) Dorr], Madagascar, Antsiranana, *R. Capuron 27349-SF* (MO-3522136), MT625296, MT625333, –, MT625372, MT625401, MT625430. *Melhanina acuminata* Mast., South Africa, Transvaal, *H. Glen 3610* (MO-5038063), MT625297, MT625334, –, MT625373, MT625402, MT625431. *Melhanina forbesii* Planch. ex Mast., Namibia, *S. Bartsch & al. SB1840* (US 976877), MT625298, MT625335, –, MT625374, MT625403, MT625432. *Melhanina phillipsiae* Baker f., Somalia, Jalaalqsi Distr., *P. Kuchar 17667* (US 3454372), MT625299, MT625336, –, MT625375, MT625404, MT625433. *Melhanina rotundata* Hochst ex Mast., Kenya, Taita-Taveta, *J. Belsky 585* (MO-5383655), MT625300, MT625337, –, MT625376, MT625405, MT625434. *Melhanina tulearensis* Arènes, Madagascar, Toliara, *F. Ratovoson 1468* (MO-6441783), MT625301, MT625338, –, MT625377, MT625406, MT625435. *Nesogordonia crassipes* (Baill.) Capuron, GU938077, –, –, GU937935, –, –, *Nesogordoniaholtzii* (Engl.) Capuron, Tanzania, Pwani, *M. Mwangoka & A. Mzibwa 2211* (MO-5569011), MT625302, MT625339, –, MT625378, MT625436. *Nesogordonia suzannae* Labat & al., GU938078, –, –, –, –, *Nesogordonia tricarpetallata* Skema & Dorr, JF939203, JF939546, JF939631, JF939459, JF939372, JF939288. *Paradombeya sinensis* Dunn [= *Corchoropsis sinensis* (Dunn) Dorr], China, Yunnan, *Li Heng & al. 8597* (MO-5316257), MT625303, MT625340, –, MT625379, MT625408, MT625437. *Paramelhanina decaryana* Arènes [= *Melhanina lisae* Dorr], Madagascar, Toliara, *M. Koopman 403* (US 3592218), MT625304, MT625341, –, MT625380, MT625409, MT625438. *Pentapetes phoenicea* L., JF939204, JF939547, JF939632, JF939460, JF939373, JF939289. *Pterospermum acerifolium* Willd., JX856493, –, –, –, –, *Pterospermum lanceifolium* Roxb., KP092998, –, –, –, –, *Pterospermum menglunense* H.H.Hsue, KR532527, –, –, –, –, *Ruizia cordata* Cav., [HC128], JF939264, JF939608, JF939693, JF939523, JF939436, JF939350. *Ruizia cordata* Cav., [VL s.n.], JF939263, JF939607, JF939692, JF939522, JF939435, JF939349. *Schoutenia accrescens* (Mast.) Merr., Malaysia, Sarawak, *G. Gentry 34080* (MO-3042822), MT625305, MT625342, –, MT625381, –, MT625439. *Theobroma cacao* L., –, plastid all HQ244500. *Tilia amurensis* Rupr., KF445432, plastid all NC_028588. *Trochetia blackburniana* Bojer ex Baker [= *Ruizia blackburniana* (Bojer ex Baker) Dorr], JF939274, JF939619, JF939704, JF939534, JF939447, JF939360. *Trochetia boutoniana* F.Friedmann [= *Ruizia boutoniana* (F.Friedmann) Dorr], GU938081, –, –, GU937940, –, –, *Trochetia granulata* Cordem. [= *Ruizia granulata* (Cordem.) Dorr], GU938082, –, –, GU937941, –, –, *Trochetia parviflora* Bojer ex Baker [= *Ruizia parviflora* (Bojer ex Baker) Dorr], JF939275, JF939620, JF939705, JF939535, JF939448, JF939361. *Trochetia triflora* DC. [= *Ruizia triflora* (DC.) Dorr], GU938084, –, –, GU937943, –, –, *Trochetia uniflora* DC. [= *Ruizia uniflora* (DC.) Dorr], JF939276, JF939621, JF939706, JF939536, JF939449, JF939362. *Trochetiopsis erythroxyton* (G.Forst.) Marais [= *Melhanina erythroxyton* (G.Forst.) R.Br.], [MC18170], JF939205, JF939548, JF939633, JF939461, JF939374, JF939290. *Trochetiopsis erythroxyton* (G.Forst.) Marais [= *Melhanina erythroxyton* (G.Forst.) R.Br.], [LP132], GU938085, –, –, GU937944, –, –,

Appendix 2. Representative specimens of *Eriolaena* examined.

Taxon, country and/or locality, collection number, and herbarium.

Eriolaena barnettiae Dorr (see text). *Eriolaena bernieri* (Baill.) Dorr, Madagascar: Antsiranana: Ankarongana (Karongana), Irodo, Analafondro forest, 26 Feb 2006, *Birkinshaw & al. 1605* (MO, P barcode P04695029, WAG 2D-barcode WAG.1833639 [image]); Baie de Rigny, s.d., *Boivin 2603* (syntype: P barcode P00547682); or S du Pic Raynaud, sur la route de la Baie de Rigny, 9 Nov 1961, *Capuron 20361-SF* (K, MO, P barcodes P00547681 [image] & P00552815 [image]); Forêt d'Orange, 22 Nov 1962, *Capuron 20937-SF* (A, K, MO, P barcodes P00552813 & P00552815 [image]); près d'Antsoha (piste d'Andofiabe à la baie de Rigny, Diégo Suarez), 17 Dec 1963, *Capuron 23039-SF* (K, MO, NY, P barcode P00552814 [image]); Antsiranana II, Ramena, Ambodivahibe, Ampio, 2.5 km au Nord Ouest du village d'Ambodivahibe, 18 May 2005, *Jullet Be & al. 99* (K, MO, P); Diana Region, Ankoriakely, Orangea Ramena, 2 km du village d'Ankoriakely, 12 Mar 2007, *Rakotondrajaona & al. 415* (K, MO); Antsiranana II, Andrafieabe, Ambolobozokely, Forêt de Nosy Voanio, à 4 km à l'Est d'Ambolobozokely, 15 Feb 2006, *Randrianaivo & al. 1370* (MO, P barcode P06721417); Diana Region: Ramena, Ankoriakely, fourée d'Orangea, vers 3 km au NE du village d'Ankoriakely, 30 Nov 2005, *Razafitsalama & Guittou 874* (MO, P barcode P06721433); Diego II, Ramena, 2.5 km est de Ramena, Forêt Orangea, Mar 2015, *Tombonirina & Andriamiharimanana 51* (MO, P, TAN). *Eriolaena boivinii* (Baill.) Dorr, Madagascar: Mahajanga: N of Majunga, vicinity of the Zaha Motel, 27 Feb 1985, *Dorr & al. 3820* (BR, K, MO, P barcode P00547707, TAN); Beanka, partie sud; Anadabomanambaditsingilo, 8 Mar 2012, *Bolliger & al. RFB 293* (MO); près d'Ampasimariny, au NE de Majunga, 26 Nov 1965, *Capuron 24317-SF* (K, MO, P barcode P00547698 [image]); Ampasimarina, au N de Majunga, Jul 1921, *Perrier de la Bâthie 13838* (syntype: P barcodes P00037208 & P00037209 [image]); Sofia Region: Mampikony, Betaramahamay, Ambohimanga, Forêt d'Ambalafomby, 4 Dec 2004, *Ramananjanaahary & al. 200* (MO, P barcode P06721413 [image]); Fiv. Ambato-Boeni, RN4, Réserve forestière

Appendix 2. Continued.

d'Ampijoroa, à l'Est du Lac Ravelobe, 9 Mar 1999, *Randrianaivo & al.* 399 (MO, P barcode P06721412 [image]); Tsaramandroso, Ambato-Boeni, Réserve Naturelle no 7, 20 Jun 1951, *Réserves Naturelles 2944-R.N.* (A, BR, K, P barcodes P00547760 [image] & P00547761 [image], TAN); à l'ouest du village de Bevezaha, Canton de Tsaramandroso, district d'Ambato-Boeni, *Service Forestier 12666-SF* (P barcodes P00547763 [image] & P00547764 [image]); Forêt Analalava, Maintirano, 23 Aug 1955, *Service Forestier 14785-SF* (MO, P barcodes P00547693 [image], P06721425 [image] & P06721427 [image]); près de Maherivaratra, village le plus proche, Ambodibonara, Canton Ankerika, District Antsohihy, sous le bas-fond de la forêt tout près de Maherivaratra, 25 Feb 1956, *Service Forestier 15782-SF* (A, BR, K, P barcodes P00547703 & P06721410, TAN, TEF). **Eriolaena calcicola** (Arènes) Dorr (see text). **Eriolaena candollei** Wall., **Bhutan**: Bootan, s.d., *Griffith 572. E. I. Co. Cat.* (K). **Cambodia**: **Mondulkiri**: Sen Monorom, Spéan méanchey, 10 Apr 2019, *Sovanmoly Hul & al.* 7102 (P barcode P00915968 [image]). **China**: **Guangxi**: Bian Chen, E Lin Yen, 5 Aug 1928, *Ching 6707* (A, W); Tai Ching Shan, Lungchow, 26 May 1935, *Ko 55141* (A); Sui-luk District: Mts. Surrounding Pa Lau village, near Sui-luk, SW of Nanning, 1–18 Mar 1933, *Tsang 21903* (P barcode P06625527 [image]). **Yunnan**: Meng-soong, Dah-meng-lung, Che-li Hsien, Sep 1936, *Wang 77962* (A, K barcode K000380332, P barcode P06625506, W); Nan-hsien-ho, Che-li Hsien, Oct 1936, *Wang 79485* (A); Meng-kuan, Jenn-yeh Hsien, Oct 1936, *Wang 79981* (A). **Laos**: **Xieng Khuang**: Phou Kabo, Apr 1952, *Vidal 1648* (P barcode P06625552 [image]); Plantes du Laos, s.d., *M. Massie s.n.* (P barcode P06625548 [image]). **Myanmar**: Magok, May 1934, *Dickason 3272* (A); Myengyan District, Popa Hill, 5 Aug 1909, *Lace 4912* (K); Amherst District, Miba, Thauingyiu [sic] Valley, 7 Feb 1912, *Lace 5673* (K); Mandalay District, Upper Burma, Satpok Chang, 13 Nov 1926, *Saw Manny Mya 3634* (K); Mandalay: Township: Kyaukpadoon, Reserve/U.C.F.: Popa, Compartment: Yonge, 25 Jun 1998, *Yin Yin Kyi 2124* (US). **Thailand**: **Chiang Mai**: Valley of Meh Kuang, Chiengrai trail 2nd day from Chiengmai, between Ban Meh Wan and Pang Kia, headwaters of the Meh Lao, 31 Dec 1921, *Rock 1566* (A, K, US, W); Route from Chiengmai to Chieng Rai, on the Wieng Papao plain, 3 Jan 1922, *Rock 1663* (A, K, US). **Lampang**: District Wahng Nua, Doi Luang National Park, Wahng Gayo Falls area, 5 Jun 1997, *Maxwell 97-600* (A, MO). **Northern Thailand**: Chiangmai Siriphum water-fall, 25 Jun 1978, *Phengkklai & al.* 4097 (NY). **South West**: Raheng, banks of Meh Ping, 4 Dec 1909, *Kerr 899* (K, P barcode P06625529 [image]); Kanchanaburi, Khaobuing, 15 Apr 1971, *Phengkklai & al.* 2963 (K). **Vietnam**: **Bac Giang**: entre Lang Met et Thanh Moi, 4 Jul 1941, *Pételot 6899* (A, MO). **Dak Lak**: Environs de Ban Me' Thuot, *Schmid 889* (P barcode P06625546 [image]). **Ninh Binh**: Magok, May 1934, *Dickason 3272* (A), 6 May 1999, *Cuong 139* (GH, MO, P barcode P06625551 [image]). **Sonla**: Thuan Chau District, Thuan Chau, Chieng Bom, Huay Pu, 14 Oct 2005, *Nguyen Quoc Binh NY-HN 232* (MO, NY). **Thanh Hoa**: Phong Y pro [sic] de Thanh hoa, 12 Jul 1920, *Poilane 1611* (A, K, P barcode P06625535 [image]). **Eriolaena cheekii** Dorr (see text). **Eriolaena ctenostegia** (Hochr.) Dorr, **Madagascar**: **Mahajanga**: Forêt d'Andranomena-Marofandilia (Morondava), 28–29 Nov 1969, *Capuron 28917-SF* (BR, K, P). **Toliara**: South edge of Kirindy Mitea, 16 Oct 2004, *Andriamahay 933* (K); Partie Sud de la forêt de Marofandilia (Morondava), aux environs de Bekonazy, 30 Mar 1970, *Capuron 29126-SF* (A, BR, K, NY, P); Tsimitia-Morondava, 24 May 1952, *Service Forestier 5302-SF* (P); Ampanasanovy [sic]: Ankazoabo, 12 Apr 1956, *Service Forestier 15797-SF* (MO, P); Betsipotika-Morondava, 24 Mar 1956, *Service Forestier 15850-SF* (K, P). **Eriolaena glaberrima** (Arènes) Dorr (see text). **Eriolaena hily** (Arènes) Dorr, **Madagascar**: **Toliara**: Forêt entre Sakaraha et Beroroka, 24 Feb 1949, *Capuron 527-SF* (K, MO, P barcodes P00547684 [image] & P00547685 [image]); Forêt de Zombitsy à l'Est de Sakaraha, Mar 1955, *Capuron 11908* (K, P barcodes P00547689 [image], P00547690 [image] & P00547691 [image]); haut bassin de la Sakoa (route Betioky-Bekily), 14 Jan 1962, *Capuron 20704ter-SF* (P barcode P00547696 [image]); Forêt d'Analalamatahitse (Analalamatahotra) entre Bekily et la Route Beraketa-Antanimora, 28 Jan 1963, *Capuron 22531-SF* (A, K, MO, P barcode P00547697 [image], WAG [image]); Forêt de Troboampamaky [sic?]-Beharona-Manja, 14 Mar 1954, *Service Forestier 9819-SF* (A, MO, P barcode P00547688 [image]); Betsako-Ankazoabo, 21 Oct 1955, *Service Forestier 15794-SF* (K, P barcode P00547695); Andranovory, Tuléar, 19 Mar 1951, *Service Forestier 3398-SF* (P barcode P00547686 [image]); Hazoroa-Sakaraha, 20 Feb 1952, *Service Forestier 4984-SF* (P barcode P00547687 [image]). **Eriolaena hily** subsp. **boinensis** (Appleq.) Dorr (see text). **Eriolaena hookeriana** Wight & Arn., **India**: Pulney hills, s.d., *Beddome 663* (BM); Flora Singhum., Jun 1900, *Haines 113* (K); Behar, s.d., *Hooker s.n.* (GH, K). Dharmapuri. Distr. Harur, Sitheri hills, Sitheri to Solakkadu, 25 Aug 1977, *Matthew & Paramasivan 24326* (US); Flora of Bengal & Borders, Bunglow height in the open, Parasnath, 9 Oct 1955, *Mukhaje 3960* (A, K). **Tamil Nadu**: Near Vilagavi, 5 mi S of Kodaikanal, 11 Jun 1928, *Bembower 95* (NY). Peninsula Indiae Orientalis, s.d., *Herb. Wight 234* (GH, K, W). **Eriolaena leandrii** (Hochr.) Dorr, **Madagascar**: **Mahajanga**: Tsingy de Bemaraha (Est Antsalova), 4 Feb 1975, *Cremers 3802* (MO, P, TAN); Tsingy de Bemaraha, 1932–33, *Leandri 1045* (syntypes: MO, P barcodes P00093411 & P00093412); Beanka, partie sud, Sarodrano, 19 Feb 2012, *Rakotozafy & al. BFL 050* (MO, US); Canton Andranomava, District Soalala, 5 Feb 1956, *Réserves Naturelles 8634-RN* (MO, P, TAN, TEF). **Eriolaena linearifolia** (Hochr.) Dorr, **Madagascar**: **Antsiranana**: Dariana: Montagne de Français: vallée de l'Andavakoera, 24 Nov 1962, *Capuron 20920-SF* (K, MO, NY, P barcodes P00547756 [image] & P00547757 [image]); P.K. 8 de la route Diégo-Suarez-Orangea, 13 Feb 1964, *Capuron 23237-SF* (BR, K, MO, NY, P barcode P00547755 [image]); Montagne des Français, Diego, 16 Mar 1950, *Service Forestier 1285-SF* (P barcodes P00044704 [image], P00044705 [image] & P00044706 [image]). **Eriolaena lushingtonii** Dunn (see text). **Eriolaena madagascariensis** (Arènes) Dorr, **Madagascar**: **Toliara**: Route Nationale 7, 90 km NE of Tuléar, 25 Mar 1985, *Barnett & al. 505* (BR, MO, TAN, TEX); entre Antanimora et la vallée de l'Ikonda (sur la piste d'Imanombo), 24 Jan 1963, *Capuron 22492-SF* (BR, MO, P); Antanimora, Dist. Ambovombe, 28 Apr 1931, *Decary 8855* (BR, K, P, TAN); Route Nationale 7, 35.6 km E of Tuléar, 21 Mar 1985, *Dorr & al. 4111* (MO, TAN); Vallée du Fiherenana, à 30–35 km en amont de Tuléar, Mar 1934, *Humbert 14351* (BR, K, P, TAN); Environs d'Antanimora (Androy), 6–9 Feb 1955, *Humbert & Capuron 28830* (BR, K, P, TAN); 16 km N of Ejeda on Route National 10, 4 Feb 1990, *Phillipson & al. 3423* (K, MO, NY); Fivondronana de Fort-Dauphin, Réserve Naturelle Intégrale d'Andohahela, Parcelle No. 2, sur la piste vers Ambatoambo, 17 Mar 1994, *Randriambololona & al. 74* (BR, GH, MO, US); Ca. 4 km W of Vohitsara, on route between Ambatry and Beheloka, 20 May 2004, *Rogers & Rakotonasolo 505* (MO, US); Belio-Bekily, 15 May 1954, *Service Forestier 10295-SF* (A, P). **Eriolaena margaritae** Dorr (see text). **Eriolaena parvifolia** (Appleq.) Dorr, **Madagascar**: **Fianarantsoa**: PK 40 route Ihosy–Ivohibe, 22 Feb 1964, *Peltier & Peltier 4381* (MO); 10 km au NE d'Ihosy, entre Ihosy et Ambararata, 22 Feb 1970, *Capuron 29070-SF* (MO, P barcode P05350164, TEF); dans le bassin de la Menarahaka, près du carrefour des routes d'Ihosy à Ivohibe et Iakora, s.d., *Service Forestier 22630-SF* (BR, G, K, MO, NY, P barcodes P05350150 [image] & P05350173 [image], US barcode 00976669). **Mahajanga**: Environ de Morafenobe, 26 May 1955, *Service Forestier 14121-SF* (K, MO, NY, P barcode P05350136 [image]); Forêt d'Andranomazava, Antsiamala, Canton Ambaratra, district Befandriana, 12 Jun 1956, *Service Forestier 15772-SF* (BR, K, MO, P barcode P05350126 [image]). **Toliara**: Forêt de Analavelona, au N du Fiherenana, Mar 1934, *Humbert 14201* (P barcodes P05350167 [image], P05350168 [image], P05350169 [image], P05350170 [image]); Ambinda, 30 Mar 1966, *Peltier & Peltier 5767* (MO, P barcode P05350165 [image]); Analavelona–Tuléar, 2 Jun 1952, *Service Forestier 5260-SF* (MO, P barcode P05350172 [image]). **Eriolaena poissonii** (Arènes) Dorr, **Madagascar**: **Antsiranana**: Montagne des Français, 19 Apr 2007, *Bardot-Vaucoulon & Véné 1723* (K, MO, P barcode P00643269 [image]), *ibid.*, 26 Nov 1958, *Capuron 20105-SF* (BR, K, MO, P, TEF); Massif de la Montagne des Français, Sommet de l'Anosiravo, 13 Feb 1962, *Capuron 20915-SF* (K, MO, P, TEF); Montagne des Français, 26 Mar 2007, *Koopman & Razafitsalama 463* (MO, US); Commune Ramena, Fok. Ankorikakely, ca. 8 km from Diego on road to Ramena at base of Montagne des Français, 16 Feb 2005, *Schatz & al. 4325* (K, MO). **Eriolaena polyandra** (Appleq.) Dorr, **Madagascar**: **Antsiranana**: Antsiranana, Forêt d'Andranomadiro (rebord S du plateau de Sahafary, entre les bassins de la Saharenana et du Rodo [= Irodo]), 27 Dec 1963, *Capuron 23078bis-SF* (P barcode P00547704 [image]); Forêt d'Analafiana, au N de la basse Manambery (au SW de Vohémar), 11 Mar 1967, *Capuron 27516-SF* (K, MO, NY, P barcode P00547699 [image]); Massif du Bezavona (entre la Fanambana et la Manambery): pentes inférieures de la rive droite de l'Andilana, 20 Mar 1967, *Capuron 27540-SF* (K, MO, P barcode P00547701 [image]); Daraina, forêt de Bobankora, 5 Mar 2003, *Gautier & al. 4237* (MO, P barcode P06737947, US barcode 00976613). **Eriolaena pseudopopulus** (Baill.) Dorr, **Madagascar**: **Antsiranana**: Montagne des Français, vallon de l'Andavakoera, 2 Mar 1964, *Capuron 23245-SF* (A, K, MO); Ankarana, près d'Ambondromifely, 28 Apr 1966, *Capuron 24730-SF* (K, MO); Daraina, forêt de Bekaraoka, partie sud, en aval d'Andranotsimaty 15 Mar 2003, *Gautier & al. LG 4383* (K, MO); Pentes du lac Sacré près Anivorano Nord, 30 Jan 1960, *Humbert 32322* (K, MO); Mantamena, part of Bekaraoka Range, 7 km NE of Daraina (Vohémar), May 1990, *Meyers & Boltz 167* (MO, P, US); Sous-préfecture de Vohémar, Daraina, forêt de Bekaraoka, 14 Feb 2004, *Nusbaumer & Ranirison LN 1177* (K, MO); Diana Region, Mangoaka, Ankorefo, au bord de la route vers la forêt de la Montagne d'Ambre, 5 Jun 2005, *Rakotonandrasana & al. 910* (MO); Ankara, Diégo Suarez, 8 Aug 1952, *Service des Eaux et Forêts 5438-SF* (K, MO, P).

Appendix 2. Continued.

Eriolaena quinquelocularis (Wight & Arn.) Drury, **India: Madras:** Billigirirangan Hills, 1938, *Barnes* 316 (A); Madurai [sic] Dt., Amarathisagaraw [sic]-Lower Camp, 22 Jun 1968, *Deb* 20159 (US). **Tamil Nadu:** Nilgiris, s.d., *Beddome* 669 (BM); Mont Nilagiri, Bende-mara, Pr. Arrehatti, s.d., *Hohenacker* 1533 (BM, K, P barcodes P04759034, P06625567, P06625578 & P06625580, S-G-4110 [image], W); Mont Nilghiri & Kurg, 1859, *Hooker & Thomson s.n.* (BM, GH, P barcode P06625573, W); Kulhuty, Nellighery, 1840, *Perrottet* 330 (P barcode P06625568). ***Eriolaena richardii*** (Baill.) Dorr, **Madagascar: Antsiranana:** Commune Ramena, forêt près camp Orangea, 20 May 2004, *Andrianjafy & al.* 433 (MO, P barcode P06721424); Antsiranana-Ambilobe: Andranonakoho Réserve Spéciale d'Ankarana, forêt de Manapisanga, 13 Apr 2007, *Bardot-Vaucoulon & al.* 1678 (K, MO); Plateau calcaire du l'Ankarana, à l'Ouest d'Ambondromifely, 24 Apr 1963, *Capuron* 22694-SF (K, MO, P barcode P00547745); Massif de l'Ambongoabo, entre la baie de Diégo et celle du Courrier, 21 Apr 1966, *Capuron* 24644-SF (K, MO); Diego Suarez, S of Anivorano N, environs of Ambalabao, *Cheek & al.* B1408 (K, P); Ankarana Special Reserve, ca. 5 km NW of Park Village near Besaboboa stream, 25 Apr 1993, *Harder & al.* 1725 (MO, WAG [image]); Environ de Diégo-Suarez, Montagne des Français, Mar 1962, *Keraudren* 1646 (K, MO); Montagne des Français, Diégo-Suarez, 12 Jul 1955, *Service Forestier* 15061-SF (K, MO, P). ***Eriolaena rigida*** (Baill.) Dorr, **Madagascar: Antsiranana:** Ambilobe, Mahamasina Réserve Spéciale d'Ankarana, chemin d'Ambohimalaza, 28 Mar 2007, *Bardot-Vaucoulon & al.* 1587 (K, MO, P barcode P00643108 [image]); Montagne des Français, 8 May 2007, *Bardot-Vaucoulon & Véné* 1777 (K, MO, P barcode P00643328 [image]); Plateau calcaire de l'Ankarana, à l'Ouest de Mahamasina (Antanatsimanaja), 23 Apr 1963, *Capuron* 22680-SF (K, MO, NY, P barcodes P05350161 [image], P05350162 [image] & P05350163 [image]); Plateau calcaire de l'Ankarana, à l'Ouest d'Ambondromifely, 24 Apr 1963, *Capuron* 22697-SF (BR, K, MO, NY, P barcode P00547747 [image]); au Sud de Marotaolana (Anivorano-Nord), 27 Apr 1966, *Capuron* 24719-SF (K, MO, NY, P barcode P00547751 [image]); Ankarana, following the dry river Apondrabe close to Mahamasina, 27 May 1999, *De Block & al.* 1064 (MO, P); Mantamena, part of Bekaroaka Range, 7 km NE of Daraina (Vohemar), Faritany Antsiranana, Apr 1990, *Meyers & Boltz* 107 (K, MO, US barcode 00976670); Diana Region, Andranovondronina, Antsiskala, à l'Ouest d'Ampasikely, 13 May 2005, *Ramananjanaahary & al.* 272 (MO, P barcode P05350108 [image]); Daraina, forêt de Bekaroaka, 14 Feb 2004, *Ranirison & Nusbaumer* PR 447 (MO, P barcode P04642198 [image]); Montagne des Français, forêt d'Antaolanaomby, 22 May 2007, *Ratovoson & al.* 1228 (MO, US barcode 00976885); District d'Ambilobe, Canton de Mahamasina, N de Mahamasina, Réserve Spéciale d'Ankarana, 14 Jun 1995, *Razafimandimbison & Andrianantoanina* 79 (US barcode 0977109); Montagne des Français, Diego-Suarez, 25 May 1955, *Service Forestier* 14228-SF (MO, P barcode P05350148 [image]). **Mahajanga:** Bords de l'Anjobona (Boeny), Aug 1905, *Perrier de la Bâthie* 5535 (G, K, P barcode P05350144 [image]); Bemarivo (Boïna), Aug 1907, *Perrier de la Bâthie* 12163 (P barcode P05350143 [image]); Bord du rivièr Marofototra, sur la route de Befandriana-Nord–Ambararata, Dt. de Befandriana, 4 Jun 1951, *Service Forestier* 3570-SF (K, P barcodes P05350132 [image] & P05350133 [image]). ***Eriolaena rulkensii*** Dorr (see text). ***Eriolaena spectabilis*** (DC.) Planch. ex Mast., **Bhutan: Wangdue Phodrang:** Nahi to Wangdu Phodrang, 29 May 1938, *Gould* 292 (K). **China: Guangxi:** Tian'e Xian: Xinlin, *Qin Hai-ning & al.* 893127 (K). **Yunnan:** Ad viam Yunnanfu-Dali (Talifu), 30 Apr 1916 (fl), v. *Handel-Mazzetti* 8649 (A, W); Mampen, Red River, s.d., *Henry* 11503 (K barcode K000380334, NY); Szemao, s.d., *Henry* 12506 (A, K barcode K000380336, NY), *ibid.*, *Henry* 12506A (K barcode K000380338, MO, US); Yunnan, s.d., *Henry* 12506B (NY, US). **India: Maharashtra:** Khandala, Sausages above Forebay, 23 May 1952, *Santapau* 440 (MO); Flora of Manipur (on the eastern frontier of India), Karongte, 18 May 1992, *Watt* 7140 (K, P barcode P06625575 [image]); Botunda Ghat, 13 May 1848, *Shurtleff Herbarium* 22 (NY). **Without precise locality:** E. Indies, s.d., *Hook.* 807 (W); East Bengal, s.d., *Herb. Griffith* 572/1 (GH, P barcode P06625554). **Myanmar:** Maymyo Plateau, 22 Apr 1910, *Lace* 5202 (K barcode K000380324 [image]). **Nepal:** “Nepalia”, s.d., [*Wallich*] *Cat. n.* 1173/1 (G barcode G00358604 [image], K, M barcode M0209773 [image]); “E Napalia”, 1819, *Sine col., s.n.* (MO barcode MO-1620495). **Cultivated specimens:** **India:** Hab. Nepaul, 1863, *Crescit* in H. B. Calc., *Herb. Pierre* 5484 (P barcode P06625571 pro parte). “Mauritius or Madagascar”, s.d., Mr. Justice *Blackburn s.n.* (GH, NY). ***Eriolaena sphaerocarpa*** (L.C.Barnett) Dorr, **Madagascar: Antsiranana:** Versant E du Massif de l'Ankarana (partie S du massif de Mafokovo) (au N de Vohémar), 17 Dec 1966, *Capuron* 27349-SF (K, MO, P barcode 00552816); Commune: Mahavanona, Fokontany: Andranomanitra, Ampitiliantsambo, à 15 km au NE d'Andranomanitra, 14 Jun 2004, *Rakotondrafara & al.* 268 (MO, P barcode 06721430); Montagne des Français, Diégo Suarez, 11 Sep 1952, *Service Forestier* 5673-SF (K, P barcodes P00552817 & P00552818). ***Eriolaena stocksii*** Hook.f. & Thomson ex Mast. (see text). ***Eriolaena wallichii*** DC., **India: Uttar Pradesh:** Flora of Upper Gangetic Plain, District Gonda (Oudh), 31 May 1898, *Harsukh* 21634 (K); Forests North Oudh, 1870, *Thomson* 32 (K). **Without precise locality:** 1862 (fl), “Donné par la *Comp^{te} des Indes*” 573/1 (P barcode P06625561); “573/1, *Herb. E. Ind. Society*” (GH); Suranaghur, s.d. (fl), *Herb. Hamilt.* [*Wallich*] *Cat. N.* 1174b (K); Ind. Or., s.d., *sine coll.* (K barcode 000380327). **Cultivated specimens:** **India:** Hort. Bot. Cal., 1866, *Anderson* 28 (P barcode P06625562); Jardin Bot., 1837, *Gaudichaud ex Wallich* 190 (P barcodes P06625564 & P06625566); Cult. in hort. Bot. Calcuttensis, Hab. Nepaul, 1863, *Pierre* 3760 (A, BM, K, L 2D-barcode L2380381 [image]); A tree introduced by Col. Thos. Hardwicke, 1811, HBC. 1845 [sic], *no.* 801 (BM). **Trinidad & Tobago:** Trinidad, Botanic Gardens, 7 Jul 1928, *Broadway* 6989 (K, US); Royal Botanic Garden, Port of Spain, 29 Jul 1966, *Nevling, Jr.* 320 (A).