REVISED CIRCUMSCRIPTIONS OF *SPHEDAMNOCARPUS* AND *PHILGAMIA* (MALPIGHIACEAE)

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Abstract. Ongoing phylogenetic investigations of the large and diverse plant clade Malpighiaceae have clarified many novel phylogenetic relationships. Results from these insights in turn have necessitated reconciling the taxonomy of numerous genera in the family. Our recent findings indicate that the genera *Sphedamnocarpus* and *Philgamia*, which collectively represent a single paleotropical clade of Malpighiaceae whose species occur in Africa and Madagascar, are not monophyletic as currently circumscribed. Here, we resolve each of these genera as monophyletic. This involves reducing the composition of *Sphedamnocarpus* to include only the African members of this genus and expanding *Philgamia* to include the Malagasy members of this clade, including former species of *Sphedamnocarpus* which compose this island radiation. In addition to geography, morphology plays an important role in justifying these divisions, which we detail here as further justification for our reclassification of these genera.

Keywords: Island endemism, taxonomy, systematics, stigmaphylloid clade

Malpighiaceae are a monophyletic angiosperm family (Chase et al., 2002; Davis and Chase, 2004; Wurdack and Davis, 2005; Davis and Anderson, 2010), whose species exhibit a pantropical distribution and a rich evolutionary and biogeographic history (Anderson, 1979; Vogel, 1990; Davis, 2002; Davis, Bell, Fritsch, et al., 2002; Davis, Bell, Mathews, et al., 2002; Davis et al., 2004; Zhang, Kramer, and Davis, 2010, 2012, 2016; Zhang et al., 2013; Davis et al., 2014; Cai et al., 2016). The center of diversity for the ~1300 species in 77 genera in this clade are the Neotropics (Anderson, 2004), although ~19% of species in Malpighiaceae (~250 spp./ 17 genera) are found in the Paleotropics, the result of at least 7 independent dispersal events from the Neotropics (Davis, Bell, Mathews, et al., 2002; Davis and Anderson, 2010; Cai et al., 2016). The family consists of trees, shrubs, and vines characterized by their simple, often opposite leaves, modified unicellular hairs, and five-petaled flowers that possess distinctly clawed petals. Most neotropical Malpighiaceae bear conspicuous paired oil glands at the base of their sepals and are implicated in specialized pollinator mutualisms with oil bees (Vogel, 1974; Anderson, 2004; Davis et al., 2014). In contrast, most paleotropical lineages, like *Sphedamnocarpus* Planchon ex. Bentham & Hooker (1862: 256) and *Philgamia* Baillon (1894: 265), exhibit a suite of floral characters that depart from the canonical New World Malpighiaceae floral morphology (Davis, 2002; Davis et al., 2014), including eglandular sepals and reduced zygomorphy.

Over the last 20 years, phylogenetic investigations in Malpighiaceae have revealed traditional generic concepts based on fruit type utilized by Niedenzu (1928) to be misleading for representing evolutionary relationships (Cameron et al., 2001; Davis, Anderson, and Donoghue, 2001; Davis, 2002; Davis et al., 2004; Davis and Anderson, 2010). These insights have prompted extensive taxonomic changes to the family, especially among genera (Anderson and Davis, 2005, 2006, 2007; Anderson, 2011).

One such example, and the focus of our present study, involves members of the informally designated stigmaphylloid clade *sensu* Davis and Anderson (2010), which, among others, includes the two paleotropical genera *Sphedamnocarpus* and *Philgamia*, whose species are distributed in Africa and Madagascar (Arènes, 1943a,b). These genera were delimited by Arènes based on their fruit type: *Philgamia* possesses a wingless nut often with a remnant dorsal crest where the samara wing would be found, as opposed to the conspicuous winged samaras of *Sphedamnocarpus*. As currently circumscribed, *Philgamia* is restricted to Madagascar, while the distribution of *Sphedamnocarpus* includes species in both Africa and Madagascar (Fig. 1).

In 1894, Baillon illustrated a single fruitless specimen of the species *P. hibbertioides* Baill. (P: P00048061). The genus was later formally described in 1908 by Dubard & Dop., remaining monotypic until 1943 when Arènes added three species to the genus: *P. brachystemon* Arènes, *P. denticulata* Arènes, and *P. glabrifolia* Arènes (Arènes, 1943a). Arènes also was the first to describe the unique wingless fruits of this genus. Both he (1943a) and William Anderson (pers. comm.) remarked on the restricted distribution of species in this genus, which only inhabit quartzite outcrops in central Madagascar. Edaphic variation is known to influence plant diversity, and unique soil types are associated with high rates of endemism (Lichter-Marck et al., 2023).

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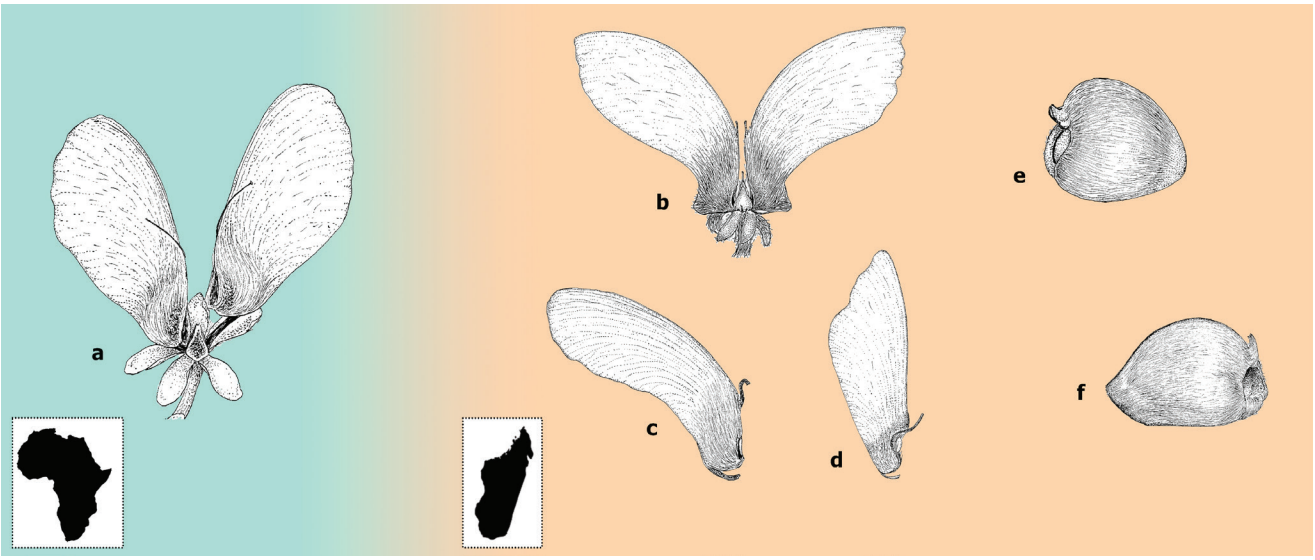

FIGURE 1. Fruit types in *Sphedamnocarpus* and *Philgamia*. **A**, *S. angolensis*; **B**, *S. poissonii*; **C**, *S. andersonii*; **D**, *S. dubardii*; **E**, *P. glabrifolia*; **F**, *P. hibbertioides*. Background colors indicate geographic distributions. Illustrations by Karin Douthit, adapted with permission from University of Michigan Malpighiaceae Nomenclature website (http://malpighiaceae.herb.lsa.umich.edu/nomhome.html).

The taxonomic history of *Sphedamnocarpus* is, in contrast, more dynamic. The genus was first published in 1862 by Bentham & Hooker and consisted of up to three species originally described as *Acridocarpus* by Adrien de Jussieu—likely *A. angolensis* A.Juss., *A. pruriens* A.Juss., and *A. argyrophyllus* A.Juss. Jussieu described these in particular as "three-styled" and indicated his uncertainty about their placement in the genus (Jussieu, 1843; Bentham & Hooker, 1862). The type species, *S. angolensis* (A. Juss.) Planch. ex. Oliv., was later published by Oliver in 1868, with a reference to Jussieu's *A. angolensis*. However, since Jussieu included no type specimen in his description, Oliver (1868) designated a lectotype for the species.

The first published Malagasy species in *Sphedamnocarpus* was *S. madagascariensis* Baker in 1884. This species was originally published by Jussieu as *Banisteria multiflora* Bojer mss., and Jussieu did highlight morphological similarities of his *Banisteria multiflora* to the "three-styled" and dubious species of *Acridocarpus* he published, expressing his doubts that the genera were distinguishable. Baker used the epithet *madagascariensis* rather than *multiflorus* for his publication because in 1924, almost 20 years before Jussieu's monograph of the Malpighiaceae, de Candolle published a different *Banisteria multiflora*, which was endemic to the neotropics (de Candolle, 1824).

Jussieu's four contentious paleotropical species were united together under *Sphedamnocarpus* when Niedenzu treated the genus in 1924. He recognized seven species, three of which were endemic to Madagascar: *S. argyrophyllus* Ndz., *S. multiflorus* (Juss.) Ndz., and *S. hibbertioides* (Baill.) Ndz. A notable expansion of *Sphedamnocarpus* was later published by Arènes as a part of his floristic treatment of the Malpighiaceae of Madagascar in 1943, in which he recognized 12 species on the island, many of them novel. He kept only one of Niedenzu's Malagasy designations (*S. multiflorus*) and transferred the others to different genera: *S. argyrophyllus* Ndz. became *Microsteira argyrophylla* (Juss.) Dub. et Dop, while *S. hibbertioides* (Baillon) Ndz. became *Philgamia hibbertioides* Baillon (Arènes, 1943b). Arènes recognized two more Malagasy species in this genus during the following several years (Arènes, 1946, 1947). He was the last researcher to publish a treatment of this genus. A most recent species from Madagascar was published in 2018, *Sphedamnocarpus andersonii* C.E. Anderson. For the species of *Sphedamnocarpus* found on continental Africa today, there is a history of taxonomic changes and shifting infraspecific arrangements, especially in *S. pruriens*, which may indicate the existence of a species complex that warrants further investigation of phenotypically and geographically variable populations with modern methods (de Villiers and Botha, 1986).

MATERIAL AND METHODS

DNA extraction, library prep, sequencing

We isolated total genomic DNA from 0.01–0.02 g of herbarium collections using the Maxwell® 16 DNA Purification Kit (Promega Corporation, Inc., Madison, Wisconsin, U.S.A.). DNA integrity and concentration were checked on a 4200 TapeStation System using D5000 ScreenTape (Agilent Technologies, Inc., Waldbronn, Germany). Genomic libraries were prepared using ca. 70 ng of genomic DNA where possible. For library preparation, we used the KAPA HyperPlus DNA library prep with IDT TrueSeq barcodes (Integrated DNA Technologies, Inc., IO, USA) and Nextflex-Ht barcodes (Bioo Scientific Corporation, Texas, U.S.A.). We fragmented DNA to an average of 350–400 base pairs (bp) and indexed for Illumina multiplex sequencing. We verified the DNA concentrations and fragment sizes of these libraries using the Qubit dsDNA HS Assay Kit on a Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, California, U.S.A.) and the 4200 Agilent

Tapestation system (Agilent Technologies, Inc., Waldbronn, Germany). All total genomic DNA libraries were pooled in equimolar rations and sequenced with the Illumina Hi-Seq 5000 (Illumina, Inc., San Diego, California, U.S.A.) at the Bauer Core Genomics Sequencing Core Facility at Harvard University, Cambridge, Massachusetts, U.S.A., which resulted in 125 bp paired-end reads. The genome skimming pipeline we applied is described by Weitemier et al. (2014).

Reads curation, assembly, and annotation

Raw reads were filtered with FastQC V0.10.1 to remove reads with average Phred scores lower than 30 (Andrews, 2010). We further trimmed the adaptors and filtered homopolymer (threshold 95%) using ea-utils and PRINSEQ-lite v0.20.4, respectively (Aronesty, 2011; Schmieder and Edwards, 2011). All reads shorter than 33 bp after trimming were discarded for downstream analysis. Plastid genome and nuclear rDNA assembly was conducted in GetOrganelle v1.7.7 (Jin et al., 2020). We used the built-in database from GetOrganelle for both assemblies and applied a wide range of kmer sizes (k = 21, 35, 55, 85, 95) to accommodate for variations in sequence coverage.

Ortholog identification and phylogenetic reconstruction

Ortholog identification was conducted using the *PhyloHerb* bioinformatic pipeline (Cai et al., 2022). Output orthologous sequences were aligned using PASTA v1.8.5 to accommodate the high sequence variation of intergenic regions (Mirarab et al., 2015). A draft maximum likelihood (ML) phylogeny was subsequently inferred from the concatenated sequences in IQTREE v2.2.2 under the default settings to facilitate manual curation of alignments (Nguyen et al., 2015). We visualized the alignment in Geneious Prime R9 (https://www.geneious.com/) to remove erroneous sequences such as paralogs. These filtered sequences were aligned in PASTA again using the ML phylogeny as the guidance. The resulting alignments were reordered and manually examined in Geneious again to remove misaligned regions. The curation of the ribosomal DNA sequences (partial ETS–18S–ITS1–5.8S–ITS2–28S) followed a similar procedure.

To infer a phylogeny based on the plastid and nuclear genes, an optimum partition scheme was determined using the AICc information criterion and the 'rcluster' search algorithm in PartitionFinder v2 (Lanfear et al., 2016). Phylogenies for individual locus, concatenated plastid loci, and combined plastid-rDNA loci were then inferred using the optimum partition and the GTR+GAMMA model with 1000 ultrafast bootstrap replicates in IQTREE (Minh et al., 2013). The phylogeny inferred from the combined plastid-rDNA dataset was used for downstream analyses. Sequence data for the species examined in this study are available in GenBank, accessions PP792599–PP792610.

Species Range Evaluations

For each species in our tree, as well as all species published but not included in our sampling, we evaluated ranges based on data available from Kew Plants of the World Online (POWO) and the type localities. Each species was scored as either African or Malagasy if its range was limited to continental Africa or Madagascar and Mauritius, respectively. There were no species with a range that spanned both of these geographic areas.

Specimen Examination

To assess morphological variation in *Sphedamnocarpus* and *Philgamia*, we used a multi-pronged approach, including examination of herbarium specimens in person at HUH, high-definition photos of specimens from multiple herbarium databases online, and data from GBIF (https://www.gbif.org/) and iNaturalist (https://www.inaturalist.org/), including photos of plants in the field. Supplemental photos for the Malagasy species were shared by Marcelo Pace, David Boufford, and Wenheng Zhang. All specimens or field photos reviewed were scored by geography (island or mainland). See Appendix I for a complete list of specimens examined.

At first, available specimens were reviewed in person to identify morphological differences between the island and mainland clades. After putative morphological differences between the clades were identified (see Results and Discussion), more specimens and photographs from the field were examined virtually, including the type specimens for each species. When syntypes existed but not a holotype, a lectotype designation was made. It was observed from field photographs of living flowers that styles that project beyond the staminal ring in the horizontal plane are abundant in African species, but not present in the Malagasy species. This trait was not always immediately apparent in dried and pressed herbarium specimens. For the Malagasy species that generally lacked many photographs of living flowers, dried flowers were extracted from available specimens at HUH, boiled and observed under a microscope to determine style orientation. Although the structural integrity of the flowers is diminished after drying and pressing, these characters were still observed and recorded (Fig. 2).

Results and Discussion

Our recent and ongoing phylogenomic investigations in Malpighiaceae reveal that *Sphedamnocarpus* and *Philgamia* are not monophyletic as currently circumscribed (Fig. 3), necessitating a recircumscription of these genera. On the basis of our results, which include both geographic and morphological evidence to support our phylogenetic findings, we propose merging the Malagasy *Sphedamnocarpus* with the genus *Philgamia* and recognize a greatly reduced *Sphedamnocarpus*, whose species are restricted to Africa. This ensures the reciprocal monophyly of both genera and recognizes an endemic island lineage in Madagascar, which exhibits among the highest rates of species endemism in the world (Antonelli et al., 2022).

Geography, not fruit type, appears to be a much better arbiter of monophyletic species groups in this clade. Here, our analyses identify two subclades, one restricted to mainland Africa, including only species of *Sphedamnocarpus*, and a second confined to Madagascar, which includes members of both *Sphedamnocarpus* and *Philgamia* (Fig. 3).

Examinations of herbarium specimens revealed that

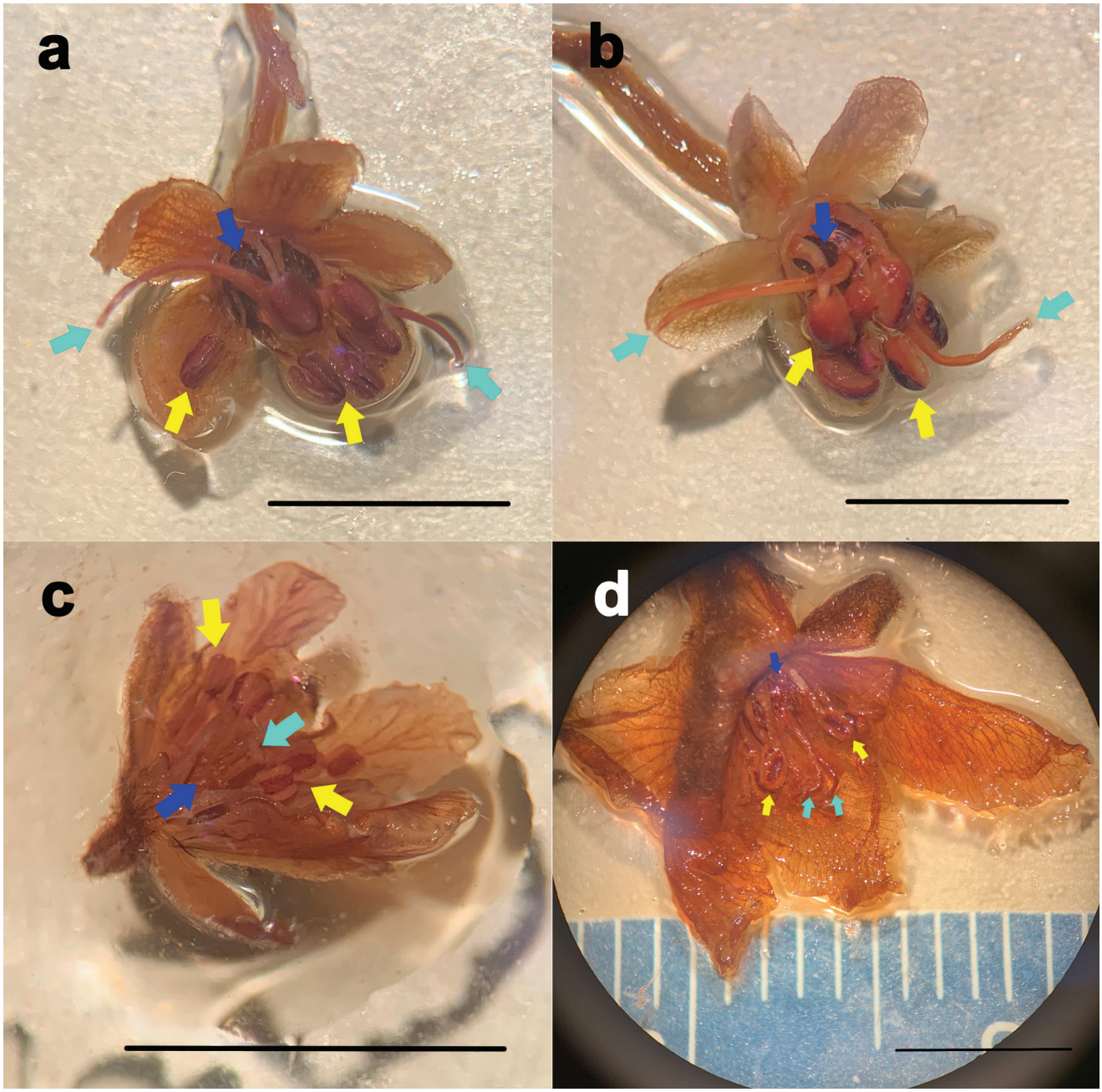

FIGURE 2. Flowers examined for investigation of morphological differences between mainland (**A, B**) and island (**C, D**) clades. Dark blue arrows indicate ovaries, light blue indicate styles, and yellow indicate anthers. **A**, *S. angolensis* (A.Juss.) Planch. ex. Oliv., based on *F. A. Rogers 13095*; **B**, *S. galphimiifolius* (A.Juss.) Szyszył., based on *Werdermann & Oberdieck 1938*; **C**, *P. glabrifolia* Arènes, based on *Zhang et. al. 129*; **D**, *S. humbertii* Arènes, based on *Phillipson et al.* 5840. Scale bars = 5.0 mm. All specimens cited in Appendix I.

continental and island lineages differ in their inflorescence and floral morphology. In both groups, flowers are umbellate and emanate in bunches, often in groups of three or four, from a node that is subtended by visible bracts. In the African *Sphedamnocarpus*, flowers are borne on a pedicel which is subtended by two bracteoles, a floriferous peduncle, and a bract (Fig. 4a–b). In contrast, the Malagasy specimens observed lack a floriferous peduncle, with bracteoles often hidden behind the bracts (Fig. 4e–f). The presence/absence of the floriferous peduncle is the most salient observable difference between these subclades and provides further support to the phylogeny for delimiting these two genera by geography.

Examinations of the flowers themselves revealed differences in style morphology across these two clades. Members of the African clade have flowers with longer, horizontally oriented styles that extend out beyond the staminal ring in the horizontal plane (Fig. 4c–d). The Malagasy clade's members exhibit shorter, vertically oriented styles that remain within the staminal ring in the horizontal plane (Fig. 4 h–j).

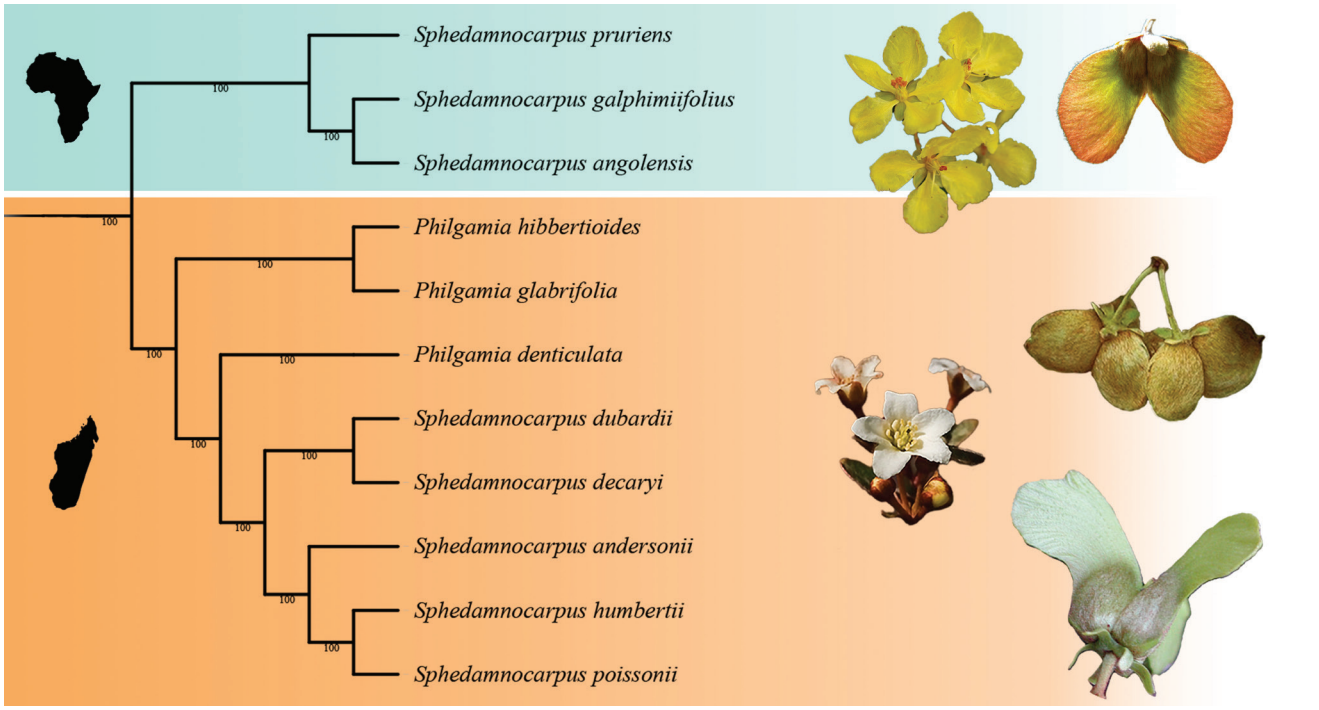

FIGURE 3. Maximum likelihood tree built with chloroplast genomes and nuclear DNA showing hypothesized evolutionary relationships between members of *Sphedamnocarpus* and *Philgamia* and revealing non-monophyly of both genera. Background colors indicate geographic distributions. Photographs from top to bottom, left to right: *S. pruriens* flower by Andre Harmse (https://www.inaturalist.org/observations/183058148); *S. pruriens* samara by JMK (https://en.wikipedia.org/wiki/Sphedamnocarpus#/media/File:Sphedamnocarpus_pruriens,_samara,_a,_Groenkloof_NR.jpg), *P. glabrifolia* fruits by G. E. Schatz (https://www.mobot.org/MOBOT/research/conspectus/malpigh.shtml), *P. hibbertioides* flowers by Fabien Rahaingoson (https://www.inaturalist.org/observations/10848867), *S. andersonii* fruits by Thomas Daniel (adapted from Anderson 2018 with permission).

In light of our results, we suggest that the Malagasy species of *Sphedamnocarpus* be transferred to *Philgamia* and list below the new combinations that we propose. To be as thorough as possible in our nomenclatural revisions, we used the names proposed by Arènes when he last treated the genus. Presently, the Missouri Botanical Gardens' Catalogue of the Plants of Madagascar (http://legacy.tropicos.org/Project/Madagascar) has combined many of the species concepts in *Sphedamnocarpus*, suggesting Arènes may have split them too finely. A fresh treatment of this group would help to resolve the issue of which species concepts best reflect biological reality.

To summarize, this study is part of a larger effort to refine the taxonomy of Malpighiaceae using new phylogenetic evidence. We propose a merging of the Malagasy members of the genus *Sphedamnocarpus* with the genus *Philgamia* and support this proposal with phylogenetic, geographic, and morphological evidence. In contrast to traditional generic delimitations founded on fruit morphology in the Malpighiaceae, our study groups together species with differing fruit morphologies. Future studies in this clade may explore the evolution of fruit type in the newly defined *Philgamia*. Additionally, notes of the late William Anderson point out that some of the Malagasy species may exhibit cryptic dioecy based on his observations of the size, shape and development of anthers and carpels across species (C. E. Anderson, pers. comm.). This is another avenue for potential future investigations of this island radiation to explore. Finally, our study did not address the taxonomy of the African *Sphedamnocarpus*, the sister genus to *Philgamia*. The existence of sympatric species, as well as sympatric subspecies with histories of taxonomic shifting, indicate this clade could benefit from more intensive studies that include phylogenetic data.

NEW COMBINATIONS PROPOSED

Philgamia ambovombensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*

Basionym: *Sphedamnocarpus ambovombensis* Arènes (1943b: 108).

TYPE: MADAGASCAR. Ambovombe District, Antanimora; 23 October 1924, *Decary 3278* (Holotype: P [P00048031], Isotype: P [P00048032]).

Philgamia andersonii (C.E. Anderson) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*

Basionym: *Sphedamnocarpus andersonii* C.E. Anderson (2018: 248).

TYPE: MADAGASCAR. Ihorombe Region: Isalo National Park, vicinity of Mangily and Tombeaux Bara on trail to Piscine Naturelle, ca. 4 km SW of Ranohira, ca. 850 m, 22°33'72"S, 45°22'95"E, 9 March 2007, *T. F. Daniel 11025* (Holotype: MICH [1566012]; Isotype: CAS [692699]).

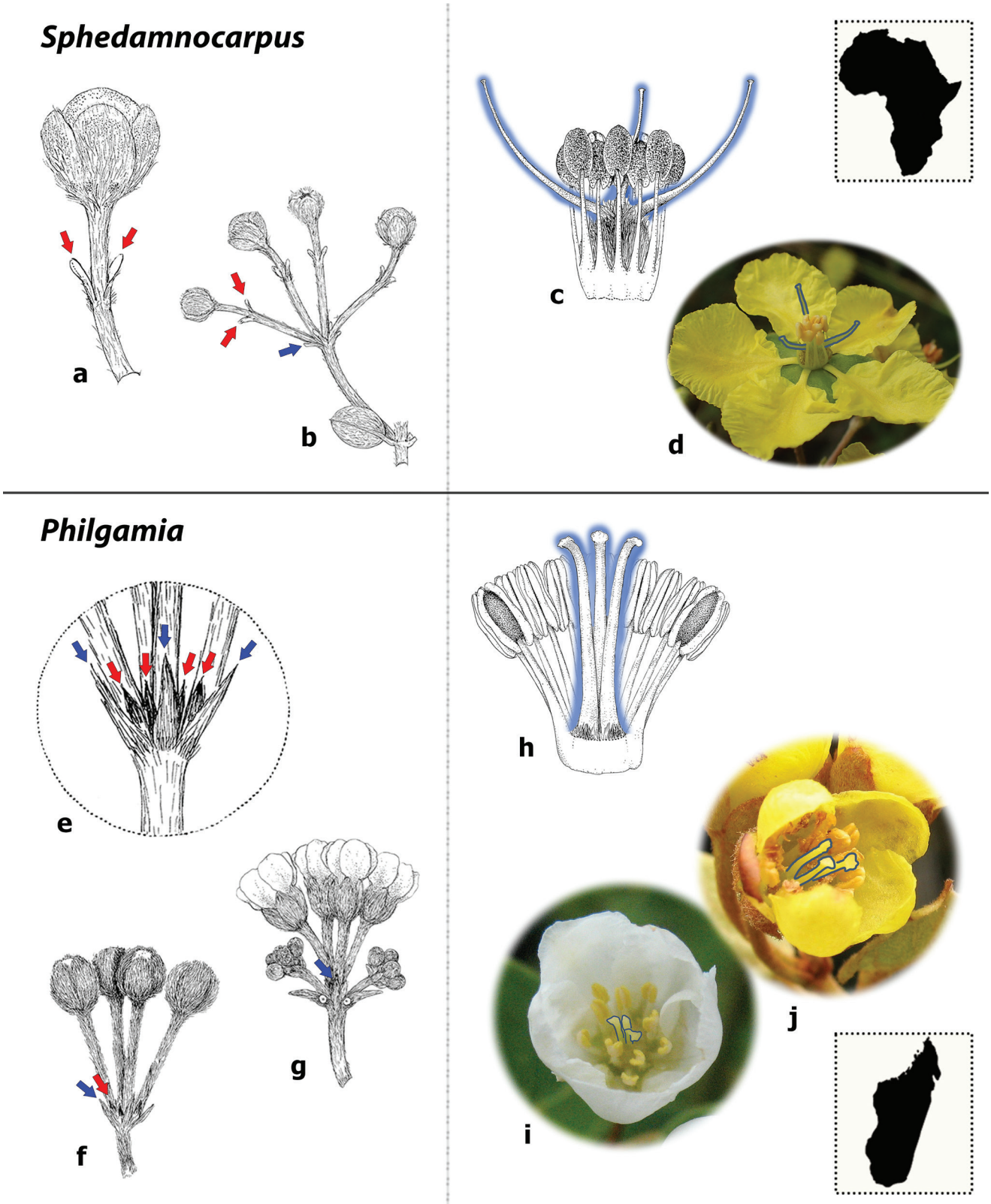

FIGURE 4. Morphological differences between the mainland (*Sphedamnocarpus*) and island (*Philgamia*) clades, highlighting inflorescence morphology on the left and floral morphology on the right. Red arrows indicate bracteoles and blue arrows indicate bracts. **A**, flower bud of *S. angolensis*; **B**, inflorescence of *S. angolensis*; **C**, reproductive parts of *S. angolensis*, with styles highlighted in blue; **D**, photograph of *S. pruriens* flower with gynoecium outlined in blue; **E**, close-up umbel base of *P. glabrifolia*; **F**, inflorescence of *P. glabrifolia*; **G**, inflorescence of *S. andersonii*; **H**, reproductive parts of *S. dubardii*, with styles highlighted in blue; **I**, photograph of *Philgamia sp.*; **J**, photograph of *S. dubardii* flower, with styles outlined in blue. Illustrations adapted from an unpublished drawing by Karin Douthit with permission from the University of Michigan Herbarium (http://malpighiaceae.herb.lsa.umich.edu/nomhome.html).

Philgamia coursii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus coursii* Arènes (1944: 185).
TYPE: MADAGASCAR. Alaotra-Mangoro region, Ambatondrazaka district, Alaotra station, 780 m, December 1937, *G. Cours 1413 (S-195)* (Holotype: P [P00048033]).

Philgamia cuspidifolia (Arenés) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus cuspidifolius* Arenés (1946: 184–185).
TYPE: MADAGASCAR. Boeny Region, Ankarafantsika (7th Reserve), Bevasaka, sandy plateau, 200 m, *Service Forstier* [Forest Service] *71* (Holotype: P [P00048034]; Isotype: P [P00048035]).

Philgamia decaryi (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus decaryi* Arènes (1943b: 109).
TYPE: MADAGASCAR. Ranopiso, District of Fort Dauphin, in the Savoka, July 1932, *R. Decary 10193* (Lectotype [designated here]: P [P06170053]; Isolectotypes: P [P06170059], [P06170054]).

Philgamia dubardii (Viguier & Humbert ex Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Tricomariopsis madagascariensis* Dubard (1907: 1191), *Sphedamnocarpus dubardi* Viguier & Humbert ex Arènes (1943b: 101).
TYPE: MADAGASCAR. Analamanga Region, Mandraka Forest, *d'Alleizette 476* (Holotype: P [P00048039]; Isotype: P [P00048040]).

Philgamia heterophylla (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus heterophyllus* Arènes (1947: 108).
TYPE: MADAGASCAR. Androy Region, Ampandrandava, east ridge, 1000 m, *Seyrig 527* (Holotype: P [P00048044]).

Philgamia humbertii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus humbertii* Arènes (1943b: 113).
TYPE: MADAGASCAR. Anosy Region, reception basin of the Mananara, tributary of the Mandraré, western slopes of the mountains between Andohahela and Elakelaka, between Ampahiso et Mahamavo (gneiss), 400–700 m, January–February 1934, *Humbert 13707* (Lectotype [designated here]: P [P00413515]; Isolectotypes: P [P00413516], [P00413517]).

Philgamia madagascariensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Banisteria multiflora* Bojer ex A. Juss. (1840: 286), non *B. multiflora* DC. (1824), *Sphedamnocarpus madagascariensis* Baker (1884: 110), *Banisterioides madagascariensis* Dubard & Dop (1908: 356), *Triaspis chrysophylla* Nied. (1915: 21), *Sphedamnocarpus multiflorus* (Bojer ex A. Juss.) Nied. (1924: 16).
TYPE: MADAGASCAR. Near Mazangay. *Bojer s.n.* (Holotype: P [P00048045]).

Philgamia orbicularis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus orbicularis* Arènes (1943b: 112).
TYPE: MADAGASCAR. Amoron'i Mania Region, woods-quartzites, 600 m, March 1919, *Perrier de la Bâthie 12537* (Holotype: P [P00048046]; Isotype: P [P00048047]).

Philgamia perrieri (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus perrieri* Arènes (1943b: 116).
TYPE: MADAGASCAR. Alaotra-Mangoro Region, between Andilamena et Mandritsara, forest, 900 m, November 1921, *Perrier de la Bâthie 14999* (Holotype: P [P00048048]; Isotypes: P [P00048049], [P00048050]).

Philgamia poissonii (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus poissonii* Arènes (1943b: 114).
TYPE: MADAGASCAR. Former Toliara Province, route from Sakaména to Ejeda, 11 April 1922, *Poisson 442* (Holotype: P [P00048051]).

Philgamia vohitrotsyensis (Arènes) Kehoe, C. Davis, & J.T. Williams, *comb. nov.*
Basionym: *Sphedamnocarpus vohitrosyensis* Arènes (1943b: 107).
TYPE: MADAGASCAR. Anosy Region, middle valley of Mandrare, near Anadabolava, Mount Vohitrotsy, 800–850 m, December 1933, *H. Humbert 12725* (Holotype: P [P00048052]; Isotypes: P [P00048053], [P00048054]).

Author Contribution Statement

C.D., J.W., and J.K. developed the study. C.D., L.C., Y.Y., and X.D. collected and curated phylogenetic data with methods they developed. J.K., L.C., and C.D. analyzed and interpreted the phylogenetic data for species included in this study. J.K. and J.W. conducted taxonomic research. J.K. examined all herbarium specimens. J.K. and C.D. wrote the main text. J.K. produced all figures and nomenclatural changes with input from C.D. and J.W.

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Appendix I

Specimens Examined

Philgamia brachystemon Arènes
MADAGASCAR. Amoron'i Mania Region, Fianarantsoa. Ambositra. Ihadilaganana, Ambohipiandrianana-Ambohibary- Montage d'Ambatonanahary. Végétation sur substrat quartzitique. 20°26'43"S 047°03'42"E; 1303 m, 04 November 2014, *S. Andriambololonera, Tefy Andriamihajarivo & Fortunat 309* (GH).

Philgamia glabrifolia Arènes
MADAGASCAR. Fianarantsoa Province: Mt. Ibity. On ridge across valley from limestome quarry and cement plant. 20°3'55"S, 47°0'3"E; 1660-1680 m, 20 January 2008, *W. H. Zhang, J. Andrianatina & D. E. Boufford 129* (AA).

Sphedamnocarpus angolensis (A.Juss.) Planch. ex. Oliv.
ZIMBABWE. Salisbury [Harare]. December 1913. *F. A. Rogers 13095* (AA).

Sphedamnocarpus decaryi Arènes
MADAGASCAR. Anosy: Environs de Fort Dauphin [Tolagnaro]. 1–25 m, 20 September–6 October 1928. *H. Humbert 5714* (AA).

Sphedamnocarpus galphimiifolius (A.Juss.) Szyszył.
SOUTH AFRICA. Transvaal: Soutpansberg, Willies Port, Louis Trichardt; 900–1000 m, 21 January 1959, *E. Werdermann & H. D. Oberdieck 1938* (AA). Mariepskop, in undergrowth in forestry reserve on the road to Klaserie. 16 January 1959, *H. P. v. d. Schiff 4509* (AA).

Sphedamnocarpus humbertii Arènes
MADAGASCAR. Atsimo-Andrefana: N of Toliara, between Fiherenana and Manombo Rivers, Ranobe Forest. Ankilimalinike Commune. About 14 km inland from RN9 on norther seismic line. 22°57'16"S, 43°39'53"E; 115 m, 12 March 2006, *P. B. Phillipson, R. Ranaivojaona, N. M. Andrianjafy & R. A. Lubke 5840* (GH).

Sphedamnocarpus madagascariensis Baker
MADAGASCAR. Boeny: Environs de Majunga. Lieux sablonneux, dunes. 2–15 m, 28–30 July 1924. *H. Humbert 2038* (AA).

Sphedamnocarpus pruriens (A.Juss.) Szyszył.
NAMIBIA. Zwischen Grootfontein und Otavi. 1400 m, 2 March 1959. *E. Werdermann et H. D. Oberdieck 2405* (AA); Otavi. 7 February 1925. *K Dinter. 5550* (AA); SOUTH AFRICA. Guatang Province, Pretoria: E of the city of Pretoria at Plumbago Conservation area. 25°46'17"S, 28°17'46"E; 1425 m, 4 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 148* (AA); Makapan Valley, near Potgietersrus, Transvaal. Sourveld, very rocky steep grassland with scattered shrubs, ca. 1500 m, 7 April 1985, *M. Bourell 2755* (GH); Waterberge, zwischen Nylstroom und Warmbad, 1150–1250 m, 21 Jan 1959. *E. Werdermann et H. D. Oberdieck 2012* (AA); *Natal s.n.* (GH).

Sphedamnocarpus pruriens *var.* ***latifolius*** Engl.
BOTSWANA. 10 miles N of Molepolole, 11 June 1955. *R. Story 4874* (ECON); NAMIBIA. Cigarette, N. E. of Karakuwise, 11 Feb 1953. *B. Maguire 2477* (ECON); SOUTH AFRICA. Nelspruit [Mbombela], Transvaal, April 1920. *F. A. Rogers 23781* (AA).

Sphedamnocarpus rehmanii Szyszył.
SOUTH AFRICA. Zoutpansberg, 1936. *M C. Gillet 4747* (GH).

Sphedamnocarpus transvaalicus (Kuntze) Burtt Davy
SOUTH AFRICA. Gauteng Province, Pretoria: Slope on N side of Fort Klapperkop. 25°46'32"S, 28°12'30"E; 1490 m, 8 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 152* (AA); Gauteng Province, Pretoria: E of the city of Pretoria at Plumbago Conservation area. 25°46'14"S, 28°17'34"E; 1390 m, 4 February 2008. *W. H. Zhang, R. H. Archer & D. E. Boufford 149* (AA).

SPHEDAMNOCARPUS INDETERMINATE

Sphedamnocarpus sp., det. C. C. Davis. MADAGASCAR. Fiannarantsoa Province, Isalo National Park, NW side of road 600m southwest from park. 24°37'54"S, 45°21'22"E; 850 m, January 18, 2001. *Charles C. Davis 03-01* (AA).

Sphedamnocarpus sp. MADAGASCAR. Fianarantsoa Province: S of Isalo National PArk and NE of the town of Ilakaka on road to Toliara at Maison de l'Isalo geological park. 22°37'09"S, 45°21'41"E; 855 m, January 22, 2008. *W. H. Zhang, J. Andrianatina & D. E. Boufford 132* (AA).

Sphedamnocarpus sp. MADAGASCAR. Toamasina (Tamatave), Forêt de Mantady, N of graphite mines. Rain forest. 18°52'20"S, 48°29'60"E; 935 m, October 27, 1993. *F. I. van Nek 1989* (AA).