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Taxonomic Studies on Malagasy *Dalbergia* (Fabaceae). III. Two New Species from Southeastern Madagascar and an Emended Description of the Rosewood Species *Dalbergia maritima*

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Abstract—The Malagasy rosewood species *Dalbergia maritima* has a long history of unsustainable exploitation for its beautiful, burgundy-colored heartwood. As currently circumscribed, *D. maritima* has a wide geographic distribution in eastern Madagascar and exhibits significant morphological, ecological, and genetic variation, suggesting it may comprise more than a single entity. Multivariate analyses of leaf, flower, and inflorescence characters as well as eco-geographic features reveal several morphologically well delimited entities with distinct habitat preferences and/or geographic ranges, which are consistent with results from recent phylogenomic and population genomic studies of Malagasy *Dalbergia*. Based on these findings, we describe and illustrate two new species from southeastern Madagascar comprising material previously assigned to *D. maritima*, viz. ***D. pseudomaritima***, characterized by paniculate inflorescences and small, broadly elliptic to orbicular, glabrous leaflets, and ***D. razakamalalae***, distinguished by racemose inflorescences with large flowers, and narrowly ovate to narrowly elliptic, glabrous leaflets. *Dalbergia maritima* is consequently re-circumscribed to include only populations from east-central Madagascar, within which we recognize two subspecies, *D. maritima* subsp. *maritima*, with glabrous leaves, inflorescence axes, and gynoecia, occurring in littoral forest habitats, and ***D. maritima* subsp. *pubescens***, with indument on these structures, and growing in evergreen humid forest farther inland. Photos are provided for each taxon, along with line drawings for the two new species. Provisional IUCN Red List assessments indicate that all three species are Endangered, *D. maritima* and *D. razakamalalae* mainly because of selective logging for trade in their high-quality heartwood, and *D. pseudomaritima* primarily because of habitat degradation due to land clearing and fire for subsistence agriculture, which has important implications for their conservation and sustainable management.

Keywords—Bois de rose, IUCN Red List, Leguminosae, multivariate analyses, Volombodipony.

The genus *Dalbergia* L.f. (Fabaceae) encompasses ca. 270 currently accepted species (World Checklist of *Dalbergia*, B. Klitgaard pers. comm. 2021; POWO 2021), which grow in a wide range of habitats throughout the tropics (Klitgaard and Lavin 2005). Phylogenetic analysis of the nuclear internal transcribed spacer (ITS) supports the monophyly of the genus (Vatanparast et al. 2013), which has been confirmed in several studies of chloroplast variation (Hartvig et al. 2015; Hassold et al. 2016; Li et al. 2017). Numerous arborescent species are known to form durable and beautifully colored heartwood (Prain 1904; De Carvalho 1997; Bosser and Rabevohitra 2002; Cervantes et al. 2019). Several species are highly sought-after, especially for the production of high-quality furniture and musical instruments (Barrett et al. 2010), and some species are used in traditional medicine (Liu et al. 2017). Increasing demand in both the national and especially the international markets for the desirable wood from several species in Madagascar has subjected them to intense, unsustainable, and often illegal logging (Schuurman and Lowry 2009; Barrett et al. 2010; Mason et al. 2016; UNODC 2016, 2020; Waeber et al. 2019), which led to the listing of the entire genus (except *D. nigra*, Appendix I) on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

The main characters of the genus, as currently understood and reported in several regional treatments (e.g. Prain 1904; De Carvalho 1997; Niyomdham et al. 1997; Bosser and Rabevohitra 2002; Dezhao et al. 2010; Adema et al. 2016; Lachenaud and van der Maesen 2016) and more global analyses (e.g. Bentham 1860; Baretta-Kuipers 1971), can be summarized as follows:

Trees, shrubs, or woody lianas. Stipules often small and usually early caducous, never spiniform. Leaves alternate, imparipinnate, with alternate (rarely subopposite) leaflets (rarely unifoliolate), stipels absent. Inflorescence paniculate, racemose, or more rarely cymose, never exclusively terminal. Bracts and bracteoles often small and usually early caducous. Flowers often small and numerous, usually pedicellate, with a pair of bracteoles at the apex of the pedicel. Calyx campanulate, usually five-lobed, upper two lobes usually broader and more connate, lower lobe usually slightly longer than the others. Petals clawed, usually glabrous. Standard petal ovate, obovate, orbicular, or panduriform, often notched at the apex. Wing petals free, often auriculate at the base, often sculpted on the abaxial surface. Keel petals usually adherent and cymbiform, often auriculate at the base. Stamens 9 or 10, monadelphous (9 or 10), diadelphous (9 + 1), or in two bundles of 4 + 5 or 5 + 5, and rarely triadelphous (4 + 1 + 4 or 4 + 1 + 5). Anthers basifixed, dehiscent by short transverse slits. Ovary stipitate, with few ovules. Style short and squat to relatively long and slender, often slightly incurved. Stigma terminal, capitate. Fruits flattened, thin samaroid to thickened and corky, with 1–3(4) seed(s) located centrally along the pod, indehiscent. Seeds flattened, reniform.

The diversity of *Dalbergia* is exceptionally high in Madagascar, and all but one species (*D. bracteolata* Baker) are endemic to the island. The last major revision of the Malagasy *Dalbergia* was done by Bosser and Rabevohitra (1996, 2002, 2005), who described 25 new species, reinstated one species, and placed three species in synonymy, thereby increasing the number of species to 48 from the 25 previously recognized by Viguier (ined. 1944), including 11 species that were posthumously described as new (Viguier 1952). Recent collection efforts, integrative analyses, and additional taxonomic work have revealed numerous problems in the application of Bosser and Rabevohitra's species-level taxonomy (Crameri 2020), despite the fact that it is relatively recent. Work towards a refined taxonomy of *Dalbergia* species from Madagascar is currently in progress, and has so far led to the description of two new species from northern Madagascar and an emended description for a third species (Wilding et al. 2021b), the proposition of required nomenclatural changes and the reinstatement of a previous synonym to species rank (Wilding et al. 2021a), and several additional manuscripts in preparation. These taxonomic changes are supported by phylogenomic and population genomic analyses based on more than 600 accessions of Malagasy *Dalbergia* (Crameri 2020).

Phylogenomic analyses including all Malagasy species recognized by Bosser and Rabevohitra (1996, 2002, 2005) have revealed that all but two Malagasy species (*D. bracteolata* and *D. xerophila* Bosser & R.Rabev.) belong to two species-rich and endemic clades that are each more closely related to mainland African or Asian species than to each other (Crameri 2020). Integrated analyses of genetic, morphometric, and eco-geographic data also confirmed further taxonomic problems, including three polyphyletic species (*D. madagascariensis* Vatke, *D. maritima* R.Vig., and *D. neoperrieri* Bosser & R.Rabev.), several cases in which apparently widely distributed species are separable into two or more morphologically and eco-geographically distinct entities, at least two cases of synonymy involving species recognized by Bosser and Rabevohitra (1996, 2002, 2005), and several potentially new species, specimens of which have questionably been included in known species or collected only recently (Crameri 2020; Madagascar Catalogue 2021). Taken together, these findings suggest that the diversity of Malagasy *Dalbergia* has been vastly underestimated, and that in reality it is comparable to or more likely exceeds the current number of recognized species in the much larger tropical zones of continental Africa, the Americas, and Southeast Asia, each of which has ca. 60–70 species (World Checklist of *Dalbergia*, B. Klitgaard pers. comm. 2021; POWO 2021), although it can be assumed that species diversity is underestimated in these areas as well.

The taxonomic inadequacies and uncertainties regarding Malagasy *Dalbergia* can in part be attributed to the previous lack of phylogenetic information, but they can also be explained by a shortage of high-quality, fertile collections documenting the full range of morphological and eco-geographic diversity found in the genus. A total of ca. 1400 databased collections were available prior to 2006, of which ca. 1000 were examined and identified by Bosser and Rabevohitra, while ca. 400 collections were either left undetermined because they were sterile or in poor condition, or had not been seen by them (Madagascar Catalogue 2021). Bosser and Rabevohitra (1996) noted that the matching of flowering collections with leafy sterile material is often difficult because some species flower before the leaves emerge. Variation in leaf characters is often large within species because the presence of indument and leaflet number, size, and shape can vary with age (Lachenaud 2016), geographic region, or branch type (fertile versus sterile or coppice shoot, pers. obs.). Consequently, several species were only known from and described on the basis of one or a few fertile specimens, resulting in a limited understanding of their range and variability. As part of an ongoing effort over the last several decades to expand our knowledge of the Malagasy flora, the number of collections of *Dalbergia* has considerably increased in recent years, amounting to over 4500 available as of October 2021, more than 2400 of which have been made since 2014 as part of a collaborative effort to better document the diversity, occurrence, growth habit, and morphological variation (Hassold 2015; Madagascar Catalogue 2021). These collections comprise herbarium specimens as well as leaf material for genetic analysis along with heartwood samples for anatomical, spectroscopic, and spectrometric characterization. Altogether this material is being used to build a reference collection of Malagasy *Dalbergia*, which can serve as a basis for forensic timber identification (Dormontt et al. 2015) while also providing an important resource for taxonomic studies.

Dalbergia maritima is one of several Malagasy species that produce high-quality rosewood (also known as bois de rose) and have a long history of exploitation (Normand 1988; Richter et al. 2014). The species was first described in Viguier (ined. 1944) and validly published several years later (Viguier 1952) based on a collection from littoral forest on sand at Tampina in east-central Madagascar (*Louvel 200*), and a second collection (*Louvel 79*) without precise locality information ("forêts côtières de l'Est"), which most likely also originates from Tampina. The two collections have glabrous leaves with small to medium-sized leaflets (Figs. 1A, 2A) and a racemose inflorescence structure (Fig. 2A). The delimitation of *D. maritima* was later broadened by Bosser and Rabevohitra (1996) to include material with pubescent leaves from the Betampona Special Reserve and the area surrounding Mahavelona (Foulpointe), respectively ca. 65 and 100 km north and further inland from Tampina, which they recognized as a new variety, *D. maritima* var. *pubescens* Bosser & R.Rabev. (Figs. 1B, 2B, 3D). In their treatment of the genus for the *Leguminosae of Madagascar*, Bosser and Rabevohitra (2002) included within an expanded delimitation of the typical variety, material with paniculate inflorescences from littoral forests on sand at Mandena and Sainte Luce (e.g. *Rabevohitra 2178*), over 700 km to the south at the southeastern extremity of the island (Figs. 1F, 2F, 3D). They further included a collection with racemose inflorescences (*Service Forestier 22334*, to be compared with Figs. 1E, 2D) from the same general area but from low-elevation evergreen humid forest on laterite farther inland (Fig. 3D). Lastly, they also included within the typical variety two collections from the SAVA Region in northeastern Madagascar (*Service Forestier 2591* and *27751*), thereby increasing its distribution range ca. 320 km farther north (Fig. 3D). Since then, numerous additional collections with glabrous or pubescent leaves, and with either racemose or paniculate inflorescences, originating from various localities ranging from Makirovana in the northeast to sites near Tolagnaro in the extreme southeast, have likewise been associated with this broad interpretation of *D. maritima* as a widely distributed, polymorphic species.

Recent phylogenomic and population genomic analyses based on more than 600 accessions of Malagasy *Dalbergia*

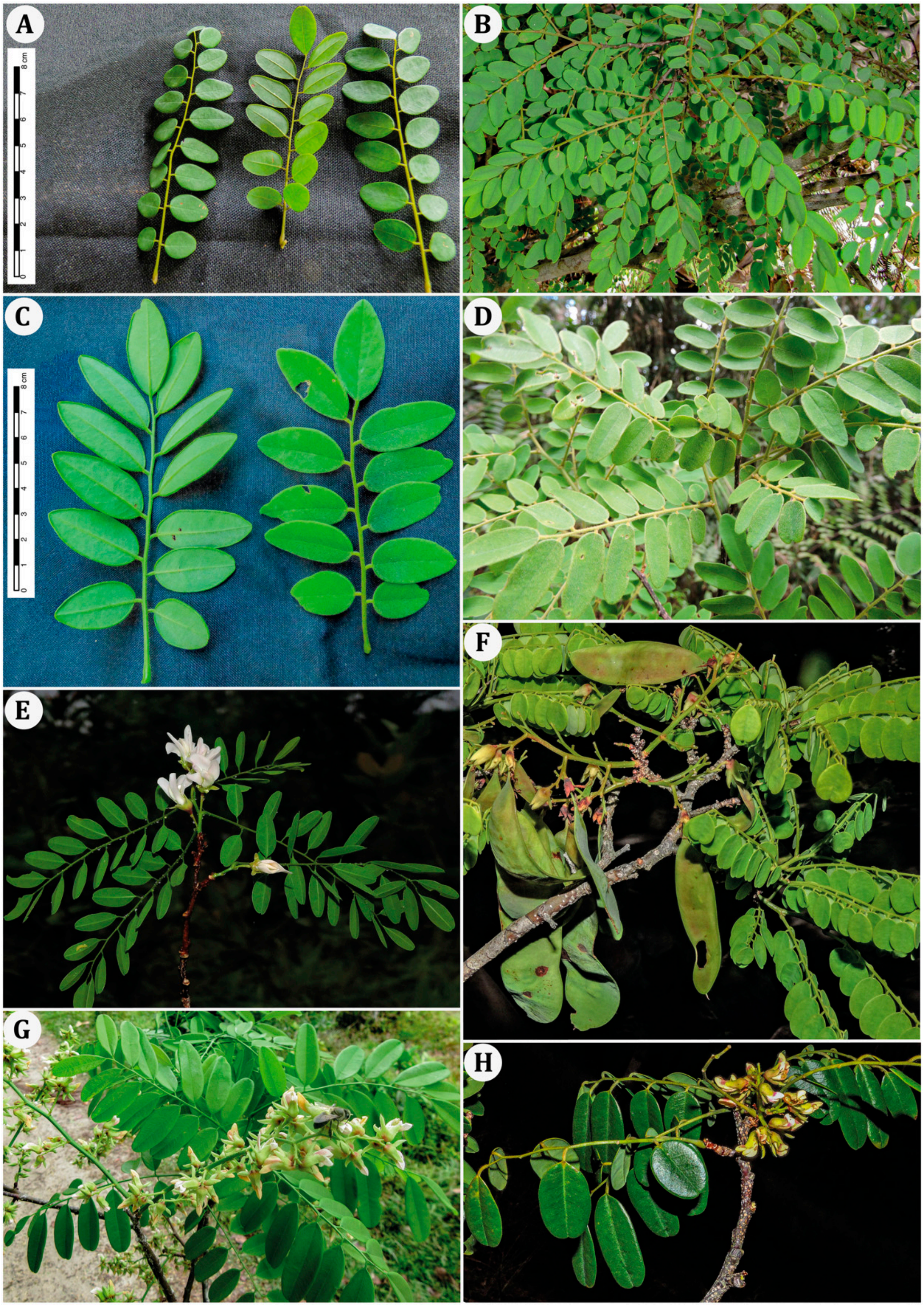

Fig. 1. Leaves and branches of selected *Dalbergia* taxa from east-central (A–C), northern central-east (D, G), and southeastern Madagascar (E–F, H). A. *D. maritima* subsp. *maritima*, Atsinanana Region (*Razakamalala & Rakotovao 8448*). B. *D. maritima* subsp. *pubescens*, Atsinanana Region (*Randrianaivo & Sylvain 2928*). C. *D. louvelii* s.s., Atsinanana Region (*Razakamalala & Rakotovao 8432*). D. *D. louvelii* s.l., Analanjirofo Region (*Rakotovao & Bernard 7299*). E. *D. razakamalalae*, Anosy Region (*Razakamalala & S. A. Andrianarivelo 8558*). F. *D. pseudomaritima*, Anosy Region (*S. A. Andrianarivelo & Razakamalala 63*). G. *D. chapelieri* s.l., Analanjirofo Region (*Lehavana 1109*). H. *D. chapelieri* s.l., Anosy Region (*S. A. Andrianarivelo & Razakamalala 51*). Photos by C. Rakotovao (A, C, D), R. Randrianaivo (B), S. A. Andrianarivelo (E, F, H), A. Lehavana (G).

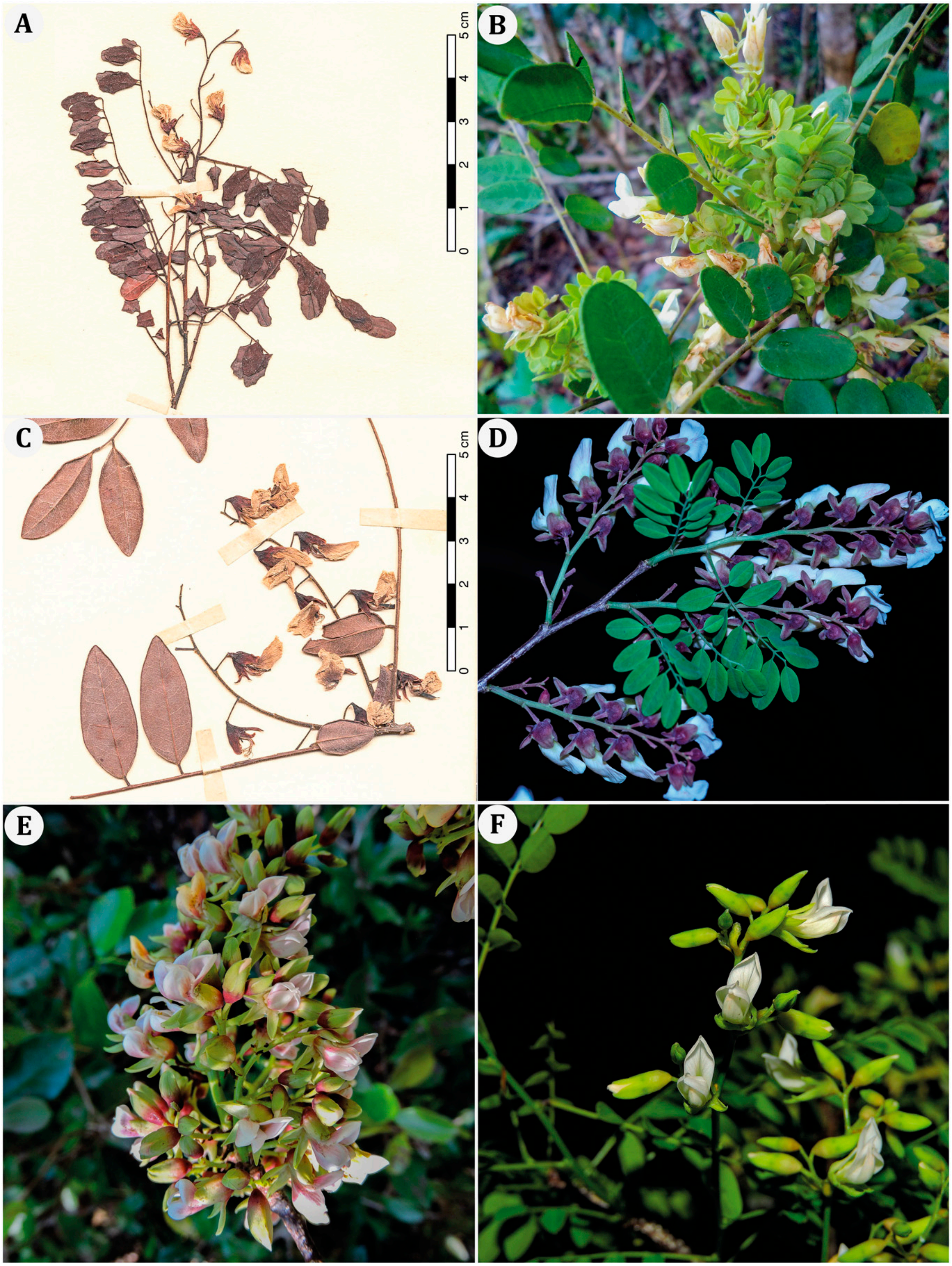

FIG. 2. Inflorescence structure and flowers of selected *Dalbergia* taxa from east-central (A–C) and southeastern Madagascar (D–F). A. *D. maritima* subsp. *maritima*, Atsinanana Region (*Louvel 79*). B. *D. maritima* subsp. *pubescens*, Atsinanana Region (*G. Rakotonirina et al. 91*). C. *D. louvelii* s.s., Atsinanana Region (*Louvel 201*). D. *D. razakamalalae*, Anosy Region (*Andriamihajarivo et al. 2455*). E. *D. chapelieri* s.l., Atsimo-Atsinanana Region (*N. Rakotonirina & Ravololomanana 1175*). F. *D. pseudomaritima*, Anosy Region (*S. A. Andrianarivelo & Razakamalala 65*). Photos by Muséum National d'Histoire Naturelle, Paris, France (A, C), F. Rakotoarivony (B), P. Antilahimena (D), N. Rakotonirina (E), S. A. Andrianarivelo (F).

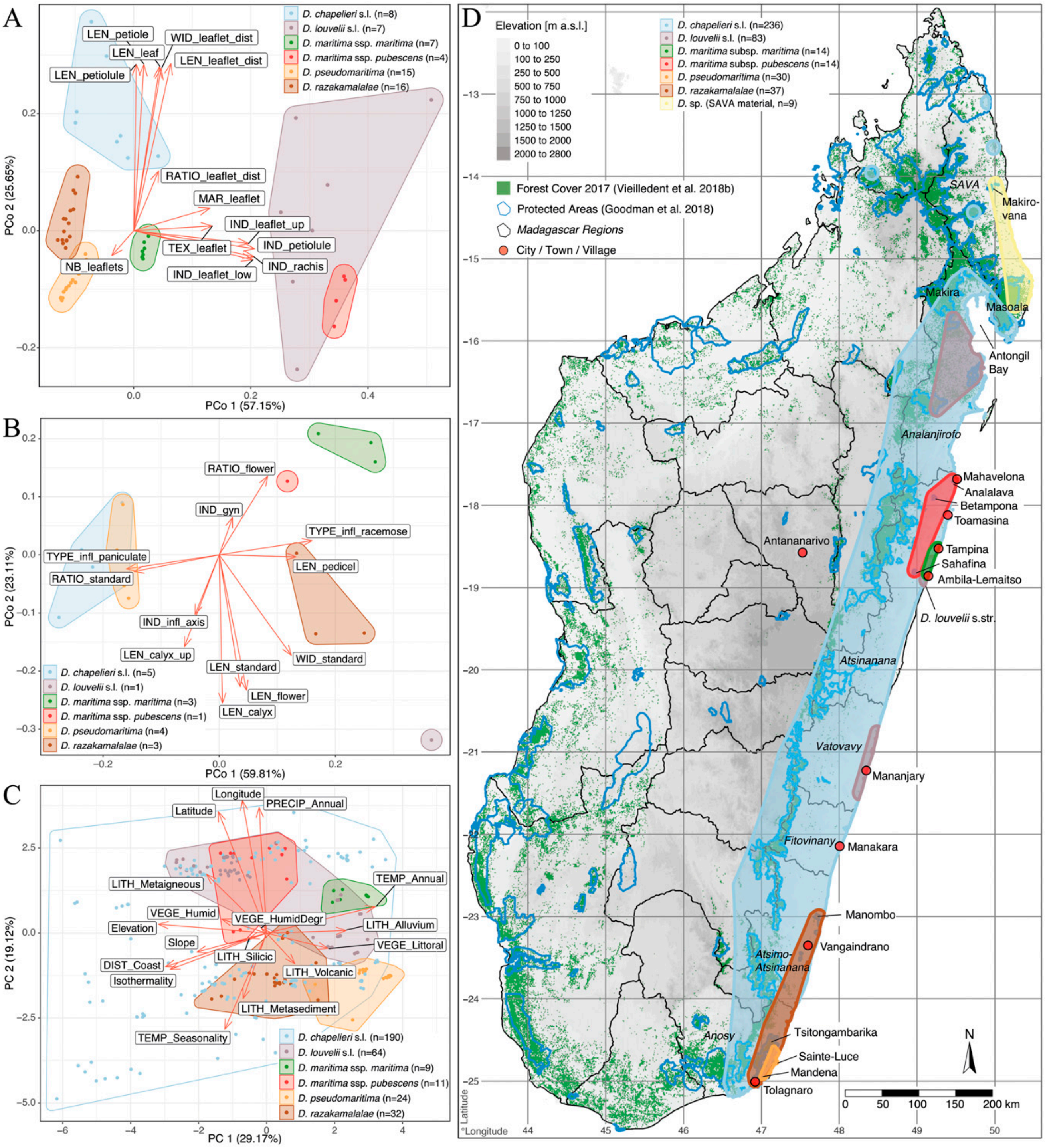

FIG. 3. Multivariate analysis of morphological and ecological data, and geographic distribution areas of selected *Dalbergia* taxa from eastern Madagascar. See Tables 1–2 for variable codes. A. PCoA biplot of 13 leaf and leaflet characters (arrows) measured in 57 collections with mature leaves. B. PCoA biplot of 11 inflorescence and flower characters (arrows) measured in 17 collections with flowers. C. PCA biplot of 17 ecological characteristics (arrows) for 330 collections made since 2000 with precise geo-coordinates. Shading for *D. chapelieri* s.l. has been omitted for clarity. D. Combined distribution map based on buffered alpha hulls drawn around 423 geolocations, including collection records from before 2000, and nine records from the undescribed SAVA material, and excluding two extreme occurrences considered extinct (*Service Forestier 38-R-118* and *34291*). Note that *D. maritima* subsp. *maritima* and *D. louvelii* s.s. co-occur in the Atsinanana Region.

have shown that this broadly circumscribed *D. maritima* is polyphyletic (see pp. 91, 117–118, and 128 in Crameri 2020). The southeastern material with paniculate inflorescences included in the typical variety by Bosser and Rabevohitra (2002), hereafter referred to as the 'southeastern paniculate material' (*D.* sp. 07 in Crameri 2020), is not closely related to *D. maritima* from the Atsinanana Region, which is hereafter referred to as 'east-central *D. maritima*', including the type specimens of both *D. maritima* and *D. maritima* var. *pubescens*. Instead, it belongs to a monophyletic and strongly divergent lineage (the Chapelieri clade) that also includes *D. chapelieri* Baill. sensu lato (s.l.), a species complex currently under study that also forms paniculate inflorescences (Figs. 1G–H, 2E) but whose leaves are longer and leaflets are larger, often more coriaceous, and elliptic to oblong-elliptic rather than broadly elliptic to orbicular (Figs. 1G–H). By contrast, east-central *D. maritima* belongs to another strongly divergent and monophyletic lineage (the Maritima clade), which includes two further described rosewood species from eastern Madagascar: (i) *D. louvelii* R.Vig. s.l. (Figs. 1C–D, 2C), a species complex with mostly pubescent leaves, larger leaflets, and larger flowers than east-central *D. maritima*, which co-occurs with the latter in littoral forests of east-central Madagascar (Figs. 3C–D), extending to the north towards the Antongil Bay (e.g. *Service Forestier 9144*) and southwards at least to littoral forests near Mananjary in the Vatovavy Region; and (ii) *D. occulta* Bosser & R.Rabev., which is characterized by its glabrous leaves, ovate leaflets with a usually emarginate apex, and large bracts (Bosser and Rabevohitra 2005), and which occurs in the Makira Natural Park and the Masoala National Park in northeastern Madagascar (Fig. 3D). Within the Maritima clade, east-central *D. maritima* forms a distinct subclade, which is sister to co-occurring *D. louvelii* sensu stricto (s.s.), but material with glabrous leaves from littoral forests cannot be clearly distinguished from material with pubescent leaves from further inland based on 2396 nuclear genetic regions (see pp. 116 and 128 in Crameri 2020). The southeastern material with racemose inflorescences included in the typical variety by Bosser and Rabevohitra (2002), hereafter referred to as the 'southeastern racemose material', forms another distinct subclade, which is separated along the second principal genetic component (*D.* sp. 06 on p. 116 in Crameri 2020). A fourth described rosewood species, *D. normandii* Bosser & R.Rabev., forms an early-branching group in the Maritima clade (Crameri 2020) and is morphologically clearly distinct from all other Malagasy species by its long, glabrous leaves, few and large leaflets with an acuminate apex, and large flowers (Bosser and Rabevohitra 2002).

The Maritima clade contains at least three further distinct entities (*D.* sp. 14, 24 and 27 in Crameri 2020), but the material available as the present paper was being completed was insufficient for description. One of these undescribed entities (*D.* sp. 27) corresponds to material from the SAVA Region mentioned above and included in *D. maritima* by Bosser and Rabevohitra (hereafter referred to as 'undescribed SAVA material'), but is much more closely related to *D. occulta* than to east-central *D. maritima* (Crameri 2020). It is thus clear that (i) the southeastern paniculate material cannot be retained in *D. maritima* because the resulting concept would be polyphyletic, (ii) the taxonomic status of the southeastern racemose material needs clarification, and (iii) the broad delimitation of *D. maritima* adopted by Bosser and Rabevohitra (2002) requires amendment.

In this study, we examine the taxonomic status of the southeastern paniculate material and the southeastern racemose material previously associated with *Dalbergia maritima*. We assess the distinctiveness of these entities using multivariate analyses of morphological features of their leaves, leaflets, inflorescences, and flowers, as well as ecological data. Our results demonstrate that these two entities are morphologically and eco-geographically coherent and distinct from one another as well as from east-central *D. maritima*, and we formally describe them as two new species, each of which is illustrated with line drawings and photographs taken in the field. We further provide an emended description for *D. maritima*, which we have re-circumscribed so that it comprises a monophyletic and morphologically coherent species from east-central Madagascar, within which we recognize two subspecies, and we present preliminary conservation assessments based on IUCN Red List categories and criteria (IUCN 2012) for each of the three species, as well as for the two subspecies of *D. maritima*.

Materials and Methods

Plant Material—We inspected *Dalbergia* collections deposited at P, K, MO, TAN, TEF, and ZT (acronyms following Thiers 2021), which together hold most type specimens and recent collections of Malagasy *Dalbergia*, including all of the material studied by Bosser and Rabevohitra. Of these, we selected 57 leafy specimens representing the following entities: *D. chapelieri* s.l. ($n = 8$), *D. louvelii* s.l. ($n = 7$), and east-central *D. maritima* ($n = 11$), as well as material of the southeastern paniculate ($n = 15$) and southeastern racemose ($n = 16$) groups, from which measurements were made of leaf and leaflet characters. We further selected 17 flowering specimens of the same entities (5 of *D. chapelieri* s.l., 1 of *D. louvelii* s.l., 4 of east-central *D. maritima*, 4 of southeastern paniculate material, and 3 of southeastern racemose collections) for measurements of inflorescence and flower characters. The leafy and flowering specimens were chosen to represent the observed morphological variation, although the selection of flowering specimens was partly limited by a lack of fully developed and intact flowers.

Morphological Measurements—We assessed 13 leaf and leaflet characters, along with 11 inflorescence and flower characters (Table 1). We initially investigated fruit characters as well, but excluded them from multivariate analyses due to the limited number of collections with mature fruits, substantial intra-individual variation owing to differences in the number of fertilized ovules, and a limited number of measurable characters. Continuous and discrete characters, which were measured several times on a given collection, were recorded as sample medians. Two or three flowers per collection were softened and rehydrated in a warm soapy solution and dissected under a stereo microscope. Measurements of continuous characters were made on digital images of leaves or dissected flower organs using ImageJ (Schneider et al. 2012) version 1.53a.

Ecological Characteristics—We downloaded specimen records from the *Catalogue of the Plants of Madagascar* (Madagascar Catalogue 2021) including all 424 currently known collections belonging to the entities for which morphological measurements were made (Supplementary Material 1, deposited in Dryad, Crameri et al. 2022). From these, we selected 330 records for collections made since 2000 that contain precise geo-coordinates obtained using a GPS device or derived post facto from precise locality data. This was done to minimize the risk of inaccurate associations between occurrences and vegetation class due to imprecise georeferencing or as a result of deforestation that has occurred in the past decades (see Vieilledent et al. 2018a).

We assessed 17 potentially relevant ecological characteristics from available spatial raster or vector data for Madagascar (Table 2). We obtained land surface boundaries from the GADM database available through the raster package (Hijmans and van Etten 2012) version 3.4.5, surface lithology classes from the SERVIR database available at http://geoportal.rcmrd.org/data/africa_surface_lithology.zip, vegetation classes from Moat and Smith (2007), and bioclimate raster data from the CHELSA version 1.2 Bioclim database (Karger et al. 2017a, 2017b). We used R (R Core Team 2020) version 4.0.2 and the elevatr package (Hollister et al. 2020) version 0.3.1, the terra package (Hijmans 2021) version 1.0.10, and the fasterRaster package (Smith 2020) version 0.6.0 to download high-resolution elevation data (3 arc seconds, ca. 90 m resolution) and to perform raster calculations. All rasters were projected to Universal Transverse Mercator (UTM) zone 38S and re-sampled to the resolution of the highest-resolved raster (30 m) when needed. We then extracted the ecological characteristics of the 330 selected collections, resulting in an ecological dataset for multivariate analysis. Commented R code documenting the download and extraction of ecological characteristics from occurrence data is available in Supplementary Material 2, deposited in Dryad (Crameri et al. 2022) and on GitHub (https://github.com/scrameri/DalbergiaTaxonomy).

We produced a combined distribution map based on 414 distinct occurrence records, supplemented by nine records of the undescribed SAVA material (Supplementary Material 1). We drew alpha convex hulls around the occurrence points of each entity using the EOO.computing function in

TABLE 1. Morphological characters of leaves and leaflets (n = 13) and of inflorescences and flowers (n = 11).

Code	Character	Type
Leaf appearance		
LEN_petiole	Petiole length (base to insertion of first basal leaflet)	Continuous
LEN_leaf	Leaf length (petiole + rachis + terminal leaflet)	Continuous
NB_leaflets	Number of leaflets per leaf	Discrete
Leaf indument	Coded as 1 = glabrous; 2 = scattered; 3 = dense	
IND_rachis	Indument on rachis	Ordinal
IND_petiolule	Indument on petiolule	Ordinal
IND_leaflet_up	Indument on upper leaflet lamina	Ordinal
IND_leaflet_low	Indument on lower leaflet lamina	Ordinal
Leaflet size (ratio)		
LEN_petiolule	Petiolule length	Continuous
LEN_leaflet_dist	Length of distal (towards the leaf apex) leaflets (including petiolule)	Continuous
WID_leaflet_dist	Width of distal leaflets at widest point	Continuous
RATIO_leaflet_dist	Ratio of distal leaflet length to width	Continuous
Leaflet texture and margins		
TEX_leaflet	Leaflet texture (thinly coriaceous or coriaceous)	Nominal
MAR_leaflet	Leaflet margin (1 = flat; 2 = thickened but not revolute; 3 = revolute)	Ordinal
Inflorescence		
TYPE_infl	Inflorescence type (racemose or paniculate)	Nominal
IND_infl_axis	Indument on inflorescence axis (coded as above)	Ordinal
Flower		
LEN_pedicel	Pedicel length	Continuous
LEN_flower	Flower length (calyx base to apex of longest petal)	Continuous
LEN_calyx	Calyx length (base to apex of longest calyx lobe)	Continuous
LEN_calyx_up	Length of upper calyx lobes (free part)	Continuous
RATIO_flower	Ratio of flower length to calyx length	Continuous
LEN_standard	Length of standard petal (height without claw)	Continuous
WID_standard	Width of standard petal at widest point	Continuous
RATIO_standard	Ratio of standard petal length to width	Continuous
IND_gyn	Indument on gynoecium (coded as above)	Ordinal

the ConR package (Dauby et al. 2017) version 1.3.0, with an entity-specific alpha parameter (1 for isolated occurrences of *D. chapelieri* s.l., and 10 for the other entities) and buffer (ca. 3 km for the southeastern paniculate material and ca. 9 km for the other entities). The map was displayed using the tmap package (Tennekes 2018) version 3.2, with the estimated forest cover for the year 2017 (Vieilledent et al. 2018b) drawn at lower resolution (ca. 700 × 1400 pixels), and including the officially recognized terrestrial protected areas in Madagascar (Goodman et al. 2018). Because these *Dalbergia* species are under threat from illegal exploitation, we have systematically refrained from making detailed distribution maps and precise geo-coordinates publicly available. Specimen records are provided in the *Catalogue of the Plants of Madagascar* (Madagascar Catalogue 2021), but with restricted public access to precise geo-locations (delivered on demand to bona fide researchers).

Multivariate Analyses—Analyses of morphological data were carried out separately for the leaf/leaflet and inflorescence/flower datasets, while ten collections with flowers and mature leaves were represented in both datasets. Two missing values in the leaf/leaflet dataset were assigned using class means. For each dataset we calculated a morphological distance matrix using the daisy function in the cluster package (Maechler et al. 2019) version 2.1.0 with variable standardization, Gower's distance (Gower 1971) as the distance metric, a specification of ordinal variables (indument and leaflet margin) as ratio-scaled variables, and binary nominal variables (leaflet texture and inflorescence type) as asymmetric binary

TABLE 2. Ecological characteristics (n = 17).

Code	Characteristic	Resolu-tion (m)	Type
Geography			
Latitude	Latitude	30	Continuous
Longitude	Longitude	30	Continuous
Elevation	Elevation	90	Continuous
Topography			
Slope	Slope	90	Continuous
DIST_Coast	Distance to the nearest coast	30	Continuous
Surface lithology			
LITH_Alluvium	Alluvium deposits (fluvial & other)	90	Nominal
LITH_Metaigneous	Metaigneous basement rock	90	Nominal
LITH_Metasediment	Metasedimentary basement rock	90	Nominal
LITH_Silicic	Silicic basement rock	90	Nominal
LITH_Volcanic	Extrusive volcanic (lavas)	90	Nominal
Vegetation class			
VEGE_HumidDegr	Degraded humid forest	30	Nominal
VEGE_Humid	Humid forest	30	Nominal
VEGE_Littoral	Littoral forest	30	Nominal
Bioclimate			
TEMP_Annual	Mean annual air temperature (bio1)	900	Continuous
Isothermality	Isothermality (bio3)	900	Continuous
TEMP_Seasonality	Temperature seasonality (bio4)	900	Continuous
PRECIP_Annual	Annual precipitation (bio12)	900	Continuous

variables. We then subjected the resulting distance matrices to principal coordinate analysis (PCoA) using the pcoa function in the ape package (Paradis and Schliep 2018) version 5.4.1, and visualized each of the first two principal coordinates and the corresponding rotation matrices as biplots using the ggplot2 package (Wickham 2016) version 3.3.3 and the ggforce package (Pedersen 2020) version 0.3.2, and a scaling factor for variable loadings of 0.8 times the smaller ratio of maximum absolute coordinate and maximum absolute variable loading.

We subjected the scaled and centered matrix of ecological data to principal component analysis (PCA) and visualized the first two axes and the rotation matrix as a biplot as above. Commented R code documenting the complete workflow for multivariate analyses and the distribution map are available in Supplementary Material 2, deposited in Dryad (Crameri et al. 2022) and on GitHub (https://github.com/scrameri/DalbergiaTaxonomy).

Species Concept and Delimitation—We follow a unified species concept (De Queiroz 2005, 2007) and its generalized view of species as "separately evolving metapopulation lineages (or, more properly, segments thereof)," where lineage separation is "the only necessary property of species" (De Queiroz 2007). We regarded evidence for genetic (population) structure, as indicated by phylogenomic data and analyses (Crameri 2020), as a starting point for species discovery sensu Carstens et al. (2013). We further considered the discovered units as putative species pending validation, and employed monophyly, genetic differentiation, morphological distinction, and eco-geographical separation or co-occurrence, along with a lack of evident admixture, as operational species criteria to assess lineage separation. Using this interpretation, taxonomic species are hypotheses of evolutionary species, which do not necessarily have to: (i) be monophyletic, (ii) exceed a particular genetic differentiation threshold, (iii) form distinct morphological clusters, (iv) occupy different adaptive niches, or (v) be intrinsically reproductively isolated, although each of these properties provides a line of evidence for lineage separation (De Queiroz 2007). The phylogenomic data collected for Malagasy *Dalbergia* provide a highly relevant line of evidence for lineage separation, because the number of assessed characters contained in this dataset (925,216 polymorphic loci distributed across 2396 nuclear regions; Crameri 2020) is much larger than the 24 morphological characters (Table 1) and the 17 eco-geographic characteristics (Table 2) available. We further assumed that the number of statistically independent characters is largest in the phylogenomic dataset because the morphological and eco-geographic datasets likely include a higher fraction of potentially inter-dependent characters, such as variables coding indument on various surfaces, or elevation and mean annual temperature. Morphological divergence, notably in leaf, inflorescence, flower, and fruit characters, is another important line of evidence for lineage separation, as variation in these characters was attributed to species-level diversity in the 49 taxonomic species delimited by Bosser and Rabevohitra (1996, 2002, 2005). Of these, at least 46 (94%) were confirmed as separately evolving lineages after incorporating phylogenomic data, even though these analyses suggested that the species diversity was underestimated and that many of the delimitations adopted by Bosser and Rabevohitra (1996, 2002, 2005) require revision (Crameri 2020). Moreover, eco-geography is known to be a major factor explaining the observed biological diversity in Madagascar (Vences et al. 2009), and it can be used to infer reproductive isolation (intrinsic or through isolation by distance or vicariance), which is especially useful when crossing experiments are unfeasible, such as for woody species with long generation times.

Conservation Assessment—The use of IUCN Red List criterion A (IUCN 2012, 2019) for many long-lived and forest-dependent species from Madagascar currently represents a major challenge, owing to the difficulty of reliably quantifying a population size reduction over three generations based on the insufficient knowledge of relevant parameters, such as generation length, effective species abundance and distribution, habitat preferences or levels of exploitation (but see Wilding et al. 2021b). We therefore applied the Red List criterion B and calculated the extent of occurrence (EOO) and area of occupancy (AOO) using the GeoCAT online tool (Bachman et al. 2011). Continuing decline was informed by a forest cover time series for Madagascar (Vieilledent et al. 2018a, 2018b) and a dedicated application (current version available at https://github.com/scrameri/ConservationAssessments), which estimates the reduction in forest cover within the minimum convex polygon encompassing known occurrences, and a user-specified elevational range.

Results

Morphological measurements (medians per individual) are presented in Supplementary Materials 3 (leaf/leaflet dataset) and 4 (inflorescence/flower dataset, all deposited in Dryad, Crameri et al. 2022). The first principal coordinate of foliar (leaf and leaflet) characters (which accounts for 57.15% of the total variation) was mainly associated with leaf indument (present in collections of *D. louvelii* s.l. and *D. maritima* var. *pubescens*, Table 3), as well as with coriaceous leaflets with revolute margins, which are typical of both varieties of east-central *D. maritima*, but also occur in *D. chapelieri* s.l. and in *D. louvelii* s.l. (Fig. 3A). The second principal coordinate of foliar characters (which explained 25.65% of the total variation) was mainly associated with leaf, petiole, and petiolule length, as well as with leaflet size, and separated collections with shorter leaves and smaller leaflets (i.e. the southeastern paniculate material) from those with longer leaves and larger leaflets (i.e. most *D. chapelieri* s.l. and some *D. louvelii* s.l.). Leaf length and leaflet size were found to be highly variable within some entities, notably *D. chapelieri* s.l., *D. louvelii* s.l., and the southeastern racemose material (Fig. 3A).

The first principal coordinate of inflorescence and flower characters (which explained 59.81% of the total variation) was mainly associated with inflorescence type, pedicel length, and the shape of the standard petal (Fig. 3B). It separated entities with paniculate inflorescences, short pedicels, and elliptic to ovate standard petals (*D. chapelieri* s.l. and the southeastern paniculate material [Fig. 4]) from material with racemose inflorescences, longer pedicels, and obovate to orbicular standard petals (*D. louvelii* type, east-central *D. maritima*, and the southeastern racemose material [Fig. 5]). The second principal coordinate of inflorescence and flower characters (which explained 23.11% of the total variation) was mainly associated with flower size (smallest in east-central *D. maritima*, largest in the *D. louvelii* type; Table 3) and the ratio of flower length to calyx length (small in *D. chapelieri* s.l. and the southeastern paniculate material, large in east-central *D. maritima*; Fig. 3B).

The extracted ecological data are presented in Supplementary Material 5, deposited in Dryad (Crameri et al. 2022). The first principal component of ecological characteristics (which explained 29.17% of the total variation) separated collections from areas at higher elevation inland and on steeper slopes, where evergreen humid forests are located (*D. maritima* var. *pubescens* and the southeastern racemose material), from sites in flat areas at low elevation and in proximity to the coast, where remnant stands of littoral forests on sand persist (*D. maritima* var. *maritima* and the southeastern paniculate material, Fig. 3C). The two species complexes (*D. chapelieri* s.l. and *D. louvelii* s.l.) occur in both littoral and inland low-elevation evergreen humid forests (Fig. 3C). The second principal component of ecological characteristics (which explained 19.12% of the total variation) was mainly associated with geography, annual precipitation (which decreases towards southeastern Madagascar), and temperature seasonality (which increases towards southeastern Madagascar), as well as with various types of surface lithology (Fig. 3C). It therefore separated populations from the northeast and the center-east (most *D. louvelii* s.l. and *D. maritima*) from those in the southeast (i.e. some *D. louvelii* s.l., the southeastern racemose and the southeastern paniculate material; Figs. 3C–D).

In summary, the southeastern paniculate material has inflorescences and flowers similar to those of *Dalbergia chapelieri* s.l. but differs by its shorter leaves with distinctly smaller and differently shaped leaflets (Table 3), supporting its recognition as a separate species, which we describe below

TABLE 3. Morphological comparison between *Dalbergia maritima*, *D. pseudomaritima*, *D. razakamalalae*, and related taxa discussed in this article. Numbers in brackets denote extreme values, such as those found on coppice shoots. Leaflet length and width and length/width ratios are given for the distal part of the leaf, where leaflet size and shape are more coherent. Diagnostic combinations of characters are shown in bold.

Taxon	Leaf length (incl. terminal leaflet, cm)	Leaflet number (per leaf)	Leaflet length (distal, mm)	Leaflet width (distal, mm)	Leaflet length/ width ratio (distal)	Leaf indument	Inflorescence type	Pedicel length (mm)	Flower length (mm)	Standard petal width (mm)	Gynoecium indument	Fruit width (mm)
D. chapelieri s.l.	**(8–)10–18(–26)**	7–15(–19)	**22–48(–90)**	**11–25(–40)**	**1.9–3.1**	Absent	**Paniculate**	1.3–4(–5)	8–11	4.0–4.5	Absent	**15–26**
D. pseudomaritima	**(4–)5–8(–10)**	(8–)10–17(–21)	**7–15(–22)**	**5–8(–12)**	**1.3–2.1**	Absent	**Paniculate**	0.5–2.5	8–11	3.5–4.5	Absent	**15–24**
D. maritima subsp. *maritima*	6–10(–12)	(8–)11–15(–18)	11–15(–19)	6–9(–11)	1.7–2.2	Absent	Racemose	(2–)3–5.5(–7)	8–9	4.0–5.0	Absent	11–16
D. maritima subsp. *pubescens*	8–13	(9–)13–21(–27)	12–20(–23)	7–9(–11)	1.8–2.3	**Present**	Racemose	1.5–2	8–10	ca. 4.5	**Present**	11–19
D. louvelii s.l.	7–19	(7–)9–15(–19)	**(16–)20–45**	**(5–)9–18**(–20)	**2.2–4.8**	**Present or Absent**	Racemose	(3.5–)5–8	**12–18**	7.5–**10.0**	Absent	15–18
D. razakamalalae	7–13(–16)	11–19(–23)	**(12–)15–25(–35)**	**5–10(–14)**	**2.1–3.2**	Absent	Racemose	2–4(–6)	**10–14**	**5.5–7.5**	Absent	9–15

as *D. pseudomaritima* sp. nov. The southeastern racemose material has an inflorescence structure similar to that of east-central *D. maritima* and *D. louvelii* s.l., but it differs by its consistently glabrous leaves (vs. with indument in most *D. louvelii* s.l. and all *D. maritima* var. *pubescens*), its thinly coriaceous and narrowly ovate to narrowly elliptic leaflets without revolute margins, and its larger flowers (vs. coriaceous and ovate to elliptic leaflets with revolute margins, and smaller flowers in *D. maritima*; Table 3). We therefore describe the southeastern racemose material as a second new species, *D. razakamalalae* sp. nov. The recognition of these two new species from southeastern Madagascar and their exclusion from *D. maritima* sensu Bosser and Rabevohitra (2002) results in a significantly narrower, more coherent, and monophyletic delimitation of *D. maritima*, which is now restricted to populations from the east-central part of the island (Fig. 3D), prompting us to provide an emended description of this economically significant rosewood species. Within *D. maritima*, we have chosen to recognize the two infraspecific entities as subspecies (rather than varieties) because of their clear distinction with regard to both morphology (glabrous vs. pubescent leaves, inflorescence axes and gynoecium; Fig. 3A–B; Table 3) and ecology (littoral forests vs. inland low-elevation evergreen humid forests, Fig. 3C), and the absence of any overlap in their documented geographic ranges (Fig. 3D).

TAXONOMIC TREATMENT

DALBERGIA MARITIMA R.Vig., Notul. Syst. (Paris) 14: 185 (1952), emend. Crameri, Phillipson & N. Wilding. TYPE: MADAGASCAR. Atsinanana [Toamasina]: Forêts côtières de l'Est [forêt côtière de Tampina], s. d. (fl), *Louvel 79* (lectotype, designated by Bosser & Rabevohitra, 2002: 346): P [P00060529]!, isolectotypes (fr): P [P00060530, P00060531]!).

Deciduous tree to at least ca. 10 m tall, or shrub-like when resprouting after felling, bole to at least ca. 8 m high, DBH to at least 20 cm; bark gray-brown, becoming fissured with age. **Branches** glabrous (*D. maritima* subsp. *maritima*) or shortly villose to tomentose on young growth (*D. maritima* subsp. *pubescens*), brown in vivo (gray-brown to dark purple in sicco) when young, becoming gray, lenticels present. **Leaves** alternate, 6–10(–12) cm long (*D. maritima* subsp. *maritima*) or 8–13 cm long (*D. maritima* subsp. *pubescens*), with (8–)11–15(–18) alternate leaflets (*D. maritima* subsp. *maritima*) or (9–)13–21(–27) alternate leaflets (*D. maritima* subsp. *pubescens*), petiole and rachis yellow-green in vivo, brown to dark purple in sicco, glabrous (*D. maritima* subsp. *maritima*) or shortly villose to tomentose (*D. maritima* subsp. *pubescens*); petiole (6–)9–12 mm long; stipules ovate, ca. 4 × 2 mm, glabrous (*D. maritima* subsp. *maritima*) or shortly villose to tomentose (*D. maritima* subsp. *pubescens*), early caducous; leaflets (7–)9–15(–19) × (4–)5–9(–11) mm (*D. maritima* subsp. *maritima*) or (7–)10–20(–23) × (5–)6–9(–11) mm (*D. maritima* subsp. *pubescens*), often noticeably smaller toward base; petiolule 1.0–1.5 mm long, yellow-green in vivo, dark brown in sicco, glabrous (*D. maritima* subsp. *maritima*) or shortly villose to tomentose (*D. maritima* subsp. *pubescens*); lamina ovate to elliptic, coriaceous, base cuneate and often asymmetric, margins revolute in vivo and in sicco, apex obtuse, sometimes

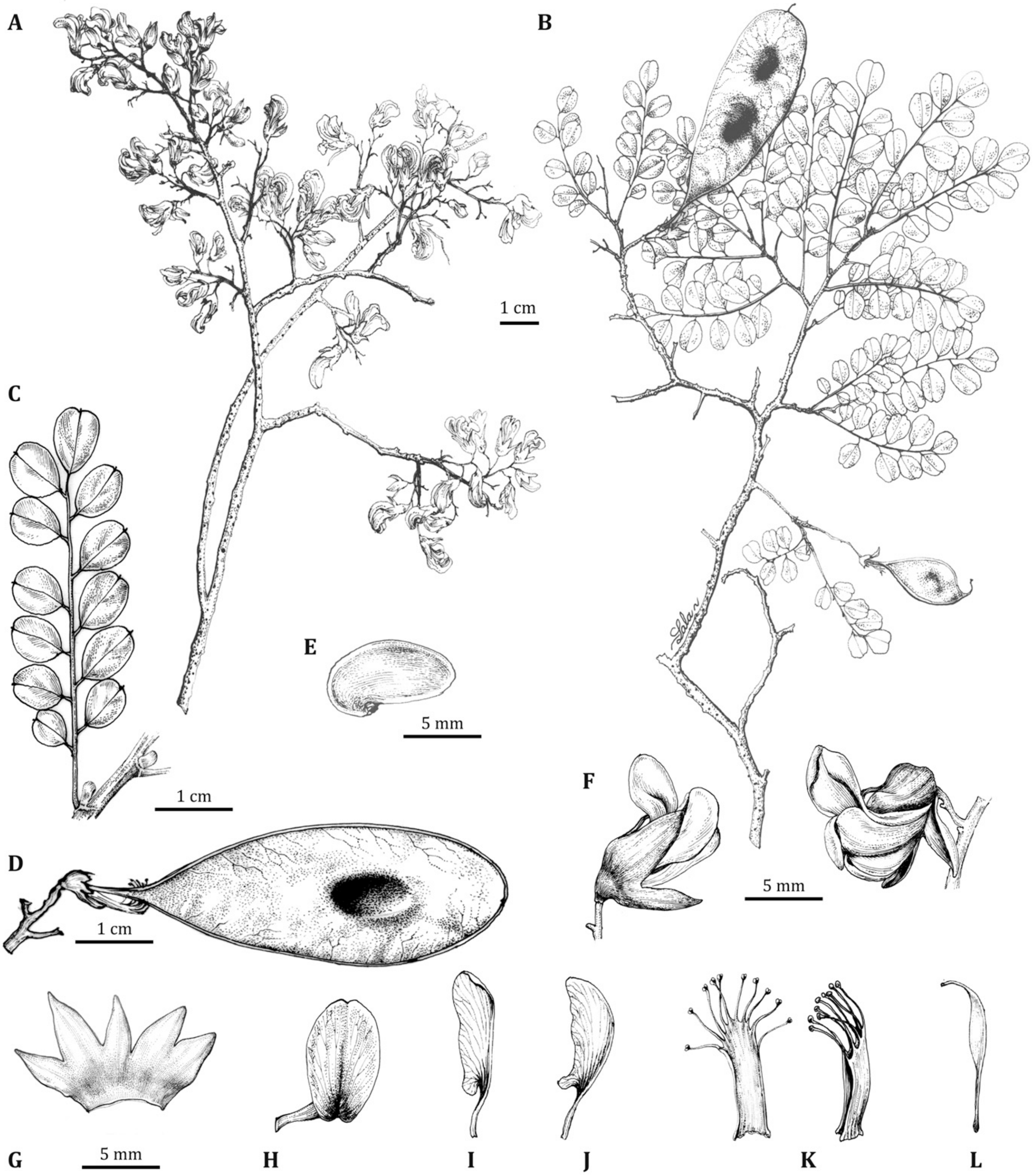

FIG. 4. *Dalbergia pseudomaritima*. A. Flowering branch. B. Fruiting branch. C. Leaf, top view. D. Fruit, single-seeded (immature). E. Seed (immature). F. Flower, side view (left) and frontal view (right). G. Calyx, abaxial surface, split open and flattened, upper lobes on right. H. Standard petal, adaxial surface. I. Wing petal, adaxial surface. J. Keel petal, adaxial surface. K. Androecium, adaxial surface, flattened, with ten fused stamens (left) or side view, with nine fused stamens (right). L. Gynoecium. Illustration by Roger Lala Andriamiarisoa from *Ramananjanahary et al. 830* (A, F–L), *Rakotonirina et al. 1190* (B, C), and *Ramison & Ramisy 109* (D, E).

shallowly emarginate, venation brochidodromous, with 5–7 principal lateral veins per side; upper surface matt, mid-green to gray-green in vivo, red-brown to dark grayish brown in sicco, glabrous (*D. maritima* subsp. *maritima*) or pubescent and glabrescent (*D. maritima* subsp. *pubescens*), venation inconspicuous (slightly raised in sicco), midrib inconspicuous or forming a groove above; lower surface matt, paler than upper in vivo and in sicco, glabrous (*D. maritima* subsp. *maritima*) or pubescent especially along the midrib, becoming puberulous (*D. maritima* subsp. *pubescens*),

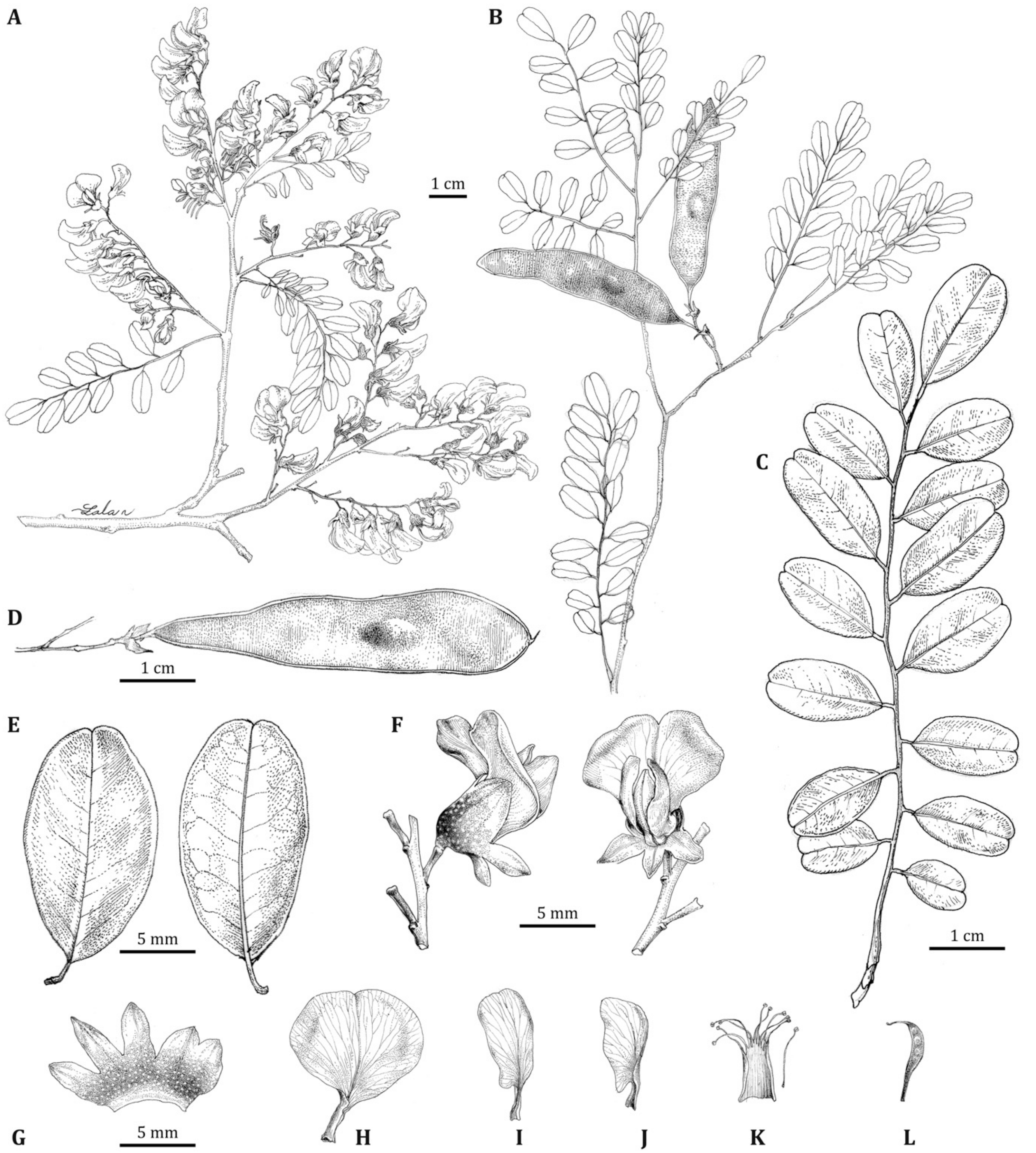

FIG. 5. *Dalbergia razakamalalae*. A. Flowering branch. B. Fruiting branch. C. Leaf, top view. D. Fruit, single-seeded (immature). E. Leaflet upper (left) and lower (right) surface. F. Flower, side view (left) and frontal view (right). G. Calyx, abaxial surface, split open and flattened, upper lobes on right. H. Standard petal, adaxial surface. I. Wing petal, adaxial surface. J. Keel petal, adaxial surface. K. Androecium, adaxial surface, with nine or ten fused stamens. L. Gynoecium. Illustration by Roger Lala Andriamiarisoa from *Andriamihajarivo et al. 2455* (A, F–L), *Ramanitrinizaka & Sandratriniaina 13* (B, C, E) and *Ramanitrinizaka & Sandratriniaina 1* (D).

venation forming a loose network of higher-order veins (often paler than matrix in sicco) below, midrib prominent. **Inflorescences** racemose, composed of (1–)4–12 alternate flowers each, often with imparipinnate reduced leaves subtending individual flowers especially near base (thus becoming single-flowered), 2–5 cm long; axes pale green in vivo, dark brown to dark purple in sicco, glabrous (*D. maritima* subsp. *maritima*) or shortly villose to tomentose (*D. maritima* subsp. *pubescens*); anthesis before or concurrent with leaf emergence; peduncle to 9 mm long. **Flowers** often subtended by glabrous (*D. maritima* subsp. *maritima*) or pubescent (*D. maritima* subsp. *pubescens*), imparipinnate reduced leaves, 12–25 mm long, with 7–13 alternate, ovate to elliptic leaflets, bracts narrowly ovate, ca. 3.0–4.0 × 1.0–1.5 mm, early caducous; pedicel (1.5–)3–6(–7) mm long, slender, glabrous; bracteoles narrowly lanceolate, ca. 2.0 × 0.6 mm, glabrous (*D. maritima* subsp. *maritima*), early caducous (none seen in *D. maritima* subsp. *pubescens*); calyx base to apex of longest petal 8–10 mm long in sicco; calyx reddish (*D. maritima* subsp. *maritima*, fide M. Louvel) or pale yellow-green (*D. maritima* subsp. *pubescens*) in vivo, purple-brown, darker at base in sicco, with a 1.8–2.8 mm long tube, 4.5–6.0 mm long from base to apex of lower lobe, glabrous (*D. maritima* subsp. *maritima*) or with often ciliate lobe margins (*D. maritima* subsp. *pubescens*), persistent, 2 upper sepals long-connate, their lobes 1.2–2.0 × 1.3–1.5 mm, apex obtuse, 2 lateral sepals triangular, 1.9–2.6 × 1.0–1.5 mm, lowest sepal triangular, margins weakly incurved, apex slightly hooked, 2.1–3.2 × 0.8–1.3 mm; petals glabrous, white at anthesis, becoming cream post anthesis, dark yellow to dark cream in sicco; standard petal elliptic to orbicular, claw and lamina forming an obtuse angle, margins incurved forwards when in full flower in vivo, base rounded, apex rounded or notched, 6.0–8.1 × 4.0–5.0 mm, including 1.6–2.6 mm long claw; wing petals 5.4–8.1 × 1.8–2.8 mm, including 1.3–1.8 mm long claw, base distinctly auriculate; keel petals 4.8–7.2 × 1.6–2.7 mm, including 1.0–1.8 mm long claw, base distinctly auriculate; androecium glabrous, monadelphous or diadelphous, 5.8–8.4 mm long; stamens 9–10 or 9 + 1, free for upper 1.5–3.2 mm; gynoecium 4.0–6.1 mm long, glabrous (*D. maritima* subsp. *maritima*) or pubescent (*D. maritima* subsp. *pubescens*); stipe ca. 2.0 mm long; ovary 2.4–3.0 mm long, with 3 or 4 ovules; style slender, slightly incurved, 1.6–2.4 mm long. **Fruits** yellow-green when immature in vivo, red-brown to purple-brown in sicco, with 1–2(–3) seeds, body oblong, 4.5–7.2 × 1.1–1.6(–1.9) cm when single-seeded, up to 8.5 × 1.9 cm when 2-seeded, base cuneate, apex rounded, surface indistinctly net-veined, glabrous; stipe ca. 8 mm long; style rarely persistent. **Seeds** (immature) sub-reniform, flattened, brown, ca. 11 × 6.5 mm. Figures 1A–B, 2A–B.

Notes—*Dalbergia maritima* was delimited by Bosser and Rabevohitra (2002) to include the populations from southeastern Madagascar recognized here as *D. pseudomaritima* and *D. razakamalalae*, as well as superficially similar collections from the northeastern part of the island (*Service Forestier 2591* and *27751*). However, the populations from the southeast and northeast are genetically distinct and less closely related to *D. maritima* than the latter is to *D. louvelii* s.s. (Crameri 2020), with which *D. maritima* co-occurs (Fig. 3D) and from which it is morphologically distinct, as summarized in Fig. 3A–B and Table 3 (but see notes below under *D. maritima* subsp. *pubescens*). The narrower circumscription of *D. maritima* adopted here avoids confusion with the distantly related *D. pseudomaritima* and results in the recognition of monophyletic as well as geographically and morphologically coherent species. The binary rather than gradual differences in indument between the two infraspecific taxa of *D. maritima* (Fig. 3A–B; Table 3), along with their non-overlapping documented geographic ranges (Fig. 3D), align better with the rank of subspecies than variety, following the infraspecific taxonomic concepts of Christensen (1987). It would not, however, be appropriate to treat these two entities as separate species because they appear to represent one metapopulation with no genetic structure that would indicate their separate evolution, and virtually no genetic differentiation between them ($F_{ST} = 0.01$, see p. 116 in Crameri 2020).

Dalbergia maritima was first described by R. Viguier (ined. 1944) as part of a comprehensive revision of the legumes of Madagascar, but this monumental work was destroyed at the printers in Saint-Lô during a bombardment in June 1944, and it was therefore not effectively published, according to Articles 29.1 and 32.1a of the Shenzhen Code (Turland et al. 2018). Several years later, H. Humbert validated the names of eleven new *Dalbergia* species described in Viguier's revision, including *D. maritima*, and acknowledging R. Viguier as their posthumous author (Viguier 1952).

Conservation Status—*Dalbergia maritima* is known from 30 positively identified collection records that represent 7 extant occurrences and 5 occurrences that appear to have been extirpated. Its former extent of occurrence (EOO) was at least 2882 km^2 and its former area of occupancy (AOO) was at least 76 km^2 (based on a 4 km^2 grid), whereas its current documented geographic range has the form of an EOO of 1883 km^2 and an AOO of 56 km^2, and comprises five subpopulations. The species occurs in forest ecosystems (Madagascar Catalogue 2021). Forest cover decline between 1953 and 2017 was estimated from the forest cover time series of Vieilledent et al. (2018a, 2018b) to be 78% in the altitudinal range of 0–450 m and within the minimum convex polygon encompassing all known collections of this species. Therefore, *D. maritima* is inferred to have undergone and to be undergoing continuing decline in EOO, AOO, quality of habitat, number of subpopulations, and number of mature individuals. This species occurs at four locations with respect to the most serious plausible threat, which is selective logging for trade in its high-quality heartwood, as inferred from older collections with exploitable diameter, its documented use for carpentry, cabinet making and construction, and tree stumps observed during recent field work in east-central Madagascar. The occurrences within the protected areas of Betampona, Sahafina, and Vohibola (where a local association provides some level of protection) represent three separate locations. All occurrences outside of protected areas can be inferred to represent a single additional (fourth) location based on the IUCN Red List guidelines (IUCN 2019), because of the large spatial scale at which illegal selective logging (or habitat degradation and loss) can severely reduce the population within a single generation (at least 30–40 yr). Moreover, most known subpopulations of this species can be accessed by road or train, and harvest intensity can be regarded as similar over large spatial scales spanning similarly accessible areas. For these reasons, *D. maritima* is assigned a preliminary IUCN conservation status of Endangered: EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

IDENTIFICATION KEY TO THE SUBSPECIES OF *DALBERGIA MARITIMA*

1. Leaves glabrous on all surfaces; inflorescence axes and gynoecium glabrous; littoral forests on sand, at 0–30 m elevation . . . ***D. maritima* subsp. *maritima***
1. Leaves with sparse to dense indumentum on all surfaces, glabrescent on upper surface of leaflets; inflorescence axes shortly villose to tomentose, gynoecium pubescent; low-elevation evergreen humid forest on laterite, at 80–450 m elevation. . . . . ***D. maritima* subsp. *pubescens***

Dalbergia maritima **subsp.** ***maritima*****—**

Vernacular Names and Uses**—**Bois de rose (*Rakotovao & Razakamalala 7467, 7474*), Hazomainty (*Rakotovao & Razakamalala 7482*), Volombodipony (*Louvel 79*), Volombodipony à petites feuilles (*Louvel 200*), Volombodipony lahy (*Louvel 200*).

The heartwood of this subspecies is burgundy in color (*Rakotovao & Razakamalala 7467*), and with time becomes blackish and similar to ebony (*Louvel 200*). It is considered to be a high-quality rosewood (Normand 1988; Richter et al. 2014).

Habitat, Distribution, and Phenology**—***Dalbergia maritima* subsp. *maritima* occurs in littoral forests on sand, at 0–30 m elevation. It is restricted to east-central Madagascar (Atsinanana Region), occurring in the littoral forests of Andranampy and Vohibola, and recorded from coastal areas between Ambila-Lemaitso and Tampina (Fig. 3D). *Dalbergia maritima* subsp. *maritima* has been collected in flower from December to March. Mature fruits (not seen) have been observed in June (fide *Rakotovao & Razakamalala 7469*).

Conservation Status**—***Dalbergia maritima* subsp. *maritima* is known from 15 positively identified collection records that represent 2 extant occurrences and 2 occurrences that appear to have been extirpated. Its former extent of occurrence (EOO) was at least 43 km^2 and its former area of occupancy (AOO) was at least 24 km^2 (based on a 4 km^2 grid), whereas its current documented geographic range has the form of an EOO of 18 km^2 and an AOO of 16 km^2, and comprises two subpopulations. The subspecies occurs in forest ecosystems (Madagascar Catalogue 2021). Forest cover decline between 1953 and 2017 was estimated from the forest cover time series of Vieilledent et al. (2018a, 2018b) to be 47% in the altitudinal range of 0–30 m and within the minimum convex polygon encompassing all known collections of this subspecies. Therefore, *D. maritima* subsp. *maritima* is inferred to have undergone and to be undergoing continuing decline in EOO, AOO, quality of habitat, number of subpopulations, and number of mature individuals. This subspecies occurs at two locations with respect to the most serious plausible threat, which is selective logging for trade in its high-quality heartwood, as inferred from older collections with exploitable diameter and tree stumps observed during recent field work in east-central Madagascar. The occurrence within the Vohibola forest (where a local association provides some level of protection) represents the first location. The subpopulation from the Andranampy forest represents the second location. For these reasons, *D. maritima* subsp. *maritima* is assigned a preliminary IUCN conservation status of Endangered: EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

Notes**—**Two specimens with glabrous leaves from the SAVA Region (*Service Forestier 2591* and *Service Forestier 27751*), which were associated with *D. maritima* by Bosser and Rabevohitra (2002), are here excluded from *D. maritima* subsp. *maritima*, since they belong to a different species (Crameri 2020) corresponding to the undescribed SAVA material (Fig. 3D).

Additional Specimens Examined**—Madagascar.** —ATSINANANA [Toamasina]: Ambila-Lemaitso, 6 Feb 1951 (fl), *Service Forestier 2860* (P, TAN); same locality, 1 Jan 1952 (st), *Service Forestier 5-R-233* (P); Andranampy forest (Vavony), 2 Jun 2019 (st), *Rakotovao & Razakamalala 7467* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Rakotovao & Razakamalala 7468* (DBEV, MO, P, TAN, ZT); same locality, same date (fr), *Rakotovao & Razakamalala 7469* (DBEV, MO, P, TAN, ZT); Tampina, Mar 1924 (fl), *Louvel 200* (P); Vohibola forest (Andranokoditra), 4 Jun 2019 (st), *Rakotovao & Razakamalala 7474* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Rakotovao & Razakamalala 7478* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Rakotovao & Razakamalala 7479* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Rakotovao & Razakamalala 7482* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Razakamalala & Rakotovao 8444* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Razakamalala & Rakotovao 8448* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Razakamalala & Rakotovao 8454* (DBEV, MO, P, TAN, ZT); same locality, 15 Dec 1982 (bud, fl), *Service Forestier 32479* (P, TEF).

Dalbergia maritima **subsp.** ***pubescens*** (Bosser & R.Rabev.) Crameri, Phillipson & N.Wilding, stat. nov. BASIONYM: *Dalbergia maritima* R.Vig. var. *pubescens* Bosser & R.Rabev., Bull. Mus. Natl. Hist. Nat., B, Adansonia Sér. 4, 18(3–4): 208 (1996). TYPE: MADAGASCAR. Atsinanana [Toamasina]: Environs de Foulpointe [Mahavelona], 1985 (fr), *Service Forestier 32824* (holotype: P [P00060551]!, isotype: TEF [TEF000141]!).

Vernacular Names and Uses**—**Andramena kely ravina (*Bernard & Razakamalala 2247*), Andramena, Hitsika, or Volombodimpona (*Service Forestier 18-R-195*).

The heartwood of *Dalbergia maritima* subsp. *pubescens* is used in carpentry, cabinet making, and construction (*Service Forestier 18-R-195*). It is considered to be a high-quality rosewood (*Razakamalala & Bernard 8368*).

Habitat, Distribution, and Phenology**—***Dalbergia maritima* subsp. *pubescens* occurs in inland low-elevation evergreen humid forests on lateritic soils, at 80–450 m elevation. It is restricted to east-central Madagascar (Atsinanana Region), occurring between and around the protected areas of Sahafina in the south and Betampona in the north, and potentially extending to the Analalava protected area (Fig. 3D). *Dalbergia maritima* subsp. *pubescens* has only been collected once in full flower, in late March (*G. Rakotonirina et al. 389*). Immature fruits have been recorded from late January, and mature fruits have been recorded from June to early August.

Conservation Status**—***Dalbergia maritima* subsp. *pubescens* is known from 15 positively identified collection records that represent 5 extant occurrences and 3 occurrences that appear to have been extirpated. Its former extent of occurrence (EOO) was at least 1355 km^2 and its former area of occupancy (AOO) was at least 52 km^2 (based on a 4 km^2 grid), whereas its current documented geographic range has the form of an EOO of 779 km^2 and an AOO of 40 km^2, and comprises three subpopulations. The subspecies occurs in forest ecosystems (Madagascar Catalogue 2021). Forest cover decline between 1953 and 2017 was estimated from the forest cover time series of Vieilledent et al. (2018a, 2018b) to be 85% in the altitudinal range of 80–450 m and within the minimum convex polygon encompassing all known collections of this subspecies. Therefore, *D. maritima* subsp. *pubescens* is inferred to have undergone and to be undergoing continuing decline in EOO, AOO, quality of habitat, number of subpopulations, and number of mature individuals. This subspecies occurs at three locations with respect to the most serious plausible threat, which is selective logging for trade in its high-quality heartwood, as inferred from older collections with exploitable diameter and its documented use for carpentry, cabinet making, and construction. The occurrences within the protected areas of Betampona and Sahafina represent two separate locations. All occurrences outside of protected areas can be inferred to represent a single additional (third) location based on the IUCN Red List guidelines (IUCN 2019), because of the large spatial scale at which illegal selective logging (or habitat degradation and loss) can severely reduce the population within a single generation (at least 30–40 yr). Moreover, most known subpopulations of this species can be accessed by road or train, and harvest intensity can be regarded as similar over large spatial scales spanning similarly accessible areas. For these reasons, *D. maritima* subsp. *pubescens* is assigned a preliminary IUCN conservation status of Endangered: EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

Notes—*Dalbergia maritima* subsp. *pubescens* is distinct from the nominal subspecies on the basis of the presence of indument on its leaves, inflorescence axes, and gynoecium, although sterile specimens can potentially be confused with *D. louvelii* s.l. (Figs. 1C–D, 2C), from which it differs in its smaller flowers (as observed in *D. louvelii* s.s., from littoral forests in east-central Madagascar) and narrower fruits, and in its smaller, more numerous, consistently pubescent, and differently shaped leaflets, as shown in Figs. 1B, 2B, 3A–B and summarized in Table 3. Moreover, the currently known geographic ranges of these two taxa do not appear to overlap, and the geographically closest similar entity (*D. louvelii* s.s., which co-occurs with *D. maritima* subsp. *maritima* in littoral forests in east-central Madagascar) occupies a different habitat type (Fig. 3C–D). Two collections (*Service Forestier 34291* and the type, *Service Forestier 32824*) increase the documented distribution range of *D. maritima* subsp. *pubescens* by ca. 50 km to the north, including the southern limits of the Analanjirofo Region and potentially the Analalava protected area, situated ca. 6 km to the southwest of Mahavelona, but no extant occurrences are known from these areas, despite intensive recent botanical inventory work at Analalava, so these populations are presumed to have been extirpated.

Additional Specimens Examined—**Madagascar.** —ANALANJIROFO [Toamasina]: Ambatomalama, 4 Jun 1991 (fr), *Service Forestier 34291* (MO, TEF); ATSINANANA [Toamasina]: Ambodiriana commune, 24 Mar 2017 (fl), *G. Rakotonirina et al. 91* (K, MO, P, TAN, UPS); Antetezambaro commune, 12 Oct 2019 (st), *Karatra & Ramanitrinizaka 190* (DBEV, MO, P, TAN, ZT); same locality, 28 Jan 2021 (y.fr), *Antilahimena 9712* (MO, P, TAN); same locality, same date (y.fr), *Antilahimena 9720* (MO, P, TAN); Betampona Special Reserve and surrounding areas, 11 Nov 2016 (st), *Randrianaivo & Sylvain* 2928 (P, TAN, ZT); same locality, 16 Feb 2018 (y.fr), *Randrianaivo 3136* (G, MO, P, TEF, ZT); same locality, 18 Jan 2014 (st), *Razakamalala & Bernard 7704* (BR, G, MO, P, ZT); same locality, 20 Jan 2014 (st), *Bernard & Razakamalala 2247* (BR, G, MO, P, ZT); same locality, 7 Aug 1986 (fr), *Service Forestier 31184* (P, TEF); Masiabarika forest, 17 Dec 1954 (st), *Service Forestier 18-R-195* (P); Sahafina protected area, 16 Apr 2019 (st), *Razakamalala & Bernard 8368* (DBEV, MO, P, TAN, ZT); same locality, 17 Apr 2019 (st), *Bernard & Razakamalala 2734* (DBEV, MO, P, TAN, ZT); Toamasina suburbaine commune, 21 Feb 2018 (y.fr), *G. Rakotonirina et al. 389* (K, MO, P, TAN, UPS).

Dalbergia pseudomaritima Crameri, Phillipson & N.Wilding, sp. nov. TYPE: MADAGASCAR. Anosy [Toliara]: Sainte Luce, 13 Feb 2019 (fr), *N. Rakotonirina, R. Razakamalala & R. Bernard 1190* (holotype: P [P01069698]!, isotypes: DBEV, MO, TAN image!, ZT [ZT-00169818]).

Dalbergia pseudomaritima is similar to *D. chapelieri* Baill. in possessing paniculate inflorescences that appear before or at the same time as the emerging, glabrous leaves, but differs by its shorter leaves [(4–)5–8(–10) cm vs. (8–)10–18(–26) cm long] with distinctly smaller leaflets [distal leaflets 7–15(–22) × 5–8(–12) mm vs. 22–48 × 11–25 mm and sometimes reaching 90 × 40 mm on coppice shoots] that are broadly elliptic to orbicular (vs. elliptic to oblong-elliptic or obovate), resembling those of *Dalbergia maritima* R.Vig. in number and size.

Deciduous tree to ca. 12 m tall, or shrub-like when resprouting after felling, bole to ca. 7 m high, DBH to at least 25 cm; bark pale gray to brown, smooth at first, becoming fissured with age. **Branches** glabrous, orange-brown in vivo (dark brown to dark purple in sicco) when young, becoming gray, lenticels present. **Leaves** alternate, (4–)5–8(–10) cm long, with (8–)10–17(–21) alternate leaflets, petiole and rachis bright green in vivo, purple-brown in sicco, glabrous; petiole (6–)8–10(–12) mm long; stipules obovate, 4.0–6.5 × 1.0–2.0 mm, glabrous, early caducous; leaflets (5–)7–14(–22) × (4–)5–8(–12) mm, sometimes noticeably smaller toward base, but often rather uniform; petiolule 0.5–2.0 mm long, yellow-green in vivo, dark brown to black in sicco, glabrous; lamina broadly elliptic to orbicular, rarely obovate, thinly coriaceous, base broadly cuneate, margins thickened but not revolute in sicco, apex shallowly retuse, sometimes mucronulate or rounded, venation brochidodromous, with 5–9 principal lateral veins per side; upper surface matt, yellow-green in vivo, olive-green to red-brown in sicco, glabrous, venation inconspicuous (slightly raised in sicco), midrib inconspicuous or forming a groove; lower surface matt, paler than upper in vivo and in sicco, glabrous, venation forming a dense network of higher-order veins, contrasting and often darker than matrix in sicco, highest-order veins often open-ended, midrib prominent. **Inflorescences** paniculate, composed of 6–20 flowers each, compact, 2–5 cm long, with (2–)4–6 partial inflorescences composed of (1–)2–6 flowers each; axes green in vivo, dark brown in sicco, glabrous or sparsely and minutely ciliate at junctions; anthesis before or concurrent with leaf emergence; peduncle to 8 mm long. **Flowers** subtended by glabrous or minutely ciliate, oblong to obovate bracts, 3.5–6.0 × 1.0–1.5 mm, early caducous; pedicel 0.5–2.5 mm long, glabrous; bracteoles obovate, (1.5–)3.5–4.5 × (0.5–)1.0–1.5 mm, glabrous or minutely ciliate, early caducous; calyx base to apex of longest petal 8–12 mm long in sicco; calyx green, reddish at base in vivo, yellow-brown to purple-brown in sicco, with a 2.5–3.4 mm long tube, 5–8 mm long from base to apex of lower lobe, glabrous or sparsely and minutely ciliate, persistent, 2 upper sepals long-connate, their lobes 1.8–2.5 × 1.9–2.5 mm, apex obtuse to subacute, 2 lateral sepals cymbiform, 3.1–4.2 × 1.3–1.9 mm, lowest sepal triangular, margins incurved, apex often distinctly hooked, 3.4–4.6 × 1.0–2.5 mm; petals glabrous, white or pinkish-white at anthesis, becoming cream post anthesis, yellow to brown in sicco; standard petal ovate to elliptic to obovate, claw and lamina almost perpendicular, margins incurved forwards in vivo, base truncate to subcordate, apex notched, 8.8–10.0 × 3.7–4.7 mm, including 2.5–3.5 mm long claw; wing petals 7.3–10.3 × 2.0–2.8 mm, including 1.5–2.9 mm long claw, base distinctly auriculate; keel petals 7.4–9.4 × 2.5–3.1 mm, including 1.8–2.7 mm long claw, base distinctly auriculate; androecium glabrous, monadelphous or diadelphous, 9.4–10.6 mm long; stamens 9–10 or 9 + 1, free for upper 2.7–4.0 mm; gynoecium 6.4–8.2 mm long, glabrous; stipe 3–4 mm long; ovary 3.5–4.5 mm long, with 3–5 ovules; style slender, slightly incurved, 1.9–2.5 mm long. **Fruits** (immature) yellow-green becoming red-brown in vivo, yellow-brown to red-brown in sicco, with 1–3(–4) seeds, body elliptic to oblong, 4.5–6.5 × 1.6–2.3 cm when single-seeded, up to 8.5 × 2.5 cm when 3-seeded, base attenuate, apex rounded or obtuse, surface with reticulate veins, glabrous; stipe 5–10 mm long; style persistent. **Seeds** (immature) sub-reniform, flattened, brown, 8.0–9.0 × 5.0–6.0 mm. Figures 1F, 2F, 4.

Etymology—The epithet reflects the superficial similarity to and confusion with *Dalbergia maritima*.

Vernacular Names and Uses—Manary (*Ramamonjiarisoa 4*), Manary toloho (*Ramamonjiarisoa 10*), Sambalahy (*Ramison & Ramisy 108*), Tombobitsy (*Razafimandimby et al. 237*).

The heartwood of *Dalbergia pseudomaritima* is orange-brown in color (*S. A. Andrianarivelo & Razakamalala 58*, *Razakamalala & S. A. Andrianarivelo 8566*). Its wood is used as firewood and for charcoal production (R. Randrianaivo pers. comm.).

Habitat, Distribution, and Phenology—*Dalbergia pseudomaritima* occurs in littoral forests on sand and adjacent swamp forests (*Razakamalala et al. 6675*), with one collection from inland low-elevation evergreen humid forests on sandy lateritic soils near a stream (*Bernard et al. 2654*), at 0–30 m elevation. It is restricted to southeastern Madagascar (Anosy Region), occurring mainly in the protected areas of Mandena and Sainte Luce (Fig. 3D). *Dalbergia pseudomaritima* has been collected in full flower from October to January. Immature fruits have been recorded from October, and mature fruits have been observed only once in late March (*Gereau et al. 3326*).

Conservation Status—*Dalbergia pseudomaritima* is known from 42 collection records that represent 5 extant occurrences and 1 occurrence that appears to have been extirpated. Its former extent of occurrence (EOO) was at least 275 km^2 and its former area of occupancy (AOO) was at least 56 km^2 (based on a 4 km^2 grid), whereas its current documented geographic range has the form of an EOO of 252 km^2 and an AOO of 44 km^2, and comprises three subpopulations. The species mainly occurs in forest ecosystems and rarely extends to marshes (Madagascar Catalogue 2021). Forest cover decline between 1953 and 2017 was estimated from the forest cover time series of Vieilledent et al. (2018a, 2018b) to be 35% in the altitudinal range of 0–30 m and within the minimum convex polygon encompassing all known collections of this species. Therefore, *D. pseudomaritima* is inferred to have undergone and to be undergoing continuing decline in EOO, AOO, quality of habitat, number of subpopulations, and number of mature individuals. This species occurs at four locations with respect to the most serious plausible threat, which is habitat degradation or loss due to land clearing and fire for subsistence agriculture. The occurrences within the protected areas of Mandena and Sainte Luce represent two separate locations. Occurrences outside of the Sainte Luce protected area, including sites north of the Ebakika river, represent the third location. The Ampasy forest subpopulation, which is comparatively less accessible, represents the fourth location. For these reasons, *D. pseudomaritima* is assigned a preliminary IUCN conservation status of Endangered: EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

Notes—Material of *Dalbergia pseudomaritima* has previously been included in or associated with *D. maritima* sensu Bosser and Rabevohitra (2002), mainly owing to their overlapping morphological variation with respect to leaflet size and number, and due to their occurrence in littoral forest. However, *D. pseudomaritima* differs by numerous characters of its leaves, inflorescences, flowers and fruits, as summarized in Fig. 3A–B and Table 3. By contrast, the inflorescence and flower characters of *D. pseudomaritima* are similar to those of the closely related *D. chapelieri* s.l., with which it shares an often conspicuous reticulate venation with open-ended highest-order veins on the lower leaflet laminae. The currently known geographic ranges of *D. chapelieri* s.l. and *D. pseudomaritima* do not appear to overlap locally, but the widely distributed *D. chapelieri* s.l. occurs both to the east and north of *D. pseudomaritima*. A single collection of *D. pseudomaritima* is known from a site located outside of the species' typical (remaining or former) littoral forest habitat (*Bernard et al. 2654*), on sandy lateritic soils near a stream. In the same general area, *D. pseudomaritima* might come into contact with neighboring populations from low-elevation evergreen humid forests attributed to the most closely related lineage within *D. chapelieri* s.l. (e.g. *Razakamalala 7739*, *Razakamalala 7765*, and *S. A. Andrianarivelo & Razakamalala 51*, Fig. 1H). However, *D. pseudomaritima* clearly differs from these individuals by its shorter leaves [(4–)5–8(–10) cm vs. (8–)10–13 cm long] with distinctly smaller leaflets [distal leaflets 7–15(–22) × 5–8(–12) mm vs. 24–40(–51) × 14–20(–25) mm] that are broadly elliptic to orbicular (vs. ovate to elliptic) and thinly coriaceous (vs. coriaceous) with plane (vs. strongly revolute) margins (Figs. 1F–H, 3A; Table 3), and no individuals with an intermediate leaf morphology (Fig. 3A) or genotype (Crameri 2020) have yet been found.

***Additional Specimens Examined*—Madagascar.** —Anosy [Toliara]: Ambanihazo village (Iabakoho commune), 31 Aug 2012 (st), *Ludovic 1570* (TAN); same locality, 25 Nov 2011 (fl), *Razakamalala et al. 6675* (MO, P, TAN); Ampasy forest (Iabakoho commune), 10 Feb 2019 (st), *Bernard et al. 2654* (DBEV, MO, P, TAN, ZT); Mandena protected area and surroundings, 21 Nov 1977 (st), *Ramamonjiarisoa 2* (P); same locality, same date (fl), *Ramamonjiarisoa 4* (P); same locality, same date (st), *Ramamonjiarisoa 5* (P); same locality, same date (st), *Ramamonjiarisoa 10* (P); same locality, 12 Jun 1991 (st), *Zarucchi et al. 7593* (K, MO, P); same locality, 7 Dec 1989 (fl), *Dumetz & McPherson 1139* (K, MO, P); same locality, 7 Apr 2014 (st), *Razakamalala 7783* (MO, P, TAN); same locality, Nov 1978 (fl), *Service Forestier 30547* (P); same locality, 16 Oct 1989 (bud), *Service Forestier 33262 = Rabevohitra 2033* (K, MO, P, TEF, WAG); Mandromodromotra, 6 Dec 2006 (fl), *Ramison & Ramisy 108* (MO, P, TAN); same locality, same date (y.fr), *Ramison & Ramisy 109* (MO, P, TAN); Sainte Luce protected area and surroundings, 22 Nov 2011 (y.fr), *Ratovoson 1713* (MO, P, TAN); same locality, 16 Jan 1990 (y.fr), *McPherson et al. 14804* (MO); same locality, 16 Oct 2008 (fl, y.fr), *Razafimandimby et al. 237* (TEF); same locality, 18 Nov 2004 (fl), *Raharimampionona et al. 1* (MO, P, TEF); same locality, 4 Nov 2003 (fl), *Rabenantoandro et al. 1556* (MO, P, TEF); same locality, 15 Dec 2000 (fl), *Faliniaina et al. 10* (L, MO, P, TEF, WAG); same locality, 18 Dec 1993 (y.fr), *Luckow 4150* (BH, K, MO, TAN, WAG, Z); same locality, 16 Jan 1990 (y.fr), *Dumetz 1195* (K, MO, P); same locality, 26 Apr 1989 (st), *Rabevohitra 1928* (MO, P); same locality, 15–16 Jan 1990 (y.fr), *Rabevohitra 2145* (K, MO, P, TEF); same locality, 17–18 Jan 1990 (fl), *Rabevohitra 2178* (K, MO, P, TEF); same locality, 6 Nov 2019 (st), *Razakamalala & S. A. Andrianarivelo 8566* (DBEV, MO, P, TAN, ZT); same locality, same date (fl), *Razakamalala & S. A. Andrianarivelo 8567* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Razakamalala & S. A. Andrianarivelo 8568* (DBEV, MO, P, TAN, ZT); same locality, same date (y.fr), *Razakamalala & S. A. Andrianarivelo 8569* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *Razakamalala & S. A. Andrianarivelo 8570* (DBEV, MO, P, TAN, ZT); same locality, same date (y.fr), *Razakamalala & S. A. Andrianarivelo 8571* (DBEV, MO, P, TAN, ZT); same locality, 5 Apr 2014 (st), *Razakamalala et al. 7767* (MO, P, TAN); same locality, 20 Oct 2012 (fl), *Razakamalala et al. 7228* (MO, P, TAN); same locality, 17 Oct 2012 (fl, y.fr), *Ramananjanahary et al. 780* (MO, P, TAN); same locality, 20 Oct 2012 (bud, fl, y.fr), *Ramananjanahary et al. 830* (MO, P, TAN); same locality, 29 Mar 1989 (fr), *Gereau et al. 3326* (K, MO, P, WAG); same locality, 7 Nov 2019 (st), *S. A. Andrianarivelo & Razakamalala 58* (DBEV, MO, P, TAN, ZT); same locality, same date (fl), *S. A. Andrianarivelo & Razakamalala 60* (DBEV, MO, P, TAN, ZT); same locality, same date (fl, y.fr), *S. A. Andrianarivelo & Razakamalala 63* (DBEV, MO, P, TAN, ZT); same locality, same date (st), *S. A. Andrianarivelo & Razakamalala 64* (DBEV, MO, P, TAN, ZT); same locality, same date (fl, y.fr), *S. A. Andrianarivelo & Razakamalala 65* (DBEV, MO, P, TAN, ZT).

Dalbergia razakamalalae Crameri, Phillipson & N.Wilding, sp. nov. Type: Madagascar. Anosy [Toliara]: Forêt d'Analamahavondjaky (commune de Iaboakoho), 7 Dec 2019 (fl), *T. Andriamihajarivo, N. H. Rakotoarivelo & F. Rakotoarivony 2455* (holotype: P [P00853053]!, isotypes: MO, TAN image!, ZT [ZT-00169820]).

Dalbergia razakamalalae is similar to *D. maritima* R.Vig. in possessing leaves with rather small leaflets and racemose inflorescences, but differs by its consistently glabrous leaves (vs. glabrous or pubescent), larger flowers (10–14 mm vs. 8–10 mm long), and narrowly ovate to narrowly elliptic leaflets (vs. ovate to elliptic) that are thinly coriaceous (vs. coriaceous) and have plane (vs. revolute) margins and frequently an emarginate (vs. obtuse to rounded) apex.

Deciduous tree to ca. 20 m tall, or shrub-like when resprouting after felling, bole to ca. 15 m high, DBH to at least 40 cm; bark gray-brown, smooth at first, becoming fissured with age. **Branches** glabrous, pale brown to purple-brown in vivo (dark brown to dark purple in sicco) when young, becoming gray-brown, lenticels present. **Leaves** alternate, 7–13(–16) cm long, with 11–19(–23) alternate leaflets, petiole and rachis purplish-green in vivo, dark brown to dark purple in sicco, glabrous; petiole (9–)12–20(–25) mm long; stipules narrowly ovate, ca. 3.0 × 1.0 mm, glabrous, early caducous; leaflets (8–)13–25(–35) × (4–)5–10(–14) mm, often noticeably smaller toward base or/and apex; petiolule 1.0–2.0 mm long, yellow-green in vivo, dark brown to dark purple in sicco, glabrous; lamina narrowly ovate to narrowly elliptic, rarely ovate to elliptic, thinly coriaceous, base cuneate, margins not revolute in sicco, apex emarginate, rarely obtuse, venation brochidodromous, with 5–7 principal lateral veins per side; upper surface matt, mid-green in vivo, dark purple-brown in sicco, glabrous, venation inconspicuous (slightly raised in sicco), midrib inconspicuous or forming a groove; lower surface paler than upper in vivo and in sicco, glabrous, venation forming a loose network with higher-order veins (often paler than matrix in sicco), midrib prominent. **Inflorescences** racemose, composed of (1–)4–12 alternate flowers each, often with imparipinnate reduced leaves subtending individual flowers especially near base (thus becoming single-flowered), sometimes pseudo-paniculate with smaller racemes (bearing abortive flower buds) branching off from close to base, 2–5 cm long; axes green to purple-green especially at apex in vivo, dark brown to dark purple in sicco, glabrous; anthesis before or concurrent with leaf emergence; peduncle to 6 mm long. **Flowers** often subtended by glabrous, imparipinnate reduced leaves, 22–57 mm long, with 7–13 alternate, narrowly ovate to narrowly elliptic leaflets, leaving visible scar, bracts not seen (early caducous and leaving visible scar); pedicel 2–4(–6) mm long, slender, glabrous; bracteoles lanceolate, ca. 2.5–3.0 × 0.6–0.8 mm, glabrous, early caducous; calyx base to apex of longest petal 10–14 mm long in sicco; calyx bright green to purple and brightly dotted especially at base in vivo, purple-brown, darker at base in sicco, with a 3.1–4.0 mm long tube, 7.0–8.2 mm long from base to apex of lower lobe, glabrous, persistent, 2 upper sepals long-connate, their lobes 2.3–3.9 × 2.5–2.9 mm, apex obtuse to rounded, 2 lateral sepals triangular, 3.2–4.2 × 1.5–2.2 mm, lowest sepal triangular, margins weakly incurved, apex slightly hooked, 3.2–4.2 × 1.4–2.2 mm; petals glabrous, white with often pink or bluish tinged veins at anthesis, dark yellow to dark cream in sicco; standard petal broadly obovate to orbicular, claw and lamina forming an obtuse angle, margins slightly incurved backwards when in full flower in vivo, base attenuate, apex notched, 9.6–11.5 × 5.8–9.2 mm, including 2.4–3.9 mm long claw; wing petals 7.3–10.8 × 2.2–3.2 mm, including 2.0–2.8 mm long claw, base distinctly auriculate; keel petals 7.3–9.3 × 2.4–2.9 mm, including 2.0–2.9 mm long claw, base distinctly auriculate; androecium glabrous, diadelphous, 6.4–10.3 mm long; stamens 9 + 1, free for upper 1.7–5.0 mm; gynoecium 7.0–7.7 mm long, glabrous; stipe ca. 3.5 mm long; ovary 4.3–5.5 mm long, with 3–5 ovules; style slender, slightly incurved, 1.4–1.8 mm long. **Fruits** (immature) purple-red to carmine in vivo, purple-brown in sicco, with 1–3 seeds, body oblong or narrowly elliptic, 3.5–5.5 × 0.8–1.5 cm when single-seeded, up to 7.5 × 1.7 cm when 3-seeded, base cuneate, apex rounded or acute, surface indistinctly net-veined, glabrous; stipe ca. 7–10 mm long; style rarely persistent. **Seeds** (immature) sub-reniform, flattened, brown, ca. 6 × 3 mm. Figures 1E, 2D, 5.

Etymology—*Dalbergia razakamalalae* is named in honor of the botanist Richardson Razakamalala, who has made more than 9000 high-quality collections over the last two decades, contributing significantly to the knowledge of the flora of Madagascar, and which have included collections of this and many other *Dalbergia* species made while working together with local guides and other members of the Missouri Botanical Garden's research team in Madagascar.

Vernacular Names and Uses—Sambalahimanga (*Andriamihajarivo et al. 2455*), Tombobitsy lahy (*Razakamalala & S. N. Andrianarivelo 8035*), Tongobitsy or Tambobitsy (*Réserves Naturelles 1689*).

The heartwood of *Dalbergia razakamalalae* is beautifully veined and burgundy-colored (*Bernard et al. 2645*, *Karatra & Rakotovao 242*, *Ramanitrinizaka & Sandratriniaina 1*). It is considered to be a high-quality rosewood (*Humbert 20607*) and is used in cabinet making (*Humbert 20355bis*).

Habitat, Distribution, and Phenology—*Dalbergia razakamalalae* occurs in inland low-elevation evergreen humid forests on lateritic soils, at 20–510 m elevation in southeastern Madagascar (Anosy and Atsimo-Atsinanana Regions). It occurs in and around the Tsitongambarika protected area, the Ankarabolava protected area, in the northern parcel of the Manombo protected area, and in the Ampotaky forest farther north and more inland of Tsitongambarika (Fig. 3D). *Dalbergia razakamalalae* has been collected in full flower from November to February. Immature to mature fruits have been recorded from December to February.

Conservation Status—*Dalbergia razakamalalae* is known from 42 positively identified collection records that represent 6 extant occurrences and 5 occurrences that appear to have been extirpated. Its former extent of occurrence (EOO) was at least 4293 km^2 and its former area of occupancy (AOO) was at least 80 km^2 (based on a 4 km^2 grid), whereas its current documented geographic range has the form of an EOO of 2096 km^2 and an AOO of 60 km^2, and comprises four subpopulations. The species occurs in forest ecosystems (Madagascar Catalogue 2021). Forest cover decline between 1953 and 2017 was estimated from the forest cover time series of Vieilledent et al. (2018a, 2018b) to be 73% in the altitudinal range of 20–510 m and within the minimum convex polygon encompassing all known collections of this species. Therefore, *D. razakamalalae* is inferred to have undergone and to be undergoing continuing decline in EOO, AOO, quality of habitat, number of subpopulations, and number of mature individuals. This species occurs at five locations with respect to the most serious plausible threat, which is selective logging for trade in its high-quality heartwood, as inferred from recent field observations of exploited trees at several sites. The occurrences within the protected areas of Ankarabolava, Manombo, and Tsitongambarika represent three separate locations. Occurrences outside of the Tsitongambarika protected area represent the fourth location. The subpopulation from the Ampotaky forest at Beampingaratry, which is situated at higher elevation and appears to be less accessible, represents the fifth location. For these reasons, *D. razakamalalae* is assigned a preliminary IUCN conservation status of Endangered: EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v).

Notes—Material of *Dalbergia razakamalalae* has previously been included in or associated with *D. maritima* sensu Bosser and Rabevohitra (2002), mainly owing to their overlapping morphological variation with respect to leaflet size, shape, and number, and to inflorescence structure. However, *D. razakamalalae* differs in its leaflet texture and margins, and in its larger flowers. Its flowers are similar in size to those of *D. louvelii* s.l., and it inhabits inland low-elevation evergreen humid forests like *D. maritima* subsp. *pubescens*, but unlike these taxa, its leaves are consistently glabrous, as summarized in Figs. 1E, 2D, 3A–B and Table 3. A specimen with both flowers (*Réserves Naturelles 1689*) and immature fruits (*Réserves Naturelles 1689bis*, collected 19 d later) was examined by Bosser and Rabevohitra in 1995, who associated it with both *D. maritima* and *D. louvelii* on account of its small and glabrous leaflets (as in *D. maritima* subsp. *maritima*) and large flowers (as in *D. louvelii*). They suggested that this collection might be a hybrid between these two taxa, without any evidence for the presence of *D. louvelii* in the region, and evidently without realizing that its morphology is consistent with other collections they saw from the same region and habitat type, viz. *Réserves Naturelles 1124* and *Service Forestier 22334*, both included in their broad definition of *D. maritima*, and potentially also *Humbert 20355bis* and *20607*, two sterile collections present in the Paris herbarium at the time. The collections made in the 1940s (*Humbert 20355bis*, *Réserves Naturelles 1689* and *1689bis*) from forests around Manantantely, and the collection from the 1960s from the Ivola forest (*Réserves Naturelles 1124*) increase the documented distribution range of *D. razakamalalae* southwards, including to the southern part of the Tsitongambarika protected area, but no extant occurrences are known from these areas, despite extensive recent collection efforts, so these populations are presumed to have been extirpated. Likewise, a sterile collection from Ambila in the Manakara district (*Service Forestier 38-R-118*) increases the documented range of *D. razakamalalae* by ca. 110 km to the north, but it probably dates from the 1950s and originates from a site that is not included in a protected area, so this possible subpopulation likewise probably no longer exists. A recently made sterile collection from the degraded forests of Fotobohitra in the Ifanadiana district (*Ravaomanalina 71*) may also represent *D. razakamalalae* and would further increase its range northwards, but the physical specimen could not yet be examined.

***Additional Specimens Examined*—Madagascar.** —Anosy [Toliara]: Ampotaky forest (Beampingaratry), 3 Dec 2019, *Karatra & Rakotovao 241* (DBEV, MO, P, TAN, ZT); same locality, 3 Dec 2019, *Karatra & Rakotovao 242* (DBEV, MO, P, TAN, ZT); Ivola forest (Tolagnaro district), s. d. (y.fr), *Réserves Naturelles 1124* (P); Manampanihy valley (Ampasimena), 18 Mar 1947, *Humbert 20607* (P); Manatantely forest (Tolagnaro district), 1 Mar 1947, *Humbert 20355bis* (MO, P, TAN); same locality, 20 Nov 1948 (fl), *Réserves Naturelles 1689* (P); same locality, 9 Dec 1948 (y.fr), *Réserves Naturelles 1689bis* (P); Tsitongambarika protected area and surroundings (Iabakoho commune), 6 Feb 2019 (fr), *Ramanitrinizaka & Sandratriniaina 1* (DBEV, MO, P, TAN, ZT); same locality, 9 Feb 2019, *Ramanitrinizaka & Sandratriniaina 12* (DBEV, P); same locality, 9 Feb 2019 (fr), *Ramanitrinizaka & Sandratriniaina 13* (DBEV, MO, P, TAN); same locality, same date, *Ramanitrinizaka & Sandratriniaina 18* (DBEV, MO, P); same locality, 12 Feb 2019, *Ramanitrinizaka & Sandratriniaina 25* (DBEV, MO, P); same locality, 7 Feb 2019, *Ramanitrinizaka & Sandratriniaina 57* (DBEV, MO, P); same locality, 16 Feb 2019, *Sandratriniaina & Ramanitrinizaka 23* (DBEV, MO, P); same locality, same date, *Sandratriniaina & Ramanitrinizaka 26* (DBEV, MO, P); same locality, same date, *Sandratriniaina & Ramanitrinizaka 27* (DBEV, MO, P); same locality, same date, *Sandratriniaina & Ramanitrinizaka 29* (DBEV, MO, P); same locality, 1 Apr 2014, *Razakamalala 7736* (MO, P, TAN); same locality, same date, *Razakamalala 7761* (MO, P, TAN); same locality, same date, *Razakamalala 7762* (MO, P, TAN); same locality, same date, *Razakamalala 7764* (MO, P, TAN); same locality, 12 Feb 2016, *Razakamalala & S. N. Andrianarivelo 8036* (MO, P, TAN, TEF, ZT); same locality, 14 Feb 2016 (fr), *Razakamalala & S. N. Andrianarivelo 8040* (MO, P, TAN, TEF, ZT); same locality, 4 Nov 2019, *S. A. Andrianarivelo & Razakamalala 53* (DBEV, MO, P, TAN, ZT); same locality, Feb 1963 (fl), *Service Forestier (Capuron) 22334* (P, TEF); Tsitongambarika protected area and surroundings (Manantenina commune/Ivohibe-Bemangidy/Antsotso), 11 Feb 2016, *Razakamalala & S. N. Andrianarivelo 8032* (MO, P, TAN, TEF, ZT); same locality, same date, *Razakamalala & S. N. Andrianarivelo 8035* (MO, P, TAN, TEF, ZT); same locality, 1 Nov 2019 (fl), *Razakamalala & S. A. Andrianarivelo 8558* (DBEV, MO, P, TAN, ZT); same locality, 2 Nov 2019, *Razakamalala & S. A. Andrianarivelo 8560* (DBEV, MO, P, TAN, ZT); same locality, 6 Feb 2019 (fr), *Razakamalala et al. 8266* (DBEV, MO, P, TAN, ZT); same locality, same date (fr), *Bernard et al. 2641* (DBEV, MO, P, TAN, ZT); same locality, 9 Feb 2019, *Bernard et al. 2645* (DBEV, MO, P, TAN, ZT); same locality, 11 Feb 2016, *S. N. Andrianarivelo & Razakamalala 255* (MO, P, TAN, TEF, ZT); Atsimo-Atsinanana [Fianarantsoa]: Amparihy (Ambitananona - Amparihy - Vangaindrano), 23 Nov 1953 (fl), *Service Forestier 7110* (P, TEF); Ankarabolava protected area, 20 Feb 2021, *Andriamiarisoa et al. 2620* (MO, P, TAN); Manombo Special Reserve, 5 Nov 2019, *Rakotovao & Andriamiarisoa 7522* (DBEV, MO, P, TAN, ZT); same locality, same date, *Rakotovao & Andriamiarisoa 7523* (DBEV, MO, P, TAN, ZT); same locality, same date, *Rakotovao & Andriamiarisoa 7528* (DBEV, MO, P, TAN, ZT); same locality, 28 Jan 2014, *Emeline 23* (MO, P, ZT); same locality, 4 Nov 2019, *Andriamiarisoa & Rakotovao 2424* (DBEV, MO, P, TAN, ZT); Fitovinany [Fianarantsoa]: Canton Ambila (Manakara district), s. d., *Service Forestier 38-R-118* (P).

Discussion

The morphological and ecological analyses presented here show that the two newly described species from southeastern Madagascar, *Dalbergia pseudomaritima* and *D. razakamalalae*, form two coherent and distinct morphological clusters (Fig. 3A–B), each associated with a different habitat type (Fig. 3C). Moreover, their geographic ranges are clearly different from those of *D. maritima* (as re-delimited here) and *D. louvelii* s.l. (Fig. 3D), which differ from one another in several characters of their leaves and flowers, co-occur in east-central Madagascar, and of which topotypic collections are more closely related to each other than either is to *D. razakamalalae* or *D. pseudomaritima* (Crameri 2020). The two subspecies of *D. maritima* can clearly be distinguished from one another based on the presence or absence of indument on the leaves, the inflorescence axis, and the gynoecium (Fig. 3A–B), as well as their apparent allopatric geographic distribution (Fig. 3D), which is associated with different habitat types (Fig. 3C).

The decision not to recognize *D. maritima* subsp. *pubescens* as a separate species reflects our adoption of a unified species concept (De Queiroz 2005, 2007), in which species are defined as segments of "separately evolving metapopulation lineages." A nested genetic analysis of over 90,000 polymorphic loci, distributed across 2396 nuclear regions, recovered 15 accessions of *D. maritima* as monophyletic and sister to *D. louvelii* s.s., but it failed to recover the two morphologically divergent subspecies as distinct genetic populations (see Fig. S5 in Crameri 2020). Due to this lack of genetic differentiation despite significant sequencing effort, a single unit encompassing both subspecies of *D. maritima* was recovered, rather than two units corresponding to the previously described infraspecific taxa, which consequently represents the single discovered group that requires species validation sensu Carstens et al. (2013). Moreover, the morphological distinction between the two subspecies relies exclusively on the consistent presence or absence of indument on various organs (leaves, inflorescence axes, and gynoecium). Although the genetics underlying plant indument are unknown for *Dalbergia*, studies from other plant groups indicate that the presence or absence of trichomes on various organs can be controlled by a single regulatory gene, with one allele dominant over the other (see e.g. Westerbergh 1992; Silvestre 2001; Kärkkäinen and Ågren 2002; Widén 2015). This fact, coupled with the generally high correlation of indument variables examined in our study (Fig. 3A–B), cast doubt on the statistical independence of these variables, reducing their cumulative relevance, and ultimately providing insufficient evidence for the recognition of separately evolving species.

Recognizing *Dalbergia maritima* subsp. *pubescens* at the infraspecific level will hopefully stimulate conservation efforts to ensure the survival of both entities, since ecological exchangeability (Crandall et al. 2000) between the two subspecies can be rejected based on their consistent differences in habitat type (Fig. 3C) and morphology. Specifically, the production of trichomes can be a defensive response to environmental stressors such as insect herbivory (see e.g. Levin 1973; Tian et al. 2012; Sato et al. 2019), and the presence of indument may therefore be of adaptive significance in *D. maritima* subsp. *pubescens*. We therefore regard the two subspecies of *D. maritima* as distinct evolutionary significant units (ESU, sensu Crandall et al. 2000) worthy of separate management and protection.

In light of the findings presented in this study and the resulting taxonomic changes, in particular the significantly narrowed delimitation of *Dalbergia maritima*, the associated trade names need to be modified accordingly. Precious wood harvested from forests in southeastern Madagascar and traded under the name *D. maritima* was presumably obtained from individuals of *D. razakamalalae*, the only known taxon in the region belonging to the Maritima clade. Normand (1988) noted more than three decades ago that rosewood attributed to *D. maritima* was being harvested especially in southeastern Madagascar because individuals of exploitable diameter had already become rare in the region of Tamatave (Toamasina) in the east-central part of the island by the 1920s, and in fact the leaf and leaflet illustrated in Normand (1988, Figs. 4–5) likely represent a specimen of *D. razakamalalae* (see our Figs. 1E, 2D). Likewise, precious wood exploited from northeastern Madagascar (Normand 1988, map on p. 91) and traded as *D. maritima* presumably was actually harvested from individuals of *D. louvelii* s.l., *D. occulta* (which was only described in 2005), and/or other taxa that occur in the region and still await formal description (Fig. 3D). This taxonomic confusion has important implications regarding the remaining number of large mature individuals of these species and the impact that further harvesting of precious wood would have on them (Waeber et al. 2019), which in turn significantly impacts whether they would meet the requirements for issuing a 'non-detriment finding,' as required for international commerce under CITES (Article IV-2a). The present study reveals the importance of conducting targeted field work, detailed taxonomic investigations, and thorough conservation assessments of tropical timber species of high economic value. It also confirms the conservation significance of Madagascar's remaining low-elevation eastern evergreen humid and littoral forests, and their importance as the habitat of a previously underestimated number of comparatively narrowly distributed and threatened rosewood species. Considerable parts of the remaining forests in the range of *D. razakamalalae*, *D. pseudomaritima*, and *D. maritima* subsp. *pubescens* are included in Madagascar's network of protected areas (but see Gardner et al. 2018 and Morelli et al. 2020). By contrast, only a small area in the distribution range of *D. maritima* subsp. *maritima* (i.e. the Vohibola forest) is currently afforded some level of protection by an association of volunteers from surrounding villages. The remaining patches of littoral forest in East Madagascar constitute a unique and highly threatened habitat (Ganzhorn et al. 2001; Bollen and Donati 2006). They harbour a disproportionally high diversity of plant species, which was estimated at 13% of Madagascar's total plant diversity, of which over 25% were considered as restricted to littoral forests (Consiglio et al. 2006). Since 2006, several patches of littoral forest have been added to Madagascar's network of protected areas (Goodman et al. 2018), but coverage of effectively protected areas remains low (Gardner et al. 2018) and should be expanded in the future.

This study, along with several others (Hassold 2015; Crameri 2020; Wilding et al. 2021a, 2021b), is part of an ongoing international effort to develop an improved taxonomy for *Dalbergia* species in Madagascar. The integration of morphological studies and eco-geographic considerations with phylogenomic and population genomic analyses, based on a much larger number of collections now available, has resulted in an increasingly comprehensive, nuanced, and informative understanding of the diversity within this taxonomically complex genus. It would likely not have been possible to resolve the taxonomic confusion regarding *D. maritima* without the significant insights provided by phylogenomic and population genomic analyses. In particular, the results of these analyses led to the important inference that differences in inflorescence structure are associated with two strongly divergent lineages (racemose in the Maritima clade, paniculate in the Chapelieri clade) within which there has been morphological convergence in leaflet size (small leaflets in *D. maritima*, the undescribed SAVA material, and *D. pseudomaritima*), while flower size, the presence or absence of indument, and eco-geography are informative at the species or subspecies level. The integration of morphology, eco-geography, and phylogenomics provides strong support for clarifying species limits and developing an improved taxonomy for the genus, and this approach is now being applied to the other groups of Malagasy *Dalbergia* that present taxonomic issues.

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Author Contributions

SC, PBP, NR, and NW carried out the taxonomic work, SC, PBP, and NR performed the morphological measurements, SC analyzed the morphological and ecological data and prepared the distribution map, NR and RLA performed field work, RLA prepared the illustrations, and SC wrote the manuscript with contributions from AW, PPL, PBP, and NW.

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