

Taxonomic studies on Malagasy Dalbergia (Fabaceae). V. Eight new large tree species and notes on related Malagasy species

Authors: Wilding, Nicholas, Phillipson, Peter B., and Crameri, Simon

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Taxonomic studies on Malagasy Dalbergia (Fabaceae). V. Eight new large tree species and notes on related Malagasy species

Nicholas Wilding, Peter B. Phillipson & Simon Crameri

Abstract

WILDING, N., P.B. PHILLIPSON & S. CRAMERI (2023). Taxonomic studies on Malagasy Dalbergia (Fabaceae). V. Eight new large tree species and notes on related Malagasy species. *Candollea* 78: 99–124. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2023v782a2

An ongoing revision of Malagasy *Dalbergia* L. f. (*Fabaceae*) has increased the number of recognized species from 48 to 64. Fifty-two (52) of the 64 are considered to grow large enough to be of potential commercial interest for their valuable timber. Eight large tree species, mostly from the north and west of Madagascar, are described and illustrated here for the first time, namely *Dalbergia bosseri* N. Wilding, Phillipson & Crameri; *D. karatrae* N. Wilding, Phillipson & Crameri; *D. rajeryi* N. Wilding, Phillipson & Crameri; *D. rajeryi* N. Wilding, Phillipson & Crameri; *D. rakotovaoi* Phillipson, N. Wilding & Crameri; *D. sambavensis* N. Wilding, Phillipson & Crameri and *D. soafarae* N. Wilding, Phillipson & Crameri. Risk of extinction assessments using the IUCN Red List criteria are provided and indicate that all eight species are threatened.

Résumé

WILDING, N., P.B. PHILLIPSON & S. CRAMERI (2023). Études taxonomiques sur les Dalbergia (Fabaceae) malgaches. V. Huit nouvelles espèces de grands arbres et notes sur les espèces malgaches apparentées. *Candollea* 78: 99–124. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2023v782a2

Une révision en cours du genre *Dalbergia* L. f. (*Fabaceae*) à Madagascar a fait passer le nombre d'espèces reconnues de 48 à 64. Cinquante-deux (52) de ces 64 espèces sont considérées comme ayant une taille suffisante pour présenter un potentiel intérêt commercial pour leur bois précieux. Huit espèces de grands arbres, principalement du nord et de l'ouest de Madagascar, sont décrites et illustrées ici pour la première fois, à savoir *Dalbergia bosseri* N. Wilding, Phillipson & Crameri; *D. karatrae* N. Wilding, Phillipson & Crameri; *D. leandrii* N. Wilding, Phillipson & Crameri; *D. oronjiae* N. Wilding, Phillipson & Crameri; *D. rakotovaoi* Phillipson, N. Wilding & Crameri; *D. sambavensis* N. Wilding, Phillipson & Crameri et *D. soafarae* N. Wilding, Phillipson & Crameri. Des évaluations du risque d'extinction utilisant les critères de la liste rouge de l'UICN sont fournies et indiquent que les huit espèces sont menacées.

Keywords

FABACEAE - Dalbergia - Madagascar - IUCN Red List - New species - Rosewood

Addresses of the authors:

NW: Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO 63110, U.S.A., Institut de Systématique, Évolution, et Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, C.P. 39, 57 rue Cuvier, 75005 Paris, France, and UMR PVBMT, Université de La Réunion, Pôle de Protection des Plantes, 7 chemin de l'IRAT, 97410 Saint-Pierre, Ile de La Réunion. E-mail: nwilding@mobot.org

PBP: Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO 63110, U.S.A. and Institut de Systématique, Évolution, et Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, C.P. 39, 57 rue Cuvier, 75005 Paris, France.

SC: Institute of Integrative Biology, ETH Zurich, Switzerland and Missouri Botanical Garden, P.O. Box 299, St. Louis, MO, 63166-0299, U.S.A.

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Introduction

A taxonomic account of Malagasy Dalbergia L. f. (Fabaceae) was published over 20 years ago as part of a monographic treatment of the Fabaceae of Madagascar (Bosser & RABEVOHITRA, 2002), which included 23 newly described species. This was followed by the publication of five additional species a few years later (Bosser & Rabevohitra, 2005), bringing the total number of native species recognized from Madagascar to 48. However, in the years following Bosser and Rabevohitra's work, it gradually became apparent that their much-improved taxonomy was not able to accommodate an increasing number of new collections, and that the genus would require additional study. Since 2018, a taxonomic revision of the Malagasy species of *Dalbergia* has been underway. This work was informed by over 2,400 new collections, and a genetic approach based on target enrichment sequencing and phylogenomic analysis targeting 2,396 nuclear loci (Crameri et al., 2022a) in 683 Dalbergia samples from Madagascar and the Comoros (Crameri, 2020). The phylogenomic analyses by Crameri (2020) have shown that all but two Malagasy species (D. bracteolata Baker and D. xerophila Bosser & R. Rabev.) belong to one of two species-rich and endemic clades (from here on Supergroup I & II), which are each more closely related to mainland African or Asian species than to each other. Careful morphological examination of the more than 5,000 collections now available has revealed numerous new species, including 5 that have already been described (Crameri et al., 2022b; Rakotonirina et al., 2023; Wilding et al., 2021a) and a further eight described in the present article. In addition, six taxa have been resurrected from synonymy (Wilding et al., 2021b; Madagascar Catalogue, 2023), and seven more new species will soon be published (Crameri et al., in prep.; Phillipson et al., in prep.). Our revised species delimitations for all the Malagasy species are available online via the Madagascar Catalogue (MADAGASCAR Catalogue, 2023).

Dalbergia trees are the primary source of rosewood, a valuable and highly prized hardwood obtained from various species throughout most of the range of this largely tropical genus. Madagascar has long been regarded as a source of high quality rosewood, but a massive increase in illegal and unsustainable exploitation of precious woods prompted CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) to place Malagasy species of Dalbergia on its Appendix II in 2013, resulting in a total embargo on international trade (Mason et al., 2016). Pressure has been mounting in Madagascar to end the embargo in order to generate badly needed foreign exchange, but sustainable exploitation would require careful control and regulation along the entire supply chain, from standing trees and cut logs to sawn wood and finished products ready for export, coupled with strict limits on the harvest of exploitable species and a

total ban on those that are assessed as threatened and that require properly planned and targeted conservation actions. An effective regulatory system would also depend on accurate identification of trees, logs, and cut wood (Schatz et al., 2021). In order to address this need, a consortium of Malagasy and international institutions established in 2017 is conducting an ambitious project that involves (1) field work to develop a reference library comprising voucher herbarium specimens, wood, bark, leaves, and silica gel-dried wood and leaf material, which is being used both for (2) taxonomic work to delimit and describe all Dalbergia species that are potential sources of precious woods and for (3) an integrated program to elucidate morphological characters, wood anatomical and spectrometric features, and DNA barcodes that can be used to (4) develop practical, reliable field identification tools and forensic wood identification protocols.

The present article is the fifth in the series of taxonomic articles, and formally describes eight additional new Dalbergia species from Madagascar. Each of these species is able to grow to a large enough size to be considered a potential source of valuable timber. This brings the total number of species of Dalbergia described and currently accepted by the project to 64, of which 52 species are known to grow into large, and potentially exploitable, trees. An additional six new large tree species are currently being described from the following three species complexes: D. chapelieri Baill., D. louvelii R. Vig., and D. maritima R. Vig., for publication in this series, thereby finalizing the process of naming all currently known potentially exploitable Dalbergia in Madagascar. We follow the criteria of Schatz et al. (2021) in considering large trees as those that attain at least a height of 20 m, and/or a diameter at breast height (DBH) of 20 cm. The DBH and height reported in our descriptions of large tree species is likely an underestimate of the actual maximum values for the species. Recorded observations of DBH and height are based on the sampling of accessible trees, and this inevitably introduces a bias towards smaller individuals.

The eight new species described in the present contribution are mostly known from the north and west of Madagascar, with one species, *Dalbergia soafarae* N. Wilding, Phillipson & Crameri, endemic to the south-east of the country (Fig. 1). *Dalbergia soafarae*, *D. bosseri* N. Wilding, Phillipson & Crameri from the north-west and *D. sambavensis* N. Wilding, Phillipson & Crameri from the north-east have highly restricted distribution ranges. With the exception of the two latter species, most of the eight species are known predominantly from within Madagascar's protected area (PA) network. Just two of the species, *D. leandrii* N. Wilding, Phillipson & Crameri and *D. rakotovaoi* Phillipson, N. Wilding & Crameri, have a relatively broad distribution range, extending over 500 km from the north to the south of their respective ranges (Fig. 1B).

The authors have the pleasure in naming six of the new species after botanists who have contributed to the exploration of the genus Dalbergia in Madagascar, while the other two are named after nearby locations. Each of the species treated below is provided with a full description, a discussion of its morphology, a comprehensive listing of specimens examined, and details of its geographic distribution, habitat, and ecogeographic preferences, along with line drawings and a map showing their approximate distribution ranges. A preliminary risk of extinction assessment is provided for each species following the IUCN Red List Categories and Criteria (IUCN, 2012), for which calculations of the area parameters of extent of occurrence (EOO) and area of occupancy (AOO) were performed using GeoCAT (BACHMAN et al., 2011). Because all the species treated here can develop into sufficiently large trees to be potential sources of valuable wood, geo-coordinates and detailed locality data have been withheld and public access to this information has been restricted. Full specimen records (with limited locality data) and colour photos are available under each species page through the Catalogue of the Plants of Madagascar (Madagascar Catalogue, 2023).

Taxonomy

Dalbergia bosseri N. Wilding, Phillipson & Crameri, **sp. nov.** (Fig. 2).

Holotypus: MADAGASCAR. Reg. Sofia [Prov. Mahajanga]: Maromandia, 4.IV.2017, y.fr., Hassold, N. Rakotonirina & Randrianaivo 711 (P [P02090166]!; iso-: MO image!, ZT [ZT-00139617, ZT-00139618]!).

Dalbergia bosseri N. Wilding, Phillipson & Crameri is most similar to D. oronjiae N. Wilding, Phillipson & Crameri and D. chlorocarpa R. Vig., but differs primarily from D. oronjiae in generally having a greater number [(17–)25–29(–31) vs. 17–23(–27)] of narrower [(2–)4–7 vs. (2–)3.5–9(–12) mm] leaflets, with margins usually recurved vs. plane in vivo, and longer (single-seeded) fruits (90–110 vs. (51–)65–95 mm), and from D. chlorocarpa by having fewer leaflets [(17–)25–29(–31) vs. (17–)29–35(–46)], which are glabrous on the upper surface.

Trees to c. 14 m or shrubs; DBH to 25 cm. Branches pubescent, yellow-green in vivo (black-brown in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, 5.5-13.5(-14.5) cm long, with (17-)25-29(-31) alternate leaflets; petioles and rachises pale green in vivo, brown to black in sicco, scattered pubescent, glabrescent; petiole 6-11 mm long; stipules caducous, 6×1.2 mm; leaflets $(6-)10-21 \times (2-)4-7$ mm, largest at mid- to upperleaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 0.3-1 mm long, pale green in vivo, brown to black in sicco, scattered pubescent; lamina oblong, oblong-ovate or elliptical, coriaceous, at times

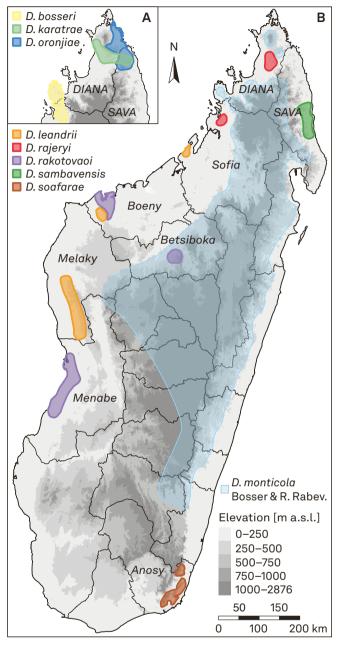


Fig. 1. – Approximate distribution ranges of the eight new large tree species of Malagasy *Dalbergia*, covering all known extant and historic collections of these species. Black borders represent regions of Madagascar, and are labeled where relevant. Elevation classes are indicated as shades of grey. A. Three new species restricted to the northern part of Madagascar; B. Three new species with disjunct distributions in northern and/or western Madagascar, and two new species with restricted distribution ranges in eastern Madagascar. The range of *D. monticola* Bosser & R. Rabev. was added to emphasize that it is not known to co-occur with the similar and closely related species *D. sambavensis* N. Wilding, Phillipson & Crameri and *D. soafarae* N. Wilding, Phillipson & Crameri.

becoming almost revolute when dry, base rounded, margin plane to strongly recurved, apex rounded or obtuse, venation

eucamptodromous, with 6–12 lateral veins per side; upper surface mid-green in vivo, pale- to dark-brown in sicco, matt, glabrous, the midrib forming a groove, the lower surface pale-green in vivo, pale- to dark-brown in sicco, matt, pubescent, higher-order veins not visible, midrib prominent. *Inflorescences* axillary or terminal, a panicle, 5–11 cm long (not seen, based on infructescence). *Flowers* not seen. *Fruits* pale-yellow green to dark green in vivo, mid- to dark-brown in sicco, the body elliptical, 90–110 × 20–30 mm when single-seeded (immature), or up to 140 mm long when multi-seeded (immature), base cuneate, apex acute or rounded, surface smooth with reticulate ribbing over the seed, glabrous; stipe 10–16 mm long, glabrous; style caducous.

Etymology. – The species epithet honors Jean Bosser (1922–2013), a French botanist employed by the Muséum national d'Histoire naturelle in Paris, and who worked extensively on the flora of Madagascar and the Mascarenes. Working with Raymond Rabevohitra, Bosser contributed significantly to knowledge of *Dalbergia* in Madagascar, through three publications on the genus, in which a total of 28 new species were described (Bosser & Rabevohitra, 1996, 2002, 2005).

Vernacular names and uses. – "Manary" (Service Forestier 38-R-152). The species has no reported uses, but given that it produces large enough trees, its hardwood is almost certainly used in the construction of furniture and housing. The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia bosseri occurs in lowland, moist-evergreen and drier forests in the Sambirano biogeographic region in the north-west (Fig. 1A), at elevations from 40 m to 300 m, on lateritic soils and sandstone outcrops. Dalbergia bosseri has not been collected in flower, but only in fruit in April and May. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia bosseri has an EOO of c. 273 km² and an estimated minimum AOO of 16 km² (based on a 4 km² grid). The species occurs in a single protected area (PA): the Ampasindava Protected Landscape (IUCN Category V), where it has been documented by two recent (< 4 years) collections, which were made within 400 m of each other. The species is further known from a single locality 5 km east of the Ampasindava PA, in the Forêt de Bongomihiravavy, and finally from a locality 5 km north of Maromandia along the RN6. The individual(s) at the locality close to the village of Ambodisaina near the town of Maromandia, recorded only by the Service Forestier de Madagascar in 1950, is considered to be extirpated. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture (known

locally as *tavy*) and wildfires. Selective logging both for construction and as a source of fuel are additional threats. These threats concern all localities both inside and outside of the Ampasindava PA (Goodman et al., 2018) to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, *D. bosseri* occurs at two locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B1ab(i,ii,iii, iv,v)+2ab(i,ii,iii,iiv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – A single specimen of this species (Service Forestier 38–R–152), determined anonymously as Dalbergia chlorocarpa, was present at P at the time that Bosser and Rabevohitra were revising the Malagasy species. This specimen was possibly seen by Bosser and Rabevohitra, but because the specimen is sterile and with immature leaves, they apparently placed it with a large pile of undetermined material. At the time of publishing this article, a single flowering collection (Randrianaivo et al. 3957) of the species was discovered. The specimen was collected during December 2021 from the same locality as the type. Only photographs of the specimen have been seen by the authors and the specimen was not yet available for examination or for measurement.

Dalbergia bosseri forms part of the group in Madagascar producing panicles with small flowers (Supergroup II sensu Crameri, 2020). The species is distinguished from other Malagasy Dalbergia by its leaves with up to 29(-31) small, oblong, oblong-ovate or elliptical leaflets. The species bears some resemblance to both *D. chlorocarpa* and *D. oronjiae*, but can be easily distinguished from these based solely on vegetative characters. Compared with D. chlorocarpa, D. bosseri possesses much fewer leaflets that are always glabrous on their upper surfaces. The leaflets of D. bosseri, while often more numerous than those of D. oronjiae, are narrower, have recurved margins (vs. plane in vivo), which can become more strongly recurved in sicco, and are glabrous on their upper surfaces. While flowers of D. bosseri have yet to be examined, the species is unique based on its vegetative morphology. In comparison to vegetative morphology, floral morphology is relatively conserved within the major Supergroups of Malagasy Dalbergia and provides little to no informative characters distinguishing among closely related and often vegetatively similar species.

The type specimen (Hassold et al. 711) and two other sequenced collections (Hassold et al. 712, Karatra & Ramanitrinizaka 155) form a coherent and distinct genetic lineage that is sister to Dalbergia oronjiae. Dalbergia bosseri, together with D. oronjiae, and two others from north Madagascar (D. abrahamii Bosser & R. Rabev. and D. urschii Bosser & R. Rabev.) compose a clade within the Chlorocarpa subgroup of Malagasy Dalbergia Supergroup II. The Chlorocarpa

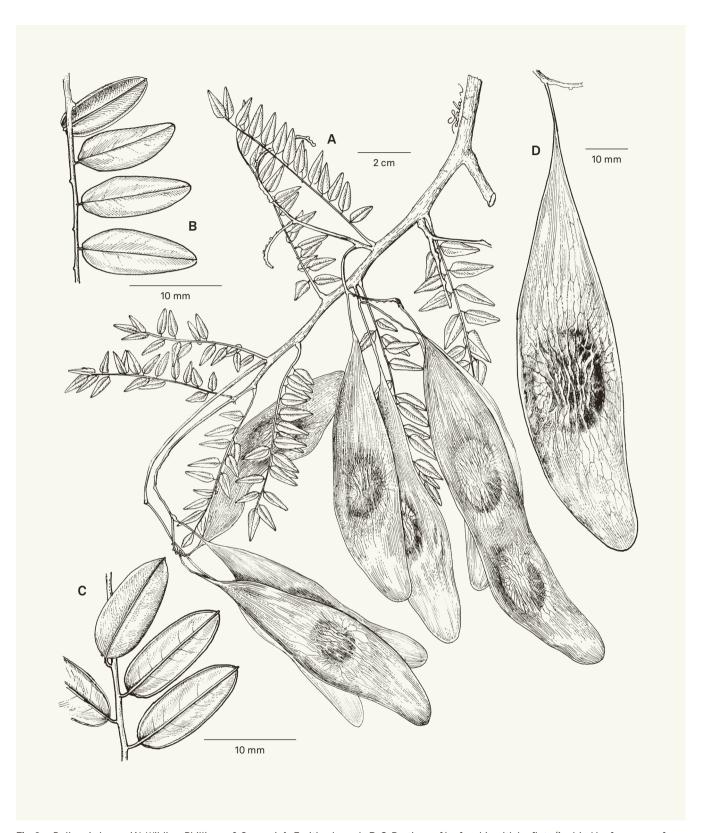


Fig. 2. – Dalbergia bosseri N. Wilding, Phillipson & Crameri. A. Fruiting branch; B, C. Portions of leaf rachis with leaflets (b: dried leaf, upper surface, the upper leaflet turned to show its lower surface; c: living leaf, lower surface, the upper leaflet turned to show its upper surface);
D. Immature fruit. [Hassold et al. 711, P] [Drawings: R.L. Andriamiarisoa]

subgroup further includes *D. chlorocarpa*, *D. davidii* Bosser & R. Rabev., *D. lemurica* Bosser & R. Rabev., and the basal lineage *D. trichocarpa* Baker (Crameri, 2020). Species of the Chlorocarpa subgroup are characterised by their leaves with leaflets that often dry to a dark brown or black colour.

Additional specimens examined. – MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: 29.VII.2019, ster., Karatra & Ramanitrinizaka 155, 160 (DBEV); 11.V.2012, y.fr., Tahinarivony & Rasoanaivo 643 (G, K, MO, P, TEF, UPS). Reg. Sofia [Prov. Mahajanga]: 4.IV.2017, ster., Hassold et al. 712 (TAN, ZT); 20.XII.2021, fl., Randrianaivo & Karatra 3957 (DBEV, G, MO, P, TAN); 29.X.1950, ster., Service Forestier 38-R-152 (P).

Dalbergia karatrae N. Wilding, Phillipson & Crameri, sp. nov. (Fig. 3).

Holotypus: MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: Ambilobe, Betsimiranja, 2.VII.2005, fl., *Guittou 155* (MO [MO-3042759]!; iso-: TAN!, CNARP).

Dalbergia karatrae N. Wilding, Phillipson & Crameri is similar to D. densicoma Baill., but differs in having leaves with a greater number of leaflets [(19-)33-43 vs. (16-)19-23], and inflorescence axes that are covered with a dense pubescent indument vs. glabrous or with a scattered indument in D. densicoma.

Trees to c. 14 m tall or shrubs; DBH to 40 cm. Branches tomentose, yellow-green in vivo (brown in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, 13-20 cm long, with (19-)33-43 alternate leaflets; petioles and rachises pale green in vivo, brown in sicco, tomentose; petiole 8-13 mm long; stipules caducous, $5-7 \times 1.2-2.3$ mm; leaflets $7-32 \times 3-7$ mm, the largest at midto upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 0.9-1.2 mm long, pale green-brown in vivo, light to dark-brown in sicco, tomentose; lamina oblong, lanceolate or less often narrowly elliptical or ovate in proximal leaflets, coriaceous, base rounded to truncate, margin strongly recurved, apex rounded, acute to obtuse, venation not visible; upper surface mid-green in vivo, brown in sicco, matt, pubescent, the midrib forming a groove, the lower surface mid-green in vivo, brown in sicco, matt, tomentose, secondary and higher-order veins not visible, midrib prominent. Inflorescences terminal, a panicle, 8-15 cm long, comprised of 10-20 paniculate secondary branches, subtended by a caducous, scale-like bract (not seen, visible scar observed); peduncle to 2 cm; terminal axes of the inflorescence short, clustered panicles comprised of up to 10 flowers, the axes densely golden-brown to reddish pubescent. Flowers subtended by a caducous, pubescent, triangular scale-like bract, $0.6-0.8 \times 0.6$ mm; pedicel 0.5-2 mm long, pubescent; bracteoles not seen (visible scars observed); calyx not seen in vivo, becoming dark orange to reddish-brown or black in sicco, glabrescent, persisting on fruits, 3.5-3.9 mm long, fused in the

lower ½, the 2 upper lobes obtuse, 1.5×1.5 mm, the 2 lateral lobes acute, $1.5-1.8 \times 0.9$ mm, the lowest lobe acute-triangular, keeled, 2×1.2 mm; petals glabrous, white in vivo becoming yellow to reddish-orange in sicco; standard petal broadly obovate, 6.3×5.1 mm, claw 1.1 mm long, apex notched; wing petals $5.5-5.8 \times 1.6-1.7$ mm, claw 0.7-0.9 mm long; keel petals 5×2 mm, claw 1 mm long; androecium glabrous, monadelphous, 5 mm long; stamens 9-10, filaments free for upper ½; gynoecium 5.7 mm long, glabrous; stipe 1.2 mm long; ovary 3.1 mm long, with up to 3 ovules; style 1.4 mm long. *Fruits* green in vivo, mid-to red-brown in sicco, the body elliptical to oblong, $30-40 \times 12-15$ mm when single-seeded (immature), to 60 mm when 2-seeded (immature), base attenuate, apex acuminate, surface smooth, glabrous; stipe 3-5 mm long, glabrous; style caducous.

Etymology. – The species epithet honors Dochard Aimé Karatra, an enthusiastic young Malagasy botanist employed on the G3D (Gestion Durable des bois précieux Dalbergia et Diospyros de Madagascar) project, who has made a significant contribution towards our improved understanding of this new species and for Malagasy Dalbergia in general, through his collecting efforts.

Vernacular names and uses. – "Manary" (Guittou 155). The species has no reported uses, but given that it produces large enough trees, its hardwood is almost certainly used in the construction of furniture and housing. The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia karatrae occurs in dry forests in the north (Fig. 1A), at elevations from 45 to 330 m, on basement rock derived substrates, including laterites over limestone. It has been collected in flower in July, and in fruit in September. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia karatrae has an EOO of c. 1,093 km² and an estimated minimum AOO of 24 km² (based on a 4 km² grid). The species occurs in three PAs: Andrafiamena-Andavakoera and Ankarana in the DIANA Region, and Loky-Manambato in the SAVA Region (IUCN categories V, IV and V, respectively). In Loky-Manambato the species is known from four recent collections, all within 2 km of each other, while only single collections are recorded from each of the other PAs. In addition, the species is known from a single locality between Ankarana and Andrafiamena-Andavakoera PAs, and from a final locality in the DIANA Region, to the west of Montagne d'Ambre National Park, in the forêt d'Antsoroby. The species is threatened from habitat loss and degradation resulting from slash and burn agriculture and wildfires. Fire is used to clear vegetation to facilitate



Fig. 3. – Dalbergia karatrae N. Wilding, Phillipson & Crameri. A. Flowering branch; B. Portion of leaf rachis with leaflets (lower surface); C. Infructescence; D. Flower; E. Calyx (outer surface, split open and flattened); F. Standard petal (adaxial surface); G. Wing petal (adaxial surface); H. Keel petal (adaxial surface); I. Androecium (adaxial surface, flattened); J. Gynoecium. [A, B, D–J: Guittou 155, MO; C: Andriamihajarivo et al. 1430, MO] [Drawings: R.L. Andriamiarisoa]

mineral extraction, and also for creating and renewing pastures. Selective logging, both for construction and as a source of fuel, is an additional threat. These threats concern all known localities both inside and outside of the PAs (Goodman et al., 2018), but to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, *D. karatrae* occurs at four locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN Blab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Most of the available collections of this species are sterile, however, we can confidently associate these with the leafy, flowering material of the type collection (Guittou 155). We also include in this species a fruiting collection (Andriamihajarivo et al. 1430), which has only very young leaves. The exceptionally large number of leaflets corresponds with that of the other material, and the structure and indument of the infructescence matches well that of the type collection.

The morphology of Dalbergia karatrae, with its large flowers and many small, oblong to lanceolate or elliptical, pubescent leaflets that dry to a reddish-orange colour, clearly allies it with D. densicoma. It can be distinguished from this species by its leaves (particularly those on sterile branches) that possess a greater number of leaflets, and its densely pubescent inflorescence axes, vs. glabrous or sparsely pubescent in D. densicoma. Among the Malagasy Dalbergia species, it has been observed that leaf size and leaflet number decrease significantly with distance to the inflorescence, hence, lowest bounds on leaf size and leaflet number often relate to leaves from flowering branches. Further work is required to establish whether this is a general characteristic of the genus. Both D. karatrae and D. densicoma appear to flourish on a diversity of substrates throughout their respective ranges and have been found growing together. Sterile specimens may also appear superficially similar to D. glaucocarpa Bosser & R. Rabev., owing to a similarly large number of leaflets observed in both species. The latter species, however, belongs to Supergroup II, which is mainly characterised by smaller flowers with a calyx that lacks soluble dark pigments (vs. larger flowers and calyx with a dark red to purplish pigment that is soluble in water and ethanol in Supergroup I), and a pubescent gynoecium (vs. a mostly glabrous gynoecium in Supergroup I). Additionally, leaflets of D. glaucocarpa also differ in shape (base shallowly cordate, apex often acute), and become brownish rather than reddish when dried.

The type specimen and two other sequenced collections (Hassold et al. 698, Karatra & Ramanantsialonina 18) form a coherent and distinct genetic lineage that represents a basal clade in the Pervillei subgroup of Supergroup I. The species is resolved in a position sister to the crown group, which

comprises *Dalbergia pervillei* Vatke and *D. tsiandalana* R. Vig. in a clade sister to *D. densicoma* (Crameri, 2020).

Additional specimens examined. — MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: 27.IX.2007, fr., Andriamihajarivo et al. 1430 (MO, P, TAN); 3.IV.2017, ster., Hassold et al. 698 (TAN, ZT); 23.III.2020, ster., Ravaoherinavalona et al. 128 (DBEV, MO, P, TAN, ZT). Reg. SAVA [Prov. Antsiranana]: 14.II.2019, ster., Karatra & Ramanantsialonina 14, 16, 17, 18 (DBEV, MO, P); 5.II.2019, ster., Karatra & Ramanantsialonina 21 (DBEV).

Dalbergia leandrii N. Wilding, Phillipson & Crameri, **sp. nov.** (Fig. 4).

Holotypus: MADAGASCAR. Reg. Menabe [Prov. Mahajanga]: Beanka Protected Area, 19.XI.2011, fl., Gautier, Tahinarivony & Bolliger 5660 (G [G00376089]!; iso-: TEF).

Dalbergia leandrii N. Wilding, Phillipson & Crameri is most similar to D. lemurica Bosser & R. Rabev. and D. davidii Bosser & R. Rabev., however, it is easily distinguished from both by having leaves with a greater number of leaflets [(10–)20–47 vs. (8–)11–17 in D. lemurica and (15–)17–22(–25) in D. davidii], which are pubescent on the upper surfaces vs. glabrous in D. lemurica and D. davidii.

Trees to c. 20 m or shrubs; DBH to 100 cm. Branches pubescent, colour unknown in vivo (black-brown in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, (3.3–)6–10 cm long, with (10–)20–47 alternate leaflets; petioles and rachises pale green in vivo, brown to black in sicco, pubescent, glabrescent; petiole 8-15 mm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets $(2.5-)5-11(-15) \times (1.3-)2-4.5$ mm, largest at mid- to upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 0.4-1 mm long, pale green in vivo, dark-brown to black in sicco, pubescent; lamina oblong, oblong-ovate or less often obovate, at times suborbicular in smaller proximal leaflets, thinly coriaceous, base rounded, margin plane to recurved, apex rounded to obtuse, sometimes retuse, venation not visible; upper surface mid-green in vivo, brown to dark brown in sicco, slightly glossy, pubescent, the midrib forming a groove, the lower surface pale grey-green in vivo, brown to dark brown in sicco, matt, pubescent, higher-order veins sometimes forming a fine network, midrib prominent. Inflorescences axillary or terminal, a panicle, 1.5-4 cm long, comprised of a series of paniculate units, subtended by a reduced pinnate leaf-like bract or a caducous, scale-like bract; peduncle to 1.2 cm long; terminal axes of the inflorescence usually short, with flowers forming clusters, the axes white to yellow pubescent. Flowers subtended by a persistent, pubescent, triangular scale-like bract, 0.6-0.8 × 0.6 mm; pedicel 0.5–1.5 mm long, pubescent; bracteoles ovate, concave, 0.9-1 × 0.6-0.7 mm, apex rounded, pubescent, dark orangebrown to black in sicco, persistent; calyx yellow-green in vivo,

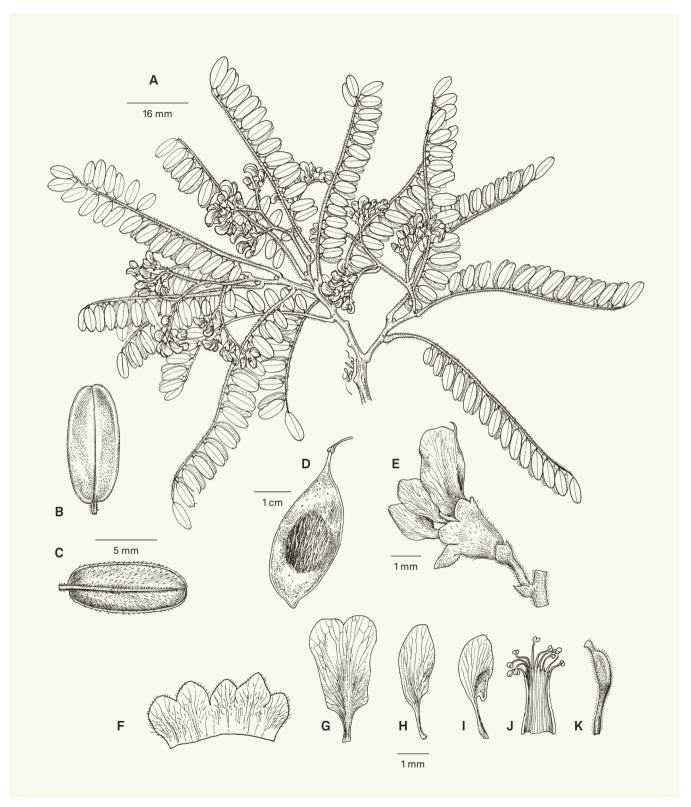


Fig. 4. – Dalbergia leandrii N. Wilding, Phillipson & Crameri. A. Flowering branch; B, C. Leaflets (b: upper surface; c: lower surface); D. Mature fruit; E. Flower; F. Calyx (outer surface, split open and flattened); G. Standard petal (adaxial surface); H. Wing petal (adaxial surface); I. Keel petal (adaxial surface); J. Androecium (adaxial surface, flattened); K. Gynoecium. [A-C, E-K: Gautier et al. 5660, G; D: Rasoafaranaivo 255, P] [Drawings: R.L. Andriamiarisoa]

becoming dark orange-brown to black in sicco, minutely pubescent, not persisting on fruits, 2–2.6 mm long, fused in the lower ½-3, the 2 upper lobes fused to form a single, rounded unit, 0.5×2 mm, the apex shallowly emarginate, the 2 lateral lobes rounded to obtuse, 0.5 × 0.8 mm, the lowest lobe acutetriangular, keeled, 1.2 × 1.1 mm; petals glabrous, white to cream in vivo becoming cream to red-orange in sicco; standard petal pandurate, $3.7-4.7 \times 2-2.6$ mm, claw 0.5-0.8 mm long, apex notched; wing petals 3.4-4.5 × 0.9-1.3 mm, claw 0.6-0.9 mm long; keel petals $3.4-3.5 \times 1.2-1.4$ mm, claw 1–1.4 mm long; androecium glabrous, monadelphous, 3–3.9 mm long; stamens 10, filaments free for upper \(\frac{1}{3}\)-\(\frac{1}{4}\); gynoecium 3-3.8 mm long; stipe densely covered in long yellowish-white hairs, 1.1-1.8 mm long; ovary densely covered in long yellowish-white hairs, 1.3 mm long, with up to 2 ovules; style glabrous, 0.7 mm long. Fruits pale yellow-green to dark green in vivo, mid-brown to black in sicco, the body broadly-elliptical, $40-60 \times 15-19$ mm when single-seeded, multi-seeded not observed, base cuneate, apex acute or rounded, surface smooth or longitudinally ribbed over the seed, glabrous; stipe 2-4 mm long, glabrous; style caducous.

Etymology. – The species epithet honors Jacques Désiré Léandri (1903–1982), a French botanist employed by the Muséum National d'Histoire Naturelle in Paris. In 1960, together with Pierre Saboureau, Leandri made the first collection of *Dalbergia leandrii* in the Bemaraha National Park during his third and last expedition to Madagascar.

Vernacular names and uses — "Manary bomby" (Rasoafaranaivo 255). The dark brown coloured heartwood (see Randrianaivo 3378) of the species is reportedly used in construction (Rasoafaranaivo 255). The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia leandrii occurs in dry deciduous forest, in the west and north-west (Fig. 1B), at elevations near sea level to 250 m, and is known to occur exclusively on limestone soils. Dalbergia leandrii has been collected in flower from November to December, and in fruit from January to March. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia leandrii has an EOO of c. 32,928 km² and an estimated minimum AOO of 32 km² (based on a 4 km² grid). The species occurs in three PAs: Beanka Protected Landscape (IUCN Category V), where it has been documented by four collections made from 2011–2012, all on the forest periphery; Bemaraha National Park (NP) (IUCN Category II), where it was first collected in 1960 and subsequently recollected in 2019; Namoroka NP (IUCN Category II), where 21 collections were made in 2021,

all within 250 m of each other. The species is also known from a single collection made in 2007 near Antsohihy, in the Sofia Region, and this is the only known locality not within a PA. The locality of the first collection of the species made by Léandri and Saboureau cannot be precisely geo-located and therefore cannot be considered in the assessment. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture and wildfires. Selective logging both for construction and as a source of fuel are additional threats. These threats concern all localities both inside and outside of the PAs (GOODMAN et al., 2018) to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, D. leandrii occurs at three locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Only one collection of Dalbergia leandrii (Léandri & Saboureau 2728) was seen by Bosser and Rabevohitra, which they included in D. lemurica with some hesitation (see Bosser & Rabevohitra, 1996). This was presumably because it was recorded from a calcareous substrate and had a much greater number of leaflets than other material they included in D. lemurica.

Morphologically, *Dalbergia leandrii* approaches *D. davidii* and *D. lemurica*, which both possess leaves with similarly small leaflets, and small-flowered panicles. However, the species can be easily distinguished from the aforementioned taxa by its leaves, which possess a greater number of leaflets with pubescent upper surfaces vs. glabrous upper surfaces in *D. davidii* and *D. lemurica*. The flowers of *D. leandrii* have been noted to have a strong odour of pea soup (fide *Gautier et al. 5660*). *Dalbergia leandrii* occurs exclusively on calcareous substrates just to the north of the known range of *D. lemurica*, which occurs on unconsolidated sands. Its range overlaps with that of *D. davidii*, but that species is found predominantly on sandy substrates, and extends much further inland notably at Ankarafantsika.

Five sequenced collections (Hanitrarivo et al. 57, 310, Leandri & Saboureau 2728, Rakotovao & Randrianaivo 7448, Randrianaivo et al. 3378) form a coherent and clearly distinct but rather isolated genetic lineage that cannot be confidently assigned to any clade within Supergroup II, however, it shows affinities to the Greveana subgroup and specifically to Dalbergia purpurascens Baill. (Crameri, 2020).

Additional specimens examined. — MADAGASCAR. Reg. Boeny [Prov. Mahajanga]: 22.VI.2021, ster., S.A.F. Andrianarivelo & Razakamalala 284, 289, 293, 294, 296, 297, 298, 299, 300, 301 (DBEV, MO, P, TAN); 24.VI.2021, ster., Razakamalala & S.A.F. Andrianarivelo 8935, 8939, 8940, 8941, 8942, 8944, 8945, 8946, 8947, 8948, 8949 (DBEV, MO, P, TAN, ZT). Reg. Melaky [Prov. Mahajanga]: 19.XII.2011, fl., Hanitrarivo et al. 57 (G, TEF); 10.III.2011,

fr., Hanitrarivo et al. 310 (G, TEF); 21.I.1960, y.fr., Leandri & Saboureau 2728 (MO, P); 12.XI.2012, fl., Rakotovao et al. 6208 (G, MO, P, TAN); 12.XI.2012, fl., Rakotovao & Randrianaivo 7448 (DBEV, MO, P, TAN, ZT); 9.IV.2019, fr., Randrianaivo et al. 3378 (DBEV, MO, P, TAN, ZT). Reg. Sofia [Prov. Mahajanga]: 19.VIII.2007, fr., Rasoafaranaivo 255 (MO, P, TAN).

Dalbergia oronjiae N. Wilding, Phillipson & Crameri, **sp. nov.** (Fig. 5).

Holotypus: MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: forêt d'Orangea, à l'E de Diégo-Suarez, 24.IV.1966, fr., Service Forestier 24684 (P [P00049309]!; iso-: MO [MO-3042697]!, P [P00049310]!, TEF [TEF000893]!).

Dalbergia oronjiae N. Wilding, Phillipson & Crameri is similar to D. lemurica Bosser & Rabev. and D. bosseri N. Wilding, Phillipson & Crameri, but primarily differs from the former in having a greater number of leaflets [(17–23(–27) vs. (8–)11–17)], and more slender fruits, and from the latter by having fewer leaflets [(17–23(–27) vs. (17–)25–29(–31)] and shorter (single-seeded) fruits [(51–)65–95 vs. 90–110 mm].

Trees to c. 20 m or shrubs; DBH to 56 cm. Branches pubescent, yellow-green in vivo (black in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, (4.5–)7–12 cm long, with 17–23(–27) alternate leaflets; petioles and rachises yellow to pale green in vivo, brown to black in sicco, pubescent, glabrescent; petiole 4-15 mm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets $(3-)9-22(-29) \times (2-)3.5-9(-12)$ mm, largest at midto upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 0.3-1 mm long, yellow to pale green or brown in vivo, dark-brown to black in sicco, pubescent; lamina oblong or obovate, coriaceous, base rounded to cuneate or subcordate, margin plane, apex rounded, obtuse or retuse, often mucronulate, venation eucamptodromous, with 5-8 lateral veins per side; upper surface bright- to mid- or blue-green in vivo, dull green to grey-black in sicco, matt, glabrescent, the midrib forming a groove, the lower surface paler, grey-green in vivo, pale green to grey or black in sicco, matt, pubescent, higher-order veins forming a fine network, midrib prominent. Inflorescences terminal, a panicle, 6-7 cm long, comprised of a series of paniculate units, subtended by a reduced pinnate leaf-like bract or a caducous, scale-like bract; peduncle to 1.5 cm long; terminal axes of the inflorescence often long, curved, secundiflorous and sub-spicate, with flowers in 2 adjacent rows with alternating insertion, the axes almost glabrous to white or yellow pubescent. Flowers subtended by a persistent, pubescent, triangular scale-like bract, 0.8-0.9 × 0.8-1 mm; pedicel 1–2 mm long, glabrous to pubescent; bracteoles ovate to elliptic, concave, 1.1–1.4 × 0.8–1.2 mm, apex rounded to acute, pubescent, dark orange-brown to black in sicco, caducous; calyx yellow-green in vivo, becoming dark orange-brown to black in

sicco, pubescent or sometimes nearly glabrous, not persisting on fruits, 3.5-4.6 mm long, fused in the lower ½-2/3, the 2 upper lobes rounded, 1.1–1.4 × 1.2–1.5 mm, the 2 lateral lobes obtuse, $0.9-1 \times 1-1.1$ mm, the lowest lobe acute-triangular, keeled, 1.5–1.9 mm × 1.2–1.4 mm; petals glabrous or with a pubescent patch on the distal surface of the standard and keel, white in vivo becoming yellow to orange-brown in sicco; standard petal pandurate, $3.6-4.6 \times 2.6-3$ mm, claw 1.1-1.5 mm long, apex notched; wing petals $3.8-4.6 \times 1.1-1.4 \text{ mm}$, claw 1.1-1.7 mmlong; keel petals $3.6-4.3 \times 1.4-1.7$ mm, claw 1.2-1.6 mm long; androecium glabrous, monadelphous, 3.6-4.5 mm long; stamens 9-10, filaments free for upper 1/3-1/4, sometimes with one or two pairs completely fused; gynoecium 3.6-4.2 mm long; stipe densely covered in long yellowish hairs, 1.6-2.1 mm long; ovary densely covered in long yellowish hairs, 1-1.3 mm long, with up to 4 ovules; style glabrous, 1–1.2 mm long. Fruits pale yellowgreen to dark green in vivo, mid- to dark-brown in sicco, the body elliptical, obovate or oblong, (51–)65–95 × 18–25 mm when single-seeded, or up to 110 mm long when multi-seeded, base cuneate, apex acute rarely rounded, surface with longitudinal ribbing, glabrous; stipe 9-20 mm long, pubescent; style caducous.

Etymology. – The species is named after its type locality, the Oronjia Protected Area, where it is particularly well-represented.

Vernacular names and uses. — "Ma(g)nary" (Randriama-hazomanana 311, 314, 328, Service Forestier 9426); "Palissandre rouge" (Service Forestier 21792). The reddish-brown coloured heartwood (see Randrianaivo 3524) of the species is reportedly used in the fabrication of furniture and housing (Louvel 2bis). The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia oronjiae occurs in dense lowland deciduous shrubland and in dry forest in the north (Fig. 1A), at elevations near sea level to 600 m, on a diversity of substrates including unconsolidated sands, laterites, and limestone. Dalbergia oronjiae has been collected in flower from November to March, and in fruit from January to May. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia oronjiae has an EOO of c. 2,025 km² and an estimated minimum AOO of 64 km² (based on a 4 km² grid). The species occurs within four PAs: Analamerana Special Reserve (IUCN Category IV), where it is known from 24 recent collections at four localities; the Loky-Manambato Protected Landscape (IUCN Category V), where it is known from 4 collections, each one at a separate locality; Montagne des Français (Ambohitr'Antsingy) Protected Landscape (IUCN Category V), where it is known

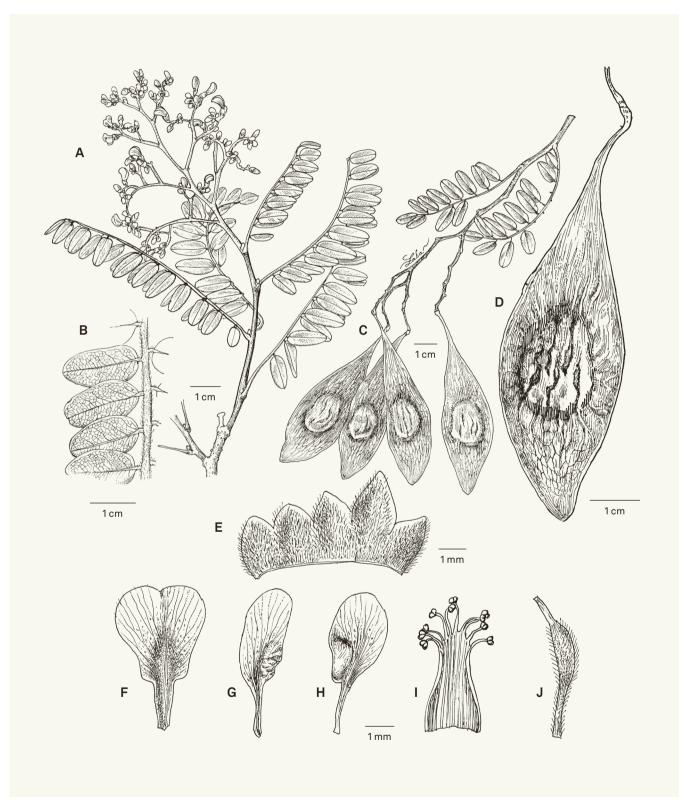


Fig. 5. – Dalbergia oronjiae N. Wilding, Phillipson & Crameri. A. Flowering branch; B. Portion of leaf rachis with leaflets (lower surface); C. Fruiting branch; D. Mature fruit; E. Calyx (outer surface, split open and flattened); F. Standard petal (adaxial surface); G. Wing petal (adaxial surface); H. Keel petal (adaxial surface); I. Androecium (adaxial surface, flattened); J. Gynoecium. [A, B, E–J: Ramanitrinizaka & Ravaomanalina 154, P; C, D: Service Forestier 24684, P] [Drawings: R.L. Andriamiarisoa]

from a single collection; Oronjia Protected Landscape (IUCN Category V), where the species is represented by over 30, mostly recent collections, and where the species appears to grow abundantly. The species is also known from a number of localities around 10 km to the north and north-west of Analamerana, and also between Oronjia and Montagne des Français. The precise localities of collections made prior to 1967 cannot be determined and therefore cannot be considered in the assessment. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture and wildfires. Selective logging both for construction and as a source of fuel are additional threats. For example, Goodman et al. (2018) report an 89% loss of moist evergreen forest in Analamerana PA between 1996 and 2016. These threats concern all localities both inside and outside of the PAs (GOODMAN et al., 2018) to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, D. oronjiae occurs at four locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Material assigned to Dalbergia oronjiae was previously treated by Bosser & Rabevohitra (2002) as a part of D. lemurica, which they considered to be distributed from the Menabe Region in the south-west to the DIANA Region, including the Forêt de Oronjia in the north.

Morphologically, *Dalbergia oronjiae* could be confused with *D. bosseri* and *D. lemurica*, both Supergroup II species that possess leaves with numerous small leaflets. In comparison with *D. bosseri*, the leaflets of *D. oronjiae* are typically fewer in number, wider, have plane margins and glabrescent upper surfaces, and shorter (single-seeded) fruits. The species differs from *D. lemurica* by its leaves, which typically possess a greater number of leaflets, and by its slender fruits. Neither of the aforementioned species are known or suspected to co-occur with *D. oronjiae*, hence, there is little possibility of confusion when geographic origin is known.

Genetic analyses based on 2,396 nuclear loci clearly show that material of *Dalbergia lemurica* (sensu Bosser & Rabevohitra, 1996), from the type locality of Kirindy in the Menabe Region, and material from the north, both form coherent but separate evolutionary lineages (Crameri, 2020), the latter of which we describe as *D. oronjiae*. According to Crameri (2020), *D. oronjiae* is most closely related to *D. bosseri* from north-west Madagascar, and to two other species from north Madagascar (*D. abrahamii* Bosser & R. Rabev. and *D. urschii* Bosser & R. Rabev.), which together compose a northern clade within the Chlorocarpa subgroup.

Additional specimens examined. - MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: 16.VII.2019, ster., Andriamiadana 2, 3, 4, 10, 11, 12 (DBEV, P, ZT); 17.VII.2019, ster., Andriamiadana 17, 18, 19, 20, 21 (DBEV, P, ZT); 18.VII.2019, ster., Andriamiadana 22, 23, 24, 25, 26, 27, 28, 29, 30 (DBEV, P, ZT); 15.XII.2019, ster., Andriamiarisoa et al. 2461 (DBEV, MO, P, TAN, ZT); 8.V.2007, fr., Bardot-Vaucoulon et al. 1773 (K, MO, P, TAN); 8.I.2009, y.fr., Christian et al. 93 (CNARP, MO, P, TAN); 1.IV.1994, fr., Du Puy et al. M771 (K, MO, P); 2.IV.2017, ster., Hassold et al. 690 (MO, TAN, ZT); 2.IV.2017, ster., Hassold et al. 691 (TAN, ZT); 17.II.2019, ster., Karatra et al. 52 (DBEV, MO, P, TAN, ZT); 29.IV.2022, fr., Karatra et al. 557 (DBEV, MO, P, TAN, ZT); [without date], ster., Louvel 2bis (P); 13.IV.2014, fr., Rakotoarisoa et al. 3426 (P); 13.XII.2019, fl., Ramanitrinizaka et al. 154 (DBEV, MO, P, TAN, ZT); 7.IV.2021, fr., Randriamahazomanana 311, 314 (MO, P, TAN); 15.IV.2021, fr., Randriamahazomanana 328 (MO, P, TAN); 21.V.2019, fr., Randriamahazomanana 64 (MO, P, TAN); 12.III.2007, fr., Randrianaivo et al. 1474 (CNARP, MO, P, TAN); 21.I.2014, y.fr., Randrianaivo et al. 2430 (BR, G, MO, P); 19.III.2014, fr., Randrianaivo et al. 2505 (K, MO, P, TAN); 6.XI.2019, ster., Randrianaivo et al. 3520 (DBEV, MO, P, TAN, ZT); 7.XI.2019, ster., Randrianaivo et al. 3524, 3525, 3526 (DBEV, MO, P, TAN, ZT); 9.III.2022, fl., y.fr., Randrianaivo et al. 3998, 4002, 4004, 4006, 4014 (DBEV, MO, P, TAN, ZT); 9.III.2022, ster., Randrianaivo et al. 3999, 4000, 4001, 4003, 4005, 4007, 4008, 4010, 4012, 4013, 4015 (DBEV, MO, P, TAN, ZT); 9.III.2022, fl., Randrianaivo et al. 4009, 4011, 4016, 4017 (DBEV, MO, P, TAN, ZT); 2.V.2004, y.fr., Ranirison 769 (G, P); 5.XI.2005, fl., Ratovoson 1066 (CNARP, MO, P, TAN); 1.V.1966, fr., Service Forestier 24695 (K, P, TEF, WAG); [without date], ster., Service Forestier 73-R-160 (P); 18.III.1954, y.fr., Service Forestier 9426 (P).

Dalbergia rajeryi N. Wilding, Phillipson & Crameri, **sp. nov.** (Fig. 6).

Holotypus: MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: District of Ambilobe, east of Mahamasina, 8.XI.2019, y.fr., Randrianaivo & Bernard 3528 (P [P02090167]!; iso-: DBEV, MO, TAN!, ZT [ZT-00241628, ZT-00241629]!).

Dalbergia rajeryi N. Wilding, Phillipson & Crameri is most similar to D. suaresensis Baill., but differs primarily in having leaves that are pubescent on both surfaces (vs. lower surface only), and fruits that are narrower (5–10 vs. 13–28 mm), and usually with several distinct, fine parallel longitudinal ribs (vs. finely reticulate, and often with a short longitudinal ridge over the seeds).

Trees to c. 9 m or shrubs; DBH to 30 cm. Branches glabrous, pale yellow-green in vivo (brown in sicco) when young, becoming pale grey-brown when old, lenticels present. Leaves alternate, (8.5-)13-22 cm long, with 7–13 alternate leaflets; petioles and rachises yellow to pale-green in vivo, black in sicco, pubescent, glabrescent; petiole 30–45 mm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets $(19-)25-60(-73)\times(7-)12-23(-30)$ mm, largest at mid- to upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 2.5–7 mm long, pale yellow-green or brown in vivo, darkbrown to black in sicco, pubescent; lamina ovate to obovate, broadly elliptical or oblong, at times suborbicular in smaller

proximal leaflets, thinly coriaceous, base rounded to cuneate, margin plane to recurved, apex acuminate to rounded, acute to obtuse, sometimes shallowly emarginate, venation eucamptodromous, with 12-20 lateral veins per side; upper surface grey-green to blue-green in vivo, dull grey-green to dark brown in sicco, slightly glossy, pubescent, the midrib forming a groove, the lower surface pale grey-green to pale blue-green in vivo, dull grey-green to dark brown in sicco, matt, pubescent, higher-order veins sometimes forming a fine network, midrib prominent. Inflorescences terminal, a panicle, 2.5-5 cm long, comprised of 2-4 short, racemose primary branches, subtended by a well-developed pinnate leaf-like bract or reduced, caducous, scale-like bract; peduncle to 1.6 cm long; terminal axes of the inflorescence usually short, straight, with flowers forming tight clusters, the axes glabrous. Flowers subtended by a caducous bract (unseen but visible scars observed); pedicel 2-2.8 mm long, glabrous; bracteoles not seen (visible scars observed), caducous; calyx yellow-green in vivo, becoming dark orange-brown to black in sicco, glabrous, persisting on fruits, 4–4.5 mm long, fused in the lower ²/₃–³/₄, the two upper lobes fused to form a single unit, 1 × 2.5 mm, the apex emarginate, the two lateral lobes obtuse, 0.7 × 0.6 mm, the lowest lobe acute-triangular, keeled, 1 × 0.9 mm; petals glabrous, white or yellow (in bud) in vivo becoming orange to brown in sicco; standard petal oblong-obovate, 5.8-7.4 × 2.5-3.2 mm, claw 1.5-2 mm long, apex weakly notched; wing petals 6.1-6.6 × 1-1.6 mm, claw 1-1.4 mm long; keel petals 5.8-6.2 × 1.1-1.6 mm, claw 1.6-2.5 mm long; androecium glabrous, monadelphous, 5.6-5.9 mm long; stamens 9-10, filaments free for upper 1/3-1/5; gynoecium 5.7-6 mm long, glabrous; stipe 2–2.5 mm long; ovary 2.5–3 mm long, with up to 3 ovules; style 0.5 mm long. Fruits pale yellow-green to dark green in vivo, mid-brown to black or red-brown in sicco, the body elongate-elliptical, elliptical, oblong or oblong-obovate, $30-43 \times 5-10$ mm when single-seeded, or up to 45-60 mm long when multi-seeded, base cuneate, apex acute or rounded, surface smooth or with fine, parallel longitudinal ribbing, glabrous; stipe 3–9 mm long, glabrous; style persistent.

Etymology. – The species epithet honors the Malagasy Forester Léopold Rajery (c. 1942–2016), who worked as an agent, then engineer for the Eaux et Forêts (Dorr, 1997), and was the first person to make a collection of the species.

Vernacular names and uses. – "Manary" (Rakotondrafara 490); "Palissandre" (N. Rakotonirina & Rakouth 1240, 1241, 1242). The species has no reported uses, but given that it produces large enough trees, its dark brown to black coloured heartwood (see Hassold 673) is almost certainly used in the construction of furniture and housing. The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. — Dalbergia rajeryi occurs in dry deciduous forest in the region south of the Ankarana plateau (DIANA Region) in the north, and near Antsohihy (Sofia Region) in the south (Fig. 1B), at elevations from near sea level to c. 500 m, on sandy and lateritic soils. Dalbergia rajeryi has been collected in flower in November, and in fruit from November to April. Collection data and field observations suggest that the species is deciduous.

Conservation status. - Dalbergia rajeryi has an EOO of c. 1,564 km² and an estimated minimum AOO of 12 km² (based on a 4 km² grid). The species occurs in a single PA: the Andrafiamena Protected Landscape (IUCN Category V), where it has been documented from a single collection. The species is better known from forest patches bordering the Andrafiamena and Ankarana PAs, where it is known from 28 recent collections, representing two subpopulations. The species is also known from a single collection in a forest patch adjacent to the Sahamalaza-Iles Radama PA (IUCN Category II). The first collection of the species, made in 1978 by L. Rajery, cannot be accurately georeferenced, and we, therefore, cannot include this locality in our threat assessment. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture and wildfires. Fire is also used to clear vegetation for mineral extraction, and for creating and renewing pasture. Selective logging both for construction and as a source of fuel are additional threats. These threats concern all localities both inside and outside of the PA (GOODMAN et al., 2018) to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, D. rajeryi occurs at two locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. - Only the sterile collection of Dalbergia rajeryi (Service Forestier 30561), made by L. Rajery himself, would have been available to Bosser and Rabevohitra at the time when they were revising the genus for Madagascar. However, it is doubtful that they saw this specimen as it bears no annotation by Bosser or Rabevohitra, and furthermore, in 2019 when we began our work on the genus, the collection was located in the "Fabaceae Genus indet." section at P. The specimen is clearly annotated, on the same label and in the same typeset, with "leg. Rajery Léopold" and the "Eaux et Forets" field code "33-R-159", which refers to collection no. 33 by Razafimandimby Solofo (collector no. 159 according to Dorr, (1997)). Presumably the two were together at the time that the collection was made and Razafimandimby's collector code was used; apparently Rajery never had a unique collector-code assigned to him (see Dorr, 1997).

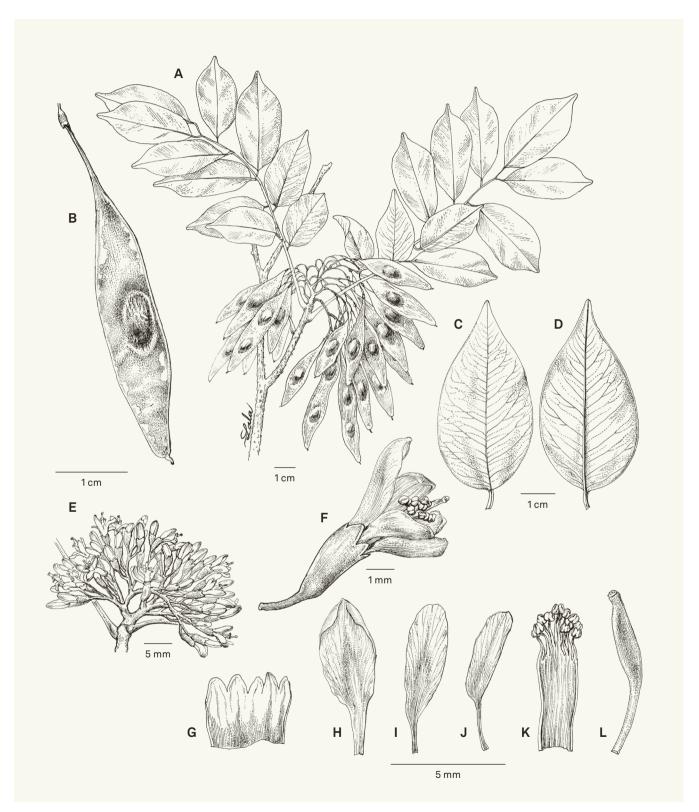


Fig. 6. – Dalbergia rajeryi N. Wilding, Phillipson & Crameri. A. Fruiting branch (immature infrutescence); B. Mature fruit; C. Leaflet upper surface; D. Leaflet lower surface; E. Inflorescence; F. Flower; G. Calyx (outer surface, split open and flattened); H. Standard petal (adaxial surface); I. Wing petal (adaxial surface); J. Keel petal (adaxial surface); K. Androecium (adaxial surface, flattened). L. Gynoecium. [A-D: Randrianaivo & Bernard 3528, P; E-L: Randrianaivo & Bernard 3532, P] [Drawings: R.L. Andriamiarisoa]

Morphologically, the species may be confused with *Dalbergia suaresensis* as both possess leaves with a similar shape, size, and number of leaflets (7–13 vs. 10–15 in *D. suaresensis*), but differs in having leaves that are pubescent on both surfaces (vs. lower surface only), shorter inflorescences (2.5–5 cm vs. 8–16 cm) and fruits that are narrower (5–10 vs. 13–28 mm), and usually with several distinct, fine parallel longitudinal ribs (vs. finely reticulate, and often with a short longitudinal ridge over the seeds). The available distribution data suggest that the ranges of the two species do not overlap. However, given that they occupy adjacent PA's, and that the limits of their current ranges are within 40 km of each other, the species may co-occur in the area between the Andrafiamena and Loky Manambato PA's.

Eight sequenced collections of the species (*Hassold et al.* 662, 665–666, 670–673; *Rakotondrafara* 490) form a coherent and clearly distinct genetic lineage that represents a basal clade in the Bemarivensis (\equiv Mollis) subgroup of Supergroup II (Crameri, 2020). Species of the Bemarivensis clade (*Dalbergia bemarivensis* Phillipson & N. Wilding, *D. chermezonii* R. Vig. & *D. hirticalyx* Bosser & R. Rabev.) are united by their fruits bearing several distinct, fine, parallel longitudinal ribs that extend over most of the pericarp. *Dalbergia rajeryi* stands out among these species by having significantly narrower fruits. In the group, only *D. chermezonii* bears remotely similar leaves but it is eco-geographically distinct and occurs further south on the island.

Additional specimens examined. - MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: 31.III.2017, ster., Hassold et al. 662, 665, 666 (TAN, ZT); 31.III.2017, fr., Hassold et al. 670, 671, 672, 673 (MO, TAN, ZT); 11.IV.2014, fr., Rakotoarisoa & Andriamahay 3419 (K, MO, P, TAN, TEF); 22.I.2007, y.fr., Rakotondrafara 490 (CNARP, MO, P, TAN); 26.II.2021, fr., N. Rakotonirina & Rakouth 1240, 1241 (DBEV, MO, P, TAN, ZT); 26.II.2021, y.fr., N. Rakotonirina & Rakouth 1242, 1244 (DBEV, MO, P, TAN, ZT); 30.XI.2021, y.fr., Randrianaivo & Karatra 3882, 3883, 3886, 3887, 3890, 3891 (DBEV, MO, P, TAN, ZT); 30.XI.2021, fl., y.fr., Randrianaivo & Karatra 3884 (DBEV, MO, P, TAN, ZT); 30.XI.2021, fl., Randrianaivo & Karatra 3885, 3888 (DBEV, MO, P, TAN, ZT); 30.XI.2021, bud, Randrianaivo & Karatra 3889 (DBEV, MO, P, TAN, ZT); 2.III.2022, fr., Randrianaivo & Karatra 3969, 3970, 3971, 3972, 3973, 3974, 3975, 3976, 3977 (DBEV, MO, P, TAN, ZT); 8.XI.2019, y.fr., Randrianaivo & Bernard 3529, 3531 (DBEV, MO, P, TAN, ZT); 8.XI.2019, fl., Randrianaivo & Bernard 3530 (DBEV, MO, P, TAN, ZT); 8.XI.2019, fl., y.fr., Randrianaivo & Bernard 3532 (DBEV, MO, P, TAN, ZT); XII.1978, ster., Service Forestier 30561 (Rajery 33-R-159) (MO, P).

Dalbergia rakotovaoi Phillipson, N. Wilding & Crameri, sp. nov. (Fig. 7).

Holotypus: MADAGASCAR. Reg. Menabe [Prov. Mahajanga]: District de Morondava, Commune Rurale de Marofandilia, 21.I.2016, y.fr., *Rakotovao 6669* (MO [MO-3066659]!; iso-: G [G00341286]!, P [P00858893]!, TAN!, ZT [ZT-00139931, ZT-00139932, ZT-00140336]!).

Dalbergia rakotovaoi Phillipson, N. Wilding & Crameri occurs on sandy substrates in western Madagascar. It is a distinctive species with its small ovate to elliptic leaflets with well-marked venation and a pale yellow puberulous to sericeous indument on the young branches and leaves. It has been confused with D. neoperrieri Bosser & Rabev., which has a similar distribution range in western Madagascar but occurs primarily on calcareous substrates. The latter species has a sparse indument and fewer, larger and more lanceolate leaflets with obscure venation. Dalbergia rakotovaoi has small racemose branches, forming terminal corymbose inflorescences, contrasting with those of many of the other species with which it co-occurs.

Trees to c. 20 m tall or shrubs; DBH to 21 cm. Branches puberulous, yellow-green in vivo (brown in sicco) when young, glabrescent, pale grey-brown when old, lenticels present (hardly visible). Leaves alternate, (5–)6–9(–16) cm long, with (3-)12-14(-21) alternate leaflets; petioles and rachises pale green in vivo, light to dark brown in sicco, puberulous, glabrescent; petiole 6-10(-18) mm long; stipules caducous, 8×2 mm; leaflets $(5-)12-24(-30) \times (3-)5-10(-15)$ mm, decreasing in size towards the proximal part of the leaf, the proximal leaflets smallest, the distal leaflet slightly longer than the rest; petiolule 1-2(-4) mm long, yellow-green to golden in vivo, dark brown in sicco, densely puberulous; lamina elliptical, ovate to obovate, thinly coriaceous, base rounded to cuneate, margin plane, apex slightly attenuate to rounded, acute to obtuse, sometimes shallowly emarginate, mucronulate, venation eucamptodromous, with 6-12 lateral veins per side; upper surface bright mid-green to dark green in vivo, pale brown in sicco, sparsely sericeous with pale yellow indument, the midrib forming a groove, the lower surface grey-green in vivo, pale brown in sicco, sericeous with pale yellow indument, higher-order veins forming a fine network, midrib prominent. Inflorescences terminal, a compact corymbose panicle, 1.5-4.0 cm long, comprised of 2-4 racemose branches, subtended by a reduced pinnate leaf-like bract or a caducous, scale-like bract; peduncle to 17 cm long; terminal axes of the inflorescence straight, secundiflorous and sub-spicate, with flowers in 2 adjacent rows with alternating insertion, the axes densely pale yellow puberulous. Flowers subtended by a caducous, densely puberulous, ovate scale-like bract, $0.8-1.1 \times 0.6-0.7$ mm; pedicel 0.1-1.5 mm long, puberulous; bracteoles ovate to elliptic, concave, 1.2–1.4 × 1.2–0.7 mm, apex rounded densely puberulous, indument yellow to orangebrown in sicco, caducous; calyx yellow-green, sometimes dark purple at the base in vivo, becoming black in sicco, densely puberulous, persisting on fruits, 2.2-2.5 mm long, fused in the lower 3/5-2/3, the 2 upper lobes fused to form a single, rounded unit, 0.8 × 1.5 mm, the apex shallowly emarginate, the 2 lateral lobes ovate-triangular, 1 × 1.2 mm, the lowest lobe acutetriangular, shallowly keeled, 1.5 × 1 mm; petals glabrous, white



Fig. 7. – Dalbergia rakotovaoi Phillipson, N. Wilding & Crameri. A. Mature fruit; B. Fruiting branch; C. Leaflet upper surface; D. Leaflet lower surface; E. Inflorescence with immature fruits; F. Flower; G. Androecium (adaxial surface, flattened); H. Gynoecium; I. Standard petal (adaxial surface); J. Wing petal (adaxial surface); L. Calyx (outer surface, split open and flattened). [S.A.F. Andrianarivelo et al. 157, P] [Drawings: R.L. Andriamiarisoa]

to yellow in vivo becoming orange in sicco; standard petal pandurate, $(4-)5-3.5 \times 2.2-3.5(-4)$ mm, claw 1-1.5 mm long, apex notched; wing petals $4-3.3 \times (1.3-)1.1-1.8 \text{ mm}$, claw 1-1.5 mmlong; keel petals $3.2-4(-5.5) \times 1-2$ mm, claw 1.5-2 mm long; androecium glabrous, monadelphous or diadelphous, 2.5-5 mm long; stamens 9-10, or more rarely 9+1, filaments free for upper 1/3-1/5 or rarely completely free; gynoecium 3.5–5(–5.7) mm long; stipe 1.2–2 mm long, sparsely covered in long yellowish hairs; ovary 2 mm long, sparsely covered in long yellowish hairs, with up to 3 ovules; style glabrous 1.5–1.7 mm long. Fruits pale yellow-green in vivo, red-brown in sicco, the body elongate-elliptical, $40-58 \times (9-)12-17$ mm when singleseeded, or 75-80 mm long when multi-seeded, base narrowly cuneate, apex acute or rounded, surface densely longitudinally ribbed especially over the immature seed, becoming somewhat smooth at maturity, sparsely pubescent towards the base and the apex, otherwise glabrous; stipe 5-7 mm long, sparsely pubescent; style caducous.

Etymology. – The species epithet honors our former colleague Charles Rakotovao, who made a total of nearly 8,000 plant collections in Madagascar from 1994 to his retirement as an employee of MBG-Madagascar in 2020. Charles is also an accomplished photographer and has taken several thousands of excellent photos of Malagasy plants associated with his and other collectors' voucher specimens.

Vernacular names and uses. — "Manary" (Bernard 2814); "Manary baomba" (Rakotovao 6512, 6672), "Manary beravy" (Rakotovao 6518); "Ma(g)nary fotsy" [= "Manarifotsy"] (Rakotovao 6508, 6667, 6668, 6669, 6682, Randriamarosoa 432); "Tsipoapoaka" (Rakotovao 6672). The wood of Dalbergia rakotovaoi is yellow-brown and its heart-wood is pink-brown; it is reported as used for furniture and as firewood (Rakotovao 6512), specifically it is reported as good for charcoal production (Du Puy & Andriantiana M761); the liquor derived from boiling the bark is reportedly used to treat post-natal bleeding (Rakotovao 6667, 6669, 6672).

Distribution, ecology and phenology. – Dalbergia rakotovaoi is known from 31 collections. It occurs predominantly in the coastal zones in the Menabe and Boeny Regions of western Madagascar (Fig. 1B), on unconsolidated sands, at elevations up to c. 100 m, with an outlying and somewhat atypical record from Betsiboka Region c. 190 km inland, at c. 700 m. The Menabe and Boeny subpopulations of the species show a remarkable range disjunction separated by over 300 km. It has been recorded in flower from November to January, and fruiting from December to April. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia rakotovaoi has an estimated EOO of 57,600 km² and an AOO of 68 km², and much of its known range falls within the protected area network of Madagascar. In the Menabe Region, it has been documented mostly from the Menabe Antimena Protected Harmonious Landscape, and with a single collection from the adjacent Andranomena Special Reserve just to the south and two from the Kirindy Mité National Park some 100 km to the southwest, with just one record from north of the Tsiribihina River outside of the protected area network. In Melaky Region it is known from three collections within the Baie de Baly National Park, and one from the edge of the Namoroka National Park (not on the limestone tsingy formation that characterises the site). The record from the Betsiboka Region was collected from a tiny unprotected forest fragment. Dalbergia rakotovaoi is known to be targeted for its useful wood, for carpentry and for charcoal, although this is not known to be high-quality rosewood, and it is also used for medicinal purposes related to childbirth. While some level of protection may be afforded to the species in the Andranomena Reserve and the Kirindy Mité Park, at Menabe Antimena the forest cover is highly fragmented, and degradation of the natural resources has been accelerating with an influx of people into the area. The northern subpopulation in the Baie de Baly National Park is probably relatively secure, but at Namoroka, where the focus is the conservation of the flora and fauna of the limestone tsingy, the single known site for the species at the edge of the park is unlikely to receive much active protection. It is believed that D. rakotovaoi is threatened by destructive exploitation of its wood throughout much of its range, with the larger more valuable trees the most sought after, and five locations can be identified in the context of this threat. Dalbergia rakotovaoi is considered to be "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,i i,iii,iv,v)].

Notes. — Only four collections of this species were known at the time when the revisionary work of Bosser & Rabevohitra (1996, 2002, 2005) was published. The older two, Service Forestier 32–R–311 collected in 1945, and Charles—Dominique 3 collected in 1973, were in young leaf and sterile condition, and the latter was annotated as not identifiable by Bosser. The other two collections were identified as Dalbergia neoperrieri Bosser & R. Rabev., one of which, Du Puy et al. M 521, is a paratype of that species, and was illustrated as such (Bosser & Rabevohitra 2002: 354). Given the ample flowering and fruiting material now available, and the results of the phylogenomic study by Crameri (2020), it is clear that D. rakotovaoi represents a coherent and separately evolving lineage that is clearly distinct from D. neoperrieri and any other Malagasy Dalbergia species.

Morphologically, *Dalbergia rakotovaoi* differs from *D. neoperrieri*, with which it had been confused by Bosser

& RABEVOHITRA (2002), by its leaflets that have a conspicuous, close lateral veins, and a distinctive yellow or yellow-green indument on its young stems and leaves. Leaflets of D. neoperrieri are lanceolate and larger than those of D. rakotovaoi, typically > 25 × 10 mm, while those of D. rakotovaoi are oblong and smaller. Both species have overlapping distribution ranges, although that of *D. neoperrieri* extends a little further to the north and south of the known range of D. rakotovaoi. While D. neoperrieri occurs primarily on calcareous substrates, D. rakotovaoi occurs primarily on unconsolidated sands. Dalbergia rakotovaoi could also be confused with D. nemoralis Rakoton., Phillipson & Crameri. Both species have leaves with few small pubescent leaflets, but the latter usually has fewer (usually < 12) leaflets than D. rakotovaoi that are often larger (frequently > 25×10 mm). The leaf indument also differs: glabrous or with a fine white puberulous indument on the upper surface, and with a glaucous bloom and fine white appressed or velutinous indument on the lower surface, mostly adjacent to the midrib for D. nemoralis; versus pale yellow, sericeous on both surfaces for D. rakotovaoi. The distribution of the two species is quite distinct with *D. nemoralis* occurring in the south (*D. nemoralis* subsp. decaryi (Bosser & R. Rabev.) Rakoton., N. Wilding, Phillipson & Crameri and south-west of the country and in the central regions (*D. nemoralis* subsp. *nemoralis*).

Population genomic analyses indicate that introgressive hybridization may occur between *Dalbergia rakotovaoi* and *D. purpurascens*, two species that overlap in their distribution and ecology. A single sequenced specimen (*Leandri 2249*) from the surroundings of Soahany in the southern Melaky Region shares many alleles with both species (Crameri, 2020), and also appears morphologically intermediate between the two putative parent species, and similar to another specimen of putative hybrid origin (*Service Forestier 6882*) from the same broader area. Intriguingly, no collection records of *D. rakotovaoi* are currently known from the Soahany area, which lies between the two disjunct subpopulations of the species.

Additional specimens examined. - MADAGASCAR. Reg. Betsiboka [Prov. Mahajanga]: 3.VI.2019, fr., Randrianaivo & Bernard 3468 (P). Reg. Boeny [Prov. Mahajanga]: 24.VI.2021, fr., S.A.F. Andrianarivelo & Razakamalala 304 (DBEV, MO, P, TAN); 27.VI.2021, fr., S.A.F. Andrianarivelo & Razakamalala 307 (DBEV, MO, P, TAN, ZT); 27.VI.2021, ster., S.A.F. Andrianarivelo & Razakamalala 308 (DBEV, MO, P, TAN, ZT); 25.VI.2021, fr., Razakamalala & S.A.F. Andrianarivelo 8951 (DBEV, MO, P, TAN, ZT); 24.I.1945, ster., Service Forestier 32-R-311 (P). Reg. Menabe [Prov. Toliara]: 16.XII.2020, fl., S.A.F. Andrianarivelo et al. 157 (DBEV, MO, P, TAN, ZT); 17.XII.2020, fl., Bernard et al. 2814 (DBEV, MO, P, TAN, ZT); 24.XI.1973, ster., Charles-Dominique 3 (P); 31.III.1990, fr., Du Puy et al. M521 (K, MO, P, TAN); 18.I.2014, ster., Rakotovao 6508 (MO, P, TAN); 19.I.2014, ster., Rakotovao 6512 (MO, P, TEF); 22.I.2014, ster., Rakotovao 6518 (MO, TEF); 20.I.2016, fl., Rakotovao 6667 (G, MO, P, TAN, TEF, ZT); 21.I.2016, fr., Rakotovao 6668 (G, MO, P, TAN, ZT); 22.I.2016, fl., Rakotovao 6672 (G, MO, P, TAN, TEF, ZT); 25.I.16, fr., Rakotovao 6682 (G, MO, P, TAN, TEF, ZT); 21-30.XI.1994,

fl., Randriamarosoa et al. 432 (MO, P, TAN); 4.IV.2019, ster., Randrianaivo et al. 3355 (DBEV, MO, P, TAN, ZT); 5.IV.2019, ster., Randrianaivo et al. 3361 (DBEV, MO, P, TAN, ZT); 5.IV.2019, ster., Randrianaivo et al. 3362 (DBEV, MO, P, TAN, ZT); 5.IV.2019, ster. Randrianaivo et al. 3363 (DBEV, MO, P, TAN, ZT); 11.IV.2019, fr., Randrianaivo et al. 3380 (DBEV, MO, P, TAN, ZT); 15.IV.2019, fr., Randrianaivo et al. 3412 (DBEV, MO, P, TAN, ZT); 5.IV.2019, fr., Randrianaivo et al. 3413 (DBEV, MO, P, TAN, ZT); 16.IV.2019, fr., Randrianaivo et al. 3421, 3422, 3423, 3426, 3427 (DBEV, MO, P, TAN, ZT).

Dalbergia sambavensis N. Wilding, Phillipson & Crameri, sp. nov. (Fig. 8).

Holotypus: Madagascar. Reg. SAVA [Prov. Antsiranana]: Distr. Sambava, Makirovana-Tsihomanaomby PA, 18.X.2013, fl., C.Z. Rakotonirina, Martial & Be 206 (P [P01069117]!; iso-: MO [MO-3065021], TAN!).

Dalbergia sambavensis N. Wilding, Phillipson & Crameri is most similar to D. monticola Bosser & R. Rabev. and D. soafarae N. Wilding, Phillipson & Crameri, but differs primarily from D. monticola in having smaller inflorescences [(1.5–5(-6) vs. (3–)6–11(–19) cm long], and from D. soafarae in having flowers with larger petals.

Trees to c. 15 m tall or shrubs; DBH to 35 cm. Branches glabrous to sparsely pubescent indument, yellow-green in vivo (red-brown in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, (4-)5-9(-10.5) cm long, with (11-)16-23(-27) alternate leaflets; petioles and rachises pale green in vivo, mid-brown to black in sicco, pubescent; petiole 6-20 mm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets (6-)10-18(-22) × 3-7 mm, largest at mid- to upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or larger than adjacent leaflets; petiolule 0.7–1.7 mm long, pale green-brown in vivo, dark-brown to black in sicco, pubescent; lamina oblong, obovate or broadly elliptical, coriaceous, base rounded to broadly cuneate, margin recurved, apex rounded, obtuse or retuse, venation not visible; upper surface mid-green in vivo, brown to green-brown in sicco, glossy or matt, glabrous, the midrib forming a groove, the lower surface pale green in vivo, light brown to pale grey-green in sicco, matt, pubescent, higher-order veins not visible, midrib prominent. Inflorescences axillary or terminal, a panicle, 1.5–5(–6) cm long, comprised of 2–5 paniculate or racemose primary branches, subtended by a reduced pinnate leaf-like bract or a caducous, scale-like bract; peduncle to 1.9 cm long; terminal axes of the inflorescence straight or curved, secundiflorous and sub-spicate, with flowers in two adjacent rows with alternating insertion, the axes white to yellowish-brown pubescent. Flowers subtended by a persistent, pubescent, triangular scale-like bract, 0.5–0.8 × 0.4–0.7 mm; pedicel 0.1–0.7 mm long, pubescent; bracteoles ovate, concave,



Fig. 8. – Dalbergia sambavensis N. Wilding, Phillipson & Crameri. A. Flowering branch; B, C. Portions of leaf rachis with leaflets (b: lower surface; c: upper surface); D. Inflorescence branch; E. Flower; F. Calyx (outer surface, split open and flattened); G. Standard petal (adaxial surface); H. Wing petal (adaxial surface); I. Keel petal (adaxial surface); J. Androecium (adaxial surface, flattened); K. Gynoecium. [Rakotonirina et al. 154, P] [Drawings: R.L. Andriamiarisoa]

 $0.7-1 \times 0.6-0.8$ mm, apex rounded to obtuse, pubescent, yellow to dark orange-brown or black in sicco, persistent; calyx pale yellow to green in vivo, becoming dark orange-brown to black in sicco, puberulous, not persisting on fruits, 2.1-2.6 mm long, fused in the lower 3/3, the 2 upper lobes fused to form a single unit, $0.5-0.6 \times 1$ mm, the 2 lateral lobes obtuse, $0.4-0.5 \times 0.5-0.6$ mm, the lowest lobe acute-triangular, keeled, $0.7-0.9 \times 0.6-0.8$ mm; petals glabrous, white to cream in vivo becoming yellow to orange-red in sicco; standard petal pandurate, $3.8-4.3 \times 2.3-2.9$ mm, claw 0.6-0.8 mm long, apex notched; wing petals $3.7-3.9 \times 1.2-1.5$ mm, claw 0.7-1 mm long; keel petals $3.3-3.9 \times 1.1-1.4$ mm, claw 1.2-1.4 mm long; androecium glabrous, monadelphous, 3.5-4 mm long; stamens (9-)10, filaments free for upper 1/3; gynoecium 3.3-4 mm long; stipe densely covered in long yellowish-white hairs, 1.3-1.7 mm long; ovary covered in long yellowish-white hairs, 1.5-1.9 mm long, with up to 3 ovules; style glabrous or sparsely pubescent, 0.4-0.5 mm long. Fruits light to midgreen in vivo, mid-to dark-brown in sicco, the body elliptical to oblong, $55 \times 12-14$ mm when single-seeded (immature), or up to 95 mm long when multi-seeded (slightly immature), base cuneate, apex acute or rounded, surface smooth with reticulate ribbing, glabrous; stipe 4-8 mm long, pubescent, glabrescent; style caducous.

Etymology. – The name Dalbergia sambavensis was chosen to reflect the species' primary distribution in the district of Sambava in the SAVA Region of Madagascar.

Vernacular names and uses. – "Andramena madinidravina" (Raharimampionona et al. 583); "Hazovola" (Service Forestier 12452); "Volomborona" (C.Z. Rakotonirina et al. 206). The reddish-brown coloured heartwood (see Razakamalala 8230) of the species is reportedly used to make furniture (C.Z. Rakotonirina et al. 206). The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia sambavensis is known from 15 collections. It occurs in lowland humid forest in the north-east (districts of Sambava and Vohemar in the SAVA Region; Fig. 1B), at elevations from c. 40 to 300 m, on substrates derived from lavas and basement rock. Dalbergia sambavensis has been collected in flower in October and November, and in fruit from November. Collection data and field observations suggest that the species is deciduous.

Conservation status. – Dalbergia sambavensis has an EOO of c. 436 km² and an estimated minimum AOO of 28 km² (based on a 4 km² grid). The species occurs in a single PA: the Makirovana Protected Landscape (IUCN Category V), where it has been documented by a single collection near the periphery of the PA. The species is further known from eight

recent collections in the areas immediately surrounding Makirovana, and from four collections in a forest patch 15 km to the south-east. The oldest known collection of this species, made by the Service Forestier de Madagascar in 1954, was collected 67 km to the south of Makirovana in Ambodimanga Farimay, however, the exact collection locality cannot be established, and we exclude it from the current assessment. This area has apparently undergone considerable forest clearance, and we consider the individual(s) to have likely been extirpated. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture and wildfires. Selective logging both for construction and as a source of fuel are additional threats. These threats concern all localities both inside and outside of the PA (GOODMAN et al., 2018) to different degrees. With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, D. sambavensis occurs at one location, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – A single fruiting collection of Dalbergia sambavensis (Service Forestier 12452) from the Antalaha area, with poorly preserved leaves, was seen by Bosser and Rabevohitra at P and determined as D. monticola, which they believed to occur in the Sambirano Region, in the central highlands, and along the east coast, from as far north as Antalaha in the district of Sambava, to Fort Carnot in the south (Bosser & Rabevohitra, 2002).

Dalbergia sambavensis is closely related to D. monticola and D. soafarae, and the three differ in relatively few morphological characters (Table 1). All three species possess leaves with small oblong to elliptical leaflets, small-flowered, paniculate inflorescences (Supergroup II), and similarly sized elliptical to oblong fruits. The species, however, differ most notably in the size of their inflorescences, and more subtly in leaf length, leaflet number, and corolla length. Morphologically, the smaller leaves and inflorescences serve to distinguish D. sambavensis from D. monticola and D. soafarae, and with the addition of elevational, geographic or genetic data there is little risk of confusing the three species. Sterile specimens of D. sambavensis may further be confused with D. baronii Baker, with which it co-occurs, and D. pseudobaronii Bosser & R. Rabev., which is known from c. 80 km to the north of its range. Dalbergia baronii is easily distinguished by its short axillary (vs. larger, terminal) inflorescences and slightly thickened rounded to obovate or oblong fruits, which are characteristically inflated over much of the body, except near the base and along a narrow margin. Dalbergia pseudobaronii possesses similarly sized leaves with leaflets of a comparable shape and size to those of D. sambavenis, D. monticola, and D. soafarae, and has been previously confused with D. monticola

in Montagne d'Ambre. *Dalbergia pseudobaronii* is, however, characterised by large fruits, and easily distinguished by leaflets that have a short scattered indument on their upper surfaces, vs. glabrous in the aforementioned species. Eco-geographically, *D. sambavensis* is well differentiated from both *D. monticola*, which is known at elevations typically above 400 m (the closest known *D. monticola* occurrences are in the forest of Antsahaberaoka, located c. 65 km inland of the Makirovana-Tsihomanaomby PA (*Razakamalala et al. 3321*), and in the Makira Natural Park and Masoala National Park, located c. 110 km to the south and west of Sambava), and *D. soafarae*, which is restricted to low elevations around Taolagnaro, and located over 1,100 km south-southwest of Sambava.

The type specimen of Dalbergia sambavensis (C.Z. Rakotonirina et al. 206) and two further collections (Bernard & Rakazamalala 2612, Phillipson et al. 6644) form a coherent and distinct genetic lineage within the Monticola subgroup, which additionally comprises D. monticola, D. orientalis Bosser & R. Rabev., D. soafarae and D. tsaratananensis Bosser & R. Rabev. Dalbergia tsaratananensis forms the most basal lineage in the Monticola subgroup, subtending a crown group, which includes D. sambavensis sister to all other species of the group (Crameri, 2020).

Additional specimens examined. – MADAGASCAR. Reg. SAVA [Prov. Antsiranana]: 26.XI.2018, ster., Bernard & Razakamalala 2612 (DBEV, MO, P, TAN, ZT); 28.XI.2019, ster., Phillipson et al. 6643 (DBEV, MO, P, TAN, ZT); 28.XI.2019, y.fr., Phillipson et al. 6644 (DBEV, MO, P, TAN, ZT); 7.XI.2021, y.fr., Rabarimampionona et al. 583 (MO, P, TAN); 13.XI.2021, y.fr., C.Z. Rakotonirina et al. 839 (MO, P, TAN); 29.XI.2021, ster., N. Rakotonirina et al. 1227 (DBEV, MO, P, TAN, ZT); 7.VII.2021, ster., Ravelonarivo 4912 (MO, P, TAN); 10.XI.2021, ster., Ravelonarivo 4989 (MO, P, TAN); 12.XI.2021, bud, fl., Ravelonarivo 5013 (MO, P, TAN); 25.XI.2018, y.fr., Razakamalala & Bernard 8230, 8232 (MO, P, TAN, TEF, ZT); 25.XI.2018, y.fr., Razakamalala & Bernard 8240 (DBEV, MO, P, TAN, ZT); 20.XII.1954, fr., Service Forestier 12452 (P, TEF).

Dalbergia soafarae N. Wilding, Phillipson & Crameri, **sp. nov.** (Fig. 9).

Holotypus: Madascar. Reg. Anosy [Prov. Toliara]: Fort Dauphin, Tsitongambarika Natural Resource Reserve, 4.IV.2016, fl., y.fr., S.N. Andrianarivelo & Razakamalala 246 (P [P00931739]!; iso-: MO [MO-3066702]!, TAN!, ZT [ZT-00140398; ZT-00140045; ZT-00140046]!).

Dalbergia soafarae N. Wilding, Phillipson & Crameri is most similar to D. monticola Bosser & R. Rabev., and to D. sambavensis N. Wilding, Phillipson & Crameri, but differs primarily from D. monticola in having smaller inflorescences [(1-)2.5-5.5 vs. (3-)6-11(-19) cm long], and from D. sambavensis in having flowers with smaller petals.

Table 1. – Comparison of morphology and elevational range between *Dalbergia sambavensis* N. Wilding, Phillipson & Crameri, *D. soafarae* N. Wilding, Phillipson & Crameri, and *D. monticola* Bosser & R. Rabev.

| | | D. sambavensis | D. soafarae | D. monticola |
|----------------|-----------------------|--|--|--|
| Leaf | length [cm] | (4-)5-9(-10.5) | (2.7–)4.5–8(–10) | (3.5-)6-14(-17) |
| Leaflets | number | (11-)16-23(-27) | 13-25(-29) | (13-)21-37(-43) |
| | lamina shape | oblong, obovate or broadly elliptical | oblong, obovate or broadly elliptical | oblong, obovate or broadly elliptical |
| | length [mm] | (6-)10-18(-22) | (5-)9-15(-27) | (3-)7-25(-30) |
| | width [mm] | 3-7 | (3-)4-9 | (2-)3-8(-11) |
| Inflorescences | length [cm] | 1.5-5(-6) | (1–)2.5–5.5 | (3-)6-11(-19) |
| Flowers | calyx length [mm] | 2.1-2.6 | 2-2.7 | 2.5-3.6 |
| | standard length [mm] | 3.8-4.3 | 3-3.6 | 4.2-5 |
| | standard width [mm] | 2.3-2.9 | 1.8-2.2 | 2.8-3.3 |
| | wing length [mm] | 3.7-3.9 | 2.7-2.9 | 4-4.8 |
| | wing width [mm] | 1.2-1.5 | c.1 | 1.2-1.4 |
| | keel length [mm] | 3.3-3.9 | 2.7-3 | 4.1-4.8 |
| | keel width [mm] | 1.1-1.4 | c.1 | 1.2-1.5 |
| Fruits | shape | elliptical to oblong | elliptical | obovate to elliptical or oblong |
| Habitat | elevational range [m] | 40-300 | 40-430 | 60-1450 |

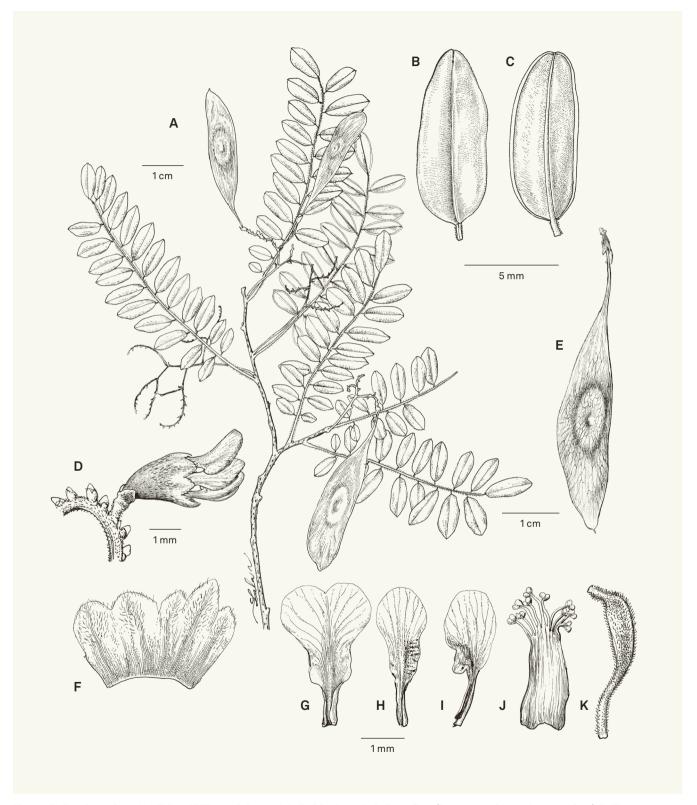


Fig. 9. – Dalbergia soafarae N. Wilding, Phillipson & Crameri. A. Fruiting branch; B, C. Leaflets (b: upper surface; c: lower surface); D. Flower; E. Immature fruit; F. Calyx (outer surface, split open and flattened); G. Standard petal (adaxial surface); H. Wing petal (adaxial surface); I. Keel petal (adaxial surface); J. Androecium (adaxial surface, flattened); K. Gynoecium.

[A-C, E: S.N. Andrianarivelo & Razakamalala 246, P; D, F-K: Razakamalala et al. 8267, P] [Drawings: R.L. Andriamiarisoa]

Trees to c. 25 m tall or shrubs; DBH to 65 cm. Branches glabrous to sparsely pubescent, yellow-green in vivo (red-brown in sicco) when young, becoming glabrous, pale grey-brown when old, lenticels present. *Leaves* alternate, (2.7–)4.5–8(–10) cm long, with 13-25(-29) alternate leaflets; petioles and rachises pale green in vivo, black in sicco, pubescent; petiole 6–13 mm long; stipules caducous, 4.5 × 1.3 mm; leaflets (5–) $9-15(-27) \times (3-)4-9$ mm, largest at mid- to upper-leaf, the proximal leaflets smallest, the distal leaflet equal to or smaller than adjacent leaflets; petiolule 0.5-1 mm long, pale greenbrown in vivo, light to dark-brown in sicco, pubescent; lamina oblong, obovate or broadly elliptical, coriaceous, base rounded to broadly cuneate, margin recurved, apex rounded, obtuse, sometimes retuse, venation not visible; upper surface midgreen in vivo, brown to green-brown in sicco, glossy or matt, glabrous, the midrib forming a groove, the lower surface pale green in vivo, brown to green-brown in sicco, matt, pubescent, higher-order veins not visible, midrib prominent. Inflorescences axillary or terminal, a panicle, (1–)2.5–5.5 cm long, comprised of 2-5 paniculate or racemose primary branches, subtended by a reduced pinnate leaf-like bract or a caducous, scale-like bract; peduncle to 1.7 cm long; terminal axes of the inflorescence straight or curved, secundiflorous and sub-spicate, with flowers in 2 adjacent rows with alternating insertion, the axes white to yellowish-brown pubescent. Flowers subtended by a persistent, pubescent, triangular scale-like bract, 0.5–1 × 0.5–1 mm; pedicel 0.4-0.6 mm long, pubescent; bracteoles ovate, concave, 1 × 0.8–1 mm, apex rounded, pubescent, yellow to dark orangebrown or black in sicco, persistent; calyx yellow-green in vivo, becoming dark orange-brown to black in sicco, puberulous, sometimes persisting on fruits, 2-2.7 mm long, fused in the lower ²/₃, the 2 upper lobes fused to form a single unit, 0.5×1.8 mm, the apex shallowly emarginate, the 2 lateral lobes obtuse, 0.5×0.5 mm, the lowest lobe acute-triangular, keeled, 0.9 mm × 0.8 mm; petals glabrous, white to yellow in vivo becoming yellow to orange-red in sicco; standard petal pandurate, 3-3.6 × 1.8-2.2 mm, claw 0.5-0.8 mm long, apex notched; wing petals 2.7-2.9 × 1 mm, claw 0.9 mm long; keel petals 2.7-3 × 1 mm, claw 1.2-1.3 mm long; androecium glabrous, monadelphous, 3 mm long; stamens (9-)10, filaments free for upper 1/3-1/4; gynoecium 2.3-2.5 mm long; stipe densely covered in long white-yellowish hairs, 1.1 mm long; ovary covered in long yellowish-white hairs, 1.1 mm long, with up to 2 ovules; style glabrous or pubescent near base, 0.5-0.7 mm long. Fruits mid- to dark-green in vivo, mid-brown to black or red-brown in sicco, the body elliptical [possibly oblong in multi-seeded fruits], 50 × 14 mm when single-seeded (immature), multi-seeded not seen, base cuneate, apex acute or rounded, surface smooth with reticulate ribbing, glabrous; stipe 4-7 mm long, pubescent, glabrescent; style caducous.

Etymology. – The species epithet honors Soafara Andrianarivelo, a Malagasy botanist, who is responsible for some of the first collections of the species, including the specimen chosen to serve as the type.

Vernacular names and uses. — "Ma(g)nary" (S.N. Andrianarivelo & Razakamalala 262, Rakotoarivelo et al. 784); "Manary mavo" (S.N. Andrianarivelo & Razakamalala 251); "Manary toloho" (Andriamiarisoa & Bernard 2714); "Sambalahy manga" (Bernard et al. 2650). The species has no reported uses, but given that it produces large enough trees, its reddish-brown coloured heartwood (see S.A.F. Andrianarivelo 48) is almost certainly used in the construction of furniture and housing. The species is also likely used as a source of fuel for cooking.

Distribution, ecology and phenology. – Dalbergia soafarae occurs in dense lowland humid forest in the south-east (Fig. 1B), at elevations from 40 to 430 m, on basement rock substrates. Dalbergia soafarae has been collected in flower in January and February, and in fruit from February. Collection data and field observations suggest that the species is deciduous.

Conservation status. - Dalbergia soafarae has an EOO of c. 1,468 km² and an estimated minimum AOO of 76 km² (based on a 4 km² grid). The species occurs in two PAs: Andohahela NP (IUCN Category II), where it is known from a single recent collection, and Tsitongambarika natural resource reserve (IUCN Category VI), where it is known from 19 recent collections. The species has also been recorded in three separate forest patches along the eastern border of Tsitongambarika, and from five collections in Beampingaratra, about 9 km north of Tsitongambarika. The species is threatened from habitat loss or degradation resulting from slash and burn agriculture and wildfires. Selective logging both for construction and as a source of fuel are additional threats. These threats concern all localities both inside and outside of the PA to different degrees (Goodman et al., 2018). With respect to habitat loss, which is considered to be the most serious plausible threat to all known localities, D. soafarae occurs at three locations, and on this basis it is assigned a preliminary conservation status of "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – No collections of *Dalbergia soafarae* are known to have been present at P at the time when Bosser and Rabevohitra revised the Malagasy *Dalbergia* species.

Morphologically, *Dalbergia soafarae* is close to *D. monticola* and *D. sambavensis* (see Table 1 and Notes under *D. sambavensis*). The three species all possess leaves with small oblong to elliptical leaflets, and similarly sized elliptical to oblong fruits. The species, however, differ most notably in the

size of their inflorescences, and more subtly in leaf length, leaflet number, and corolla length. Young sterile leafy material of *D. soafarae* can easily be distinguished from *D. sambavensis* on the basis of its geographical separation of over 1,100 km. Similarly, *D. monticola* is not known from the Anosy Region, as its southernmost known collection records originate from the Vondrozo District (*Razakamalala 8461, 8466*), over 150 km north of the northern limit of *D. soafarae*. Unlike *D. sambavensis*, *D. soafarae* is not known to co-occur with *D. baronii*, with which it has previously been confused, and whose southernmost collections originate from over 100 km to the north-east of the range of *D. soafarae*.

The species forms a distinct genetic lineage (see Notes under *Dalbergia sambavensis*) within the Monticola subgroup, sister to *D. orientalis*, separating it from *D. monticola* and *D. soafarae* (Crameri, 2020).

Additional specimens examined. - MADAGASCAR. Reg. Anosy [Prov. Toliara]: 7.VII.2021, ster., Andriamiarisoa & Bernard 2640 (DBEV, MO, P, TAN, ZT); 18.X.2021, ster., Andriamiarisoa & Bernard 2675, 2676, 2677, 2679, 2682 (DBEV, MO, P, TAN, ZT); 19.X.2021, ster., Andriamiarisoa & Bernard 2685, 2686, 2689 (DBEV, MO, P, TAN, ZT); 27.X.2021, ster., Andriamiarisoa & Bernard 2709 (DBEV, MO, P, TAN, ZT); 28.X.2021, ster., Andriamiarisoa & Bernard 2714 (DBEV, MO, P, TAN, ZT); 12.IX.2018, y.fr., fr., Andriamihajarivo et al. 2193 (MO, P, TAN, UPS); 9.II.2016, bud, y.fr., S.N. Andrianarivelo & Razakamalala 251 (MO, P, TAN, TEF, ZT); 13.II.2016, bud, y.fr., S.N. Andrianarivelo & Razakamalala 262 (G, MO, P, TAN, TEF, ZT); 27.X.2019, ster., S.A.F. Andrianarivelo & Razakamalala, 41 (DBEV, MO, P, TAN, ZT); 2.XI.2019, ster., S.A.F. Andrianarivelo & Razakamalala 48 (DBEV, MO, P, TAN, ZT); 9.II.2019, y.fr., Bernard et al. 2650 (DBEV, MO, P, TAN, ZT); 5.XII.2019, ster., Karatra & Rakotovao 258 (DBEV, MO, P, TAN, ZT); 10.I.2016, bud, fl., Rakotoarivelo et al. 784 (MO, P, TAN); 10.II.2019, ster., N. Rakotonirina et al. 1182 (DBEV, MO, P, TAN, ZT); 29.XI.2009, fl., Rakotovao et al. 4901 (MO, P, TAN); 14-17.XII.2009, fl., Rakotovao et al. 5008 (MO, P, TAN); 1.XII.2019, ster., Rakotovao et al. 7600 (DBEV, MO, P, TAN, ZT); 4.XII.2019, ster., Rakotovao et al. 7613, 7614, 7617, 7619 (DBEV, MO, P, TAN, ZT); 6.II.2019, y.fr., Ramanitrinizaka & Sandratriniaina 6 (DBEV, MO, P); 17.II.2019, ster., Ramanitrinizaka & Sandratriniaina 30 (DBEV, MO, P); 21.II.2019, ster., Ramanitrinizaka & Sandratriniaina 41, 43, 47 (DBEV, MO, P); 6.II.2019, fl., Razakamalala et al. 8267 (DBEV, MO, P, TAN, ZT); 8.II.2019, ster., Razakamalala et al. 8274 (DBEV, MO, P, TAN, ZT); 22.II.2019, ster., Sandratriniaina & Ramanitrinizaka 47 (DBEV, MO, P); 24.II.2019, ster., Sandratriniaina & Ramanitrinizaka 53 (DBEV, MO, P).

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