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Taxonomic studies on Malagasy *Dalbergia* (Fabaceae). I. Two new species from northern Madagascar, and an emended description for *D. manongarivensis*

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Abstract

WILDING, N., P.B. PHILLIPSON, S. CRAMERI, S. ANDRIAMBOLOLONERA, R.L. ANDRIAMIARISOA, S.A.F. ANDRIANARIVELO, R. BERNARD, N. RAKOTONIRINA, C. RAKOTOVAO, R.I. RANDRIANAIVO, R. RAZAKAMALALA & P.P. LOWRY II (2021). Taxonomic studies on Malagasy *Dalbergia* (Fabaceae). I. Two new species from northern Madagascar, and an emended description for *D. manongarivensis*. *Candollea* 76: 237–249. In English, English and French abstracts. DOI: <http://dx.doi.org/10.15553/c2021v762a4>

Two new species of *Dalbergia* L. f. (Fabaceae: Dalbergieae) are described from northern Madagascar: *Dalbergia antsirananae* Phillipson, Crameri & N. Wilding and *Dalbergia obcordata* N. Wilding, Phillipson & Crameri, and an emended description is provided for a third species, *Dalbergia manongarivensis* Bosser & R. Rabev. All three species are illustrated with line drawings and photographs, and each is provided with a risk of extinction assessment using the IUCN Red List criteria: all three species are assessed as “Endangered”. *Dalbergia antsirananae* and *Dalbergia manongarivensis* are closely related, and both appear to be a source of valuable wood, while *Dalbergia obcordata* is only known as a shrub and is assumed not to produce wood of commercial value.

Résumé

WILDING, N., P.B. PHILLIPSON, S. CRAMERI, S. ANDRIAMBOLOLONERA, R.L. ANDRIAMIARISOA, S.A.F. ANDRIANARIVELO, R. BERNARD, N. RAKOTONIRINA, C. RAKOTOVAO, R.I. RANDRIANAIVO, R. RAZAKAMALALA & P.P. LOWRY II (2021). Études taxonomiques sur le genre *Dalbergia* (Fabaceae) à Madagascar. I. Deux nouvelles espèces du nord de Madagascar, et une description amendée de *D. manongarivensis*. *Candollea* 76: 237–249. En anglais, résumés anglais et français. DOI: <http://dx.doi.org/10.15553/c2021v762a4>

Deux nouvelles espèces de *Dalbergia* L. f. (Fabaceae: Dalbergieae) sont décrites du nord de Madagascar: *Dalbergia antsirananae* Phillipson, Crameri & N. Wilding et *Dalbergia obcordata* N. Wilding, Phillipson & Crameri. Une description amendée est donnée pour une troisième espèce, *Dalbergia manongarivensis* Bosser & R. Rabev. Les trois espèces sont illustrées par des dessins au trait et des photographies, et leur risque d'extinction est évalué selon les critères de la Liste rouge de l'IUCN. Les trois espèces sont évaluées comme «En danger». *Dalbergia antsirananae* et *Dalbergia manongarivensis* sont étroitement apparentées et semblent toutes deux être une source de bois précieux, tandis que *Dalbergia obcordata* n'est connu que comme arbuste et ne semble pas produire de bois à valeur commerciale.

Keywords

FABACEAE – Leguminosae – *Dalbergia* – Madagascar – IUCN Criterion A – IUCN Red List – New species – Precious wood – Rosewood

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Introduction

Dalbergia L. f. (Fabaceae: *Dalbergieae*) is a pantropical genus of c. 270 species (POWO, 2021; TROPICOS, 2021) with centres of diversity in Africa, the Americas and Asia. The genus includes woody climbers (lianas), shrubs and trees, present in a wide range of vegetation types, including tropical rainforest, seasonally dry tropical to subtropical humid and dry forest, woodland, bushland, thicket, and wooded grassland (KLITGAARD & LAVIN, 2005). Among members of the tribe *Dalbergieae*, species of *Dalbergia* are recognisable by their non-woody indehiscent samaroid fruits, 5-lobed calyces and basifixed anthers that usually dehisce via small transverse slits (BARETTA-KUIPERS, 1971; LACHENAUD & VAN DER MAESEN, 2016).

As the primary source of rosewood, one of the world's most valuable and highly prized precious woods, the genus has been subjected to significant over-exploitation and illegal trade. For example, between 2004 and 2015, rosewood accounted for 35% of the value of all wildlife seizures, more than that of elephants, pangolins, rhinoceros and big cats combined (UNODC, 2016). The problem has been particularly acute in Madagascar (MASON et al., 2016), the origin of more than 50% of the approximately 10,000 metric tons of rosewood seized globally during the period 2005–2015 (UNODC, 2016).

Dalbergia is especially diverse in Madagascar, and in a series of publications, Jean Bosser and Raymond Rabevohitra accepted a total of 48 species (BOSSE & RABEVOHITRA, 1996, 2002, 2005), 24 of them newly described. This diversity contrasts with the 64 native species known from continental Africa (APD, 2021), a land area more than 50 times larger than Madagascar. Just one species, *D. bracteolata* Baker, is present in both Madagascar and continental Africa, while the remaining 47 Malagasy species recognised to date are endemic to the island. Although no formal infrageneric classification has been established for the endemic Malagasy species of *Dalbergia*, BOSSE & RABEVOHITRA (2002) identified two broad groups: Group 1, comprising 14 species with relatively large flowers, a strongly pigmented calyx, a glabrous gynoeceum and a long slender style; and Group 2, comprising 29 species with relatively small flowers, a green calyx, a pubescent gynoeceum and a short robust style.

A renewed focus on *Dalbergia* in the context of a project that aims to improve knowledge of precious wood genera across Madagascar's diverse habitats has generated significant numbers of new field collections for targeted regions and taxa. The new field collections have already served as an important source of voucher material for phylogenomic and population genomic analyses based on more than 600 accessions of Malagasy *Dalbergia* (CRAMERI, 2020). These new data, in combination with observations by local botanists and the study of herbarium material collected since Bosser and Rabevohitra worked on the genus, have revealed numerous shortcomings with the current taxonomy of the Malagasy species and

demonstrated the urgent need for taxonomic revision. Aided by the ongoing phylogenetic studies, we estimate that about 75% of the currently recognised *Dalbergia* species in Madagascar present problems with regard to their current delimitation, seriously hindering other areas of study, most notably the development of an effective conservation strategy for this targeted group. The phylogenetic data also provide support for the two major species groups identified in Madagascar by BOSSE & RABEVOHITRA (2002) and suggest furthermore that these two separate lineages represent independent colonisations of Madagascar (CRAMERI, 2020).

This article is the first in a series of papers on the taxonomy of Malagasy *Dalbergia*, in which new taxa will be described and revised species circumscriptions will be presented. In this first contribution we describe two new species from northern Madagascar: *D. antsirananae* Phillipson, Crameri & N. Wilding and *D. obcordata* N. Wilding, Phillipson & Crameri. Previously, certain specimens that we now place in *D. antsirananae* were identified by Bosser and Rabevohitra as *D. madagascariensis* Vatke, a Group 2 species for which the delimitation has long been problematic. BOSSE & RABEVOHITRA (2002) took a broad view of *D. madagascariensis*, which also included material that we now refer to *D. manongarivensis* Bosser & R. Rabev., for which we provide an emended description in this article. According to CRAMERI (2020), *D. antsirananae* and *D. manongarivensis* are resolved as part of a highly supported clade that also includes *D. viguieri* Bosser & R. Rabev. The distribution ranges of these three species are narrow and non-overlapping, with *D. antsirananae* occurring in the far north, *D. manongarivensis* in the northwest, and *D. viguieri* in the northeast (MADAGASCAR CATALOGUE, 2021), all north of a line from Antalaha in the northeast to Antsohihy in the northwestern part of the island (Fig. 1). In contrast, *D. madagascariensis* (including its infraspecific taxa) is much more widely distributed, also occurring in the north, but present as well on the Masoala Peninsula, at scattered locations along the eastern escarpment, and in the southeast, but is not known from the far north where *D. antsirananae* occurs. *Dalbergia madagascariensis* is phylogenetically and morphologically most closely related to *D. delphinensis* Bosser & R. Rabev., which is restricted to the southeast (Fig. 1), and together these two species are sister to the clade that includes *D. antsirananae*, *D. manongarivensis*, and *D. viguieri* (CRAMERI, 2020). The second new species described in this article, *D. obcordata*, is only known from two recent collections in northern Madagascar. In contrast to the previously mentioned species, the structure of the inflorescence in *D. obcordata* clearly distinguishes it as a Group 1 species.

The treatment of each of the three species presented in this article is accompanied by line drawings, field photographs, and a risk of extinction assessment according to the IUCN Red List Categories and Criteria (IUCN, 2012). Since

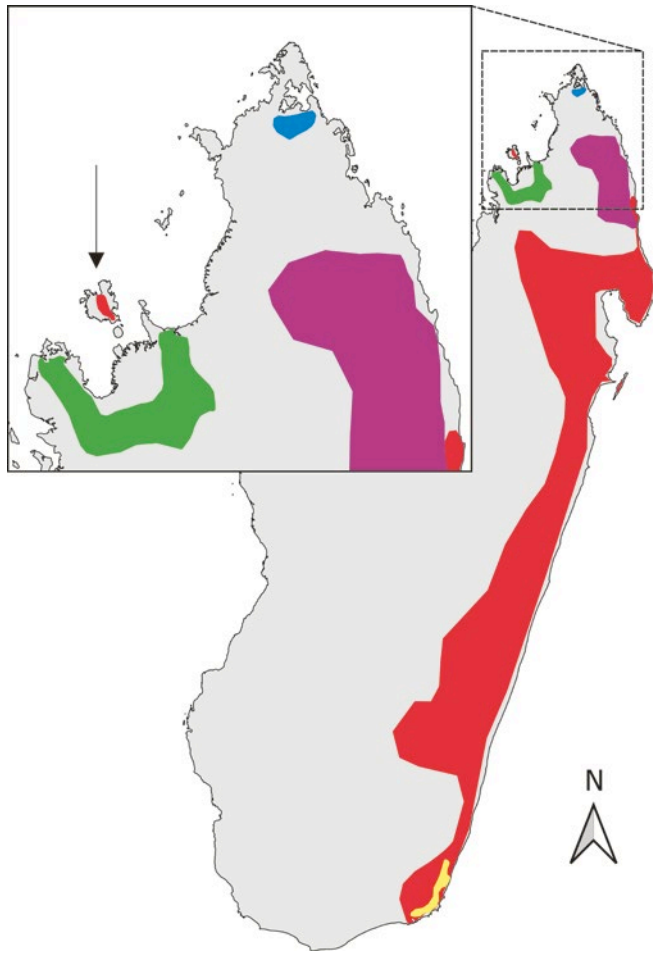


Fig. 1. – Map showing the approximate distribution ranges for *Dalbergia* Group II species treated in the text. From north to south: *D. antsirananae* Phillipson, Cramer & N. Wilding (blue); *D. viguieri* Bosser & R. Rabev. (purple); *D. manongarivensis* Bosser & R. Rabev. (green); *D. madagascariensis* Vatke (red; note small subpopulation on Nosy Be, indicated by an arrow); *D. delphinensis* Bosser & R. Rabev. (yellow).

Dalbergia antsirananae and *D. manongarivensis* can develop into sufficiently large trees to be potential sources of valuable wood, geo-coordinates and detailed locality data have been withheld for them in this article, and public access to this information through the MADAGASCAR CATALOGUE (2021) has been restricted. For *D. obcordata* full specimen records and distribution maps are available in the MADAGASCAR CATALOGUE (2021), and scanned images can also be found in the SONNERAT (2021) database. Post-facto georeferencing of historical specimens is indicated by square brackets.

Material and methods

With the knowledge that one of the most serious threats to many forest species in Madagascar is the loss of suitable habitat, primarily as a result of agricultural practices, we devel-

oped a novel integrative approach to estimate the decline of forested area within the modelled ecological niche for a given forest species. This method was conceived specifically for conducting conservation assessments under IUCN Criterion A, which is concerned with assessing threat based on reduction in population size, as per the indicators “a-e” (IUCN, 2012). Under Criterion A, one of the ways to determine a “suspected” population reduction involves using indirect evidence that can reasonably be supported as a proxy for the number of mature individuals. Indicator “c” under Criterion A is uniquely concerned with this type of evidence as it is based on “a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality” for suspecting population reductions.

The method we developed takes advantage of a time series of historical forest cover data for Madagascar (see VIEILLEDENT et al., 2018) to infer past and future loss of forest cover as a proxy for demonstrating a decline in habitat quality. We used binary logistic regression in a hierarchical Bayesian framework (VIEILLEDENT et al., 2013) to fit numerous potentially informative predictors (including topography, climate, soil, distance to settlements or transport routes, land policy and time-varying forest characteristics such as connectivity or distance to forest edge) to the locations of observed past deforestation during four periods spanning the years 2000 and 2017. We projected future (loss of) forest cover following MORELLI et al. (2020) but for the whole of Madagascar based on a series of local sub-models. Forest loss projections were intersected with a model of the species’ ecological niche to produce an estimate of the total loss of forest cover during a predefined time interval and within the potential distribution of the species.

Taxonomy

Dalbergia antsirananae Phillipson, Cramer & N. Wilding, **sp. nov.** (Fig. 2, 3).

Holotypus: MADAGASCAR. **Reg. DIANA [Prov. Antsiranana]:** Montagne des Français, 30.III.1994, fl., Du Puy & Andriantiana M761 (P [P00059481]!; iso-: K [K001351089]!, MO-3065175 image!, PRE, TAN, WAG [WAG1014216, WAG1014217 2-sheet specimen] images!).

Dalbergia antsirananae Phillipson, Cramer & N. Wilding differs from *D. madagascariensis* Vatke by its smaller flowers (petal length c. 5 mm vs. at least 6 mm) and leaves with (5–)7–9 membranous, ovate-triangular leaflets, each with a shortly acuminate apex (vs. 5–7(–9) subcoriaceous, ovate-oblong leaflets, each with an attenuate apex).

Trees to c. 15 m tall; bole to 3.5 m high, DBH to c. 50 cm. Branches glabrous, yellow-green *in vivo* (black *in sicco*) when young, becoming pale grey-brown when old, coppice shoots with a fine brown pubescence on the branches and the leaves (RIR, pers. obs.; Fig. 2C), lenticels present. Leaves alternate,



Fig. 2. – *Dalbergia antsirananae* Phillipson, Cramer & N. Wilding. **A.** Flowering branch; **B.** Fruiting branch; **C:** Leafy branch from coppice shoot, showing underside of leaves with distinctive pale brown indument on the laminae, contrasting with leaves on fertile branches; **D:** Bole of large felled tree (foreground) and large standing tree (background).

[**A:** Randrianaivo 3675; **B:** Razafitsalama1504; **C–D:** Randrianaivo 3506] [Photos: **A, C–D:** R. Randrianaivo; **B:** J. Razafitsalama]

c. 12–20 cm long, with (5–)7–9 alternate leaflets; petiole and rachis yellow-green *in vivo*, dark brown to black *in sicco*, glabrous except for a very fine, scattered, white, puberulous indument forming a line on the upper surface of the rachis, with a fine brown pubescence on coppice shoots; petiole 2.5–3.5 cm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets (5–)40–55(–70) × (3–)20–25(–30) mm, the proximal leaflets sometimes smaller than the rest, the distal leaflet slightly larger, the others often relatively uniform; petiolule (2–)3.5–5 mm long, yellow-green *in vivo*, very dark brown to black *in sicco*, with a very fine, scattered, white, puberulous

indument on the upper surface, with a fine brown pubescence on the lower surface on coppice shoots; lamina ovate-triangular, membranous, base truncate to broadly obtuse, margin very slightly revolute, apex acute to obtuse, shortly acuminate, venation brochidodromous, with 7–9 principal lateral veins per side; upper and lower surface bright mid-green *in vivo*, dark brown *in sicco*, upper surface slightly glossy, glabrous, the midrib forming a groove, with a very fine, scattered, white, puberulous indument on the proximal portion, lower surface matt, glabrous, higher-order veins forming a fine network, midrib prominent. *Inflorescences* terminal, corymbose panicles, corymbs



Fig. 3. – *Dalbergia antsirananae* Phillipson, Crameri & N. Wilding. **A.** Flowering branch; **B.** Fruiting branch; **C.** Part of young inflorescence; **D.** Leaflet (lower surface); **E.** Flower; **F.** Fruit; **G:** Calyx (split open and flattened) inner surface (left) and outer surface (right); **H.** Standard petal (adaxial surface); **I.** Wing petal (adaxial surface); **J.** Keel petal (adaxial surface); **K.** Androecium (split open to show adaxial surface); **L.** Gynoecium.

[**A, C–E, G–L:** Service Forestier 13215, TEF; **B:** Randriambololomamonjy 23, TAN; **F:** Randrianarivelo et al. 138, TAN] [Drawings: R.L. Andriamiarisoa]

decreasing in size towards the apex, the basal units subtended by well-developed pinnate leaf-like bracts, the apical units with reduced, caducous scale-like bracts or caducous leafy bracts, distal portions curved, sub-spicate, secundiflorous, axes sparsely pubescent; peduncle 2–3 cm long. *Flowers* subtended by a caducous, triangular, sparsely puberulous (mostly near the margins) bract, c. $0.5\text{--}1.5 \times 0.5\text{--}1.5$ mm; pedicel 0.5–1.2 mm long, very sparsely puberulous or glabrous (pedicels of apical flowers shorter than of basal flowers); bracteoles ovate, c. 1.2×1 mm, apex rounded, sparsely ciliate, yellow-green *in vivo*, brown to dark brown *in sicco*, caducous; calyx yellow-green *in vivo* (or cream *fide Du Puy M761*), becoming brown to dark brown *in sicco*, glabrous except for minutely ciliate apices of lower 3 lobes, persisting on fruits, c. 3 mm long, fused in the lower $\frac{2}{3}$, the 2 upper lobes fused to form a single, rounded unit, c. 2×3 mm, the apex shallowly emarginate, the 2 lateral lobes triangular, c. 1×1 mm, the lowest lobe triangular, keeled, c. 1.8×1.4 mm; petals glabrous, white *in vivo*, becoming pale brown *in sicco*; standard petal pandurate, c. 5×3 mm, claw c. 1 mm long, apex notched; wing petals c. 5×1.2 mm, claw c. 0.8 mm long; keel petals c. 5×1.5 mm, claw c. 1.8 mm long; androecium glabrous, monadelphous, c. 4 mm long; stamens 10, filaments free for the upper $\frac{1}{3}$; gynoecium c. 4.7 mm long; stipe densely pubescent, c. 1.9 mm long; ovary glabrous, c. 2 mm long, with 4 ovules; style glabrous, c. 0.8 mm long. *Fruits* green *in vivo* (*fide Rakotonandrajaona 316*), dark brown *in sicco*, the body oval, $5.0\text{--}6.0 \times 1.9\text{--}2.1$ cm when single-seeded (multi-seeded fruits not seen), base cuneate, apex rounded, surface smooth but with a coarse network of mostly longitudinal ribs over the seed not extending to the edges, glabrous; stipe c. 4 mm long, glabrescent but with some persistent indument at the base; style caducous; seeds 7×3.5 mm, reniform, flattened, brown, smooth.

Etymology. – The name *Dalbergia antsirananae* was chosen to reflect the species' restricted distribution near the city of Antsiranana in northern Madagascar.

Vernacular names and uses. – “Ma(g)nary” (*Du Puy M761*, *Randriamahazomanana 130*, *Service Forestier 13215*); “Tsian-dalana” (*Randriambolomamonjy 12*, *Randrianarivelo et al. 138*).

The wood of *Dalbergia antsirananae* is strong and durable, and red-brown in colour; it is used in carpentry and for furniture, and it is also reported as good for charcoal production (*Du Puy & Andriantiana M761*).

Distribution, ecology and phenology. – *Dalbergia antsirananae* occurs in intact and degraded, dry, dense deciduous forest and gallery forest at low- to mid-elevations (55–450 m) in the north of Madagascar. It occurs mainly on tertiary limestone (tsingy) and on alluvial or white sandy soils over limestone, but also on basaltic substrates. The species has been collected in flower from April to May, just after the rainy season, and

in fruit in June and from September to October, during the dry season. A single record of young fruit in March 2004 at the start of the dry season is probably due to exceptionally dry weather in February of that year (SZABÓ et al., 2015).

Conservation status. – *Dalbergia antsirananae* has an EOO of c. 128 km² and an estimated minimum AOO of 36 km² (based on a 4 km² grid). The species occurs in two protected areas: the Montagne des Français (Ambohitratsingy) Protected Landscape, a category V protected area, where it has been documented by nine collections at scattered localities, and by seven collections from two separate low-lying areas in the north of the Montagne d'Ambre National Park, a category II protected area, that are atypical of the National Park as a whole, most of which is over 500 m in elevation and covered primarily by humid forest and with little, if any, dry forest. These three areas represent three separate subpopulations. Within the Montagne des Français protected area, where the largest sub-population of *D. antsirananae* occurs, the species is threatened by wild fires related to charcoal production, as exemplified by a fire that destroyed a 4 ha block of forest in November 2020 within the protected area (C. Frasier, pers. comm.), while illegal timber harvesting may also occur. Recent observations of the two subpopulations in Montagne d'Ambre National Park have provided valuable information on their status. The species is abundant at one of the sites (RIR, pers. obs., Feb. 2021), and this important subpopulation should be targeted by park authorities for conservation measures because it is easily accessed and therefore particularly vulnerable. The second subpopulation within the National Park is less accessible and the species apparently less abundant (RIR, pers. obs., Oct. 2019), but at this site a large, recently felled tree of *D. antsirananae* with a bole of c. 50 cm diameter was documented in October 2019 (*Randrianaivo 3506*; Fig. 2D) although coppice shoots were developing from its base. With respect to wild fires, which are considered to be the most serious plausible threat, *D. antsirananae* occurs at three locations corresponding to the three known subpopulations, and on this basis it is assigned a preliminarily 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). The impact of recent fires at the Montagne des Français on this important subpopulation should be evaluated, and the three subpopulations should be closely monitored.

Notes. – The currently available material of *Dalbergia antsirananae* includes two collections that were seen by Bosser and Rabevohitra in 1992 (*Service Forestier 3557*, *13215*) and one (*Du Puy & Andriantiana M761*) examined by Bosser in 1997. These specimens were identified and annotated by Bosser as *D. madagascariensis*, and no doubt for this reason, in their treatment of the genus, BOSSER & RABEVOHITRA (2002)

indicated that *D. madagascariensis* occurred as far north as the city of Antsiranana. However, these and other specimens now available from the same area are morphologically distinct from *D. madagascariensis* (see Table 1), which, as now circumscribed, does not occur in this area.

Differences in habitat further support the recognition of *Dalbergia antsirananae* as a coherent taxonomic entity distinct from *D. madagascariensis*: *D. antsirananae* occurs in dry deciduous forest whereas *D. madagascariensis* occurs in humid and sub-humid evergreen forest. In addition to differences in the morphology of the flowers and leaves of *D. antsirananae*, which separate it from *D. madagascariensis* (see diagnosis), it can further be distinguished from its allies by a combination of vegetative and floral characters (see Table 1).

Additional specimens examined. – MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: Distr. d'Antsiranana II, Montagne des Français PA (Pay-sage Harmonieux Protégé d'Ambohitr'Antsingy), 30.III.2004, y.fr., Rakotondrajaona et al. 316 (CNARP, MO, P, TAN); *ibid. loco*, 14.XII.2019, ster., Ramanitrinizaka & Ravaomanalina 158 (DBEV, MO, P, TAN, ZT); *ibid. loco*, 12.VI.2019, fr., Randriamahazomanana 130 (MO, P, TAN); *ibid. loco*, 5.X.2004, fr., Randriambololomamonjy 23 (MO, P, TAN); *ibid. loco*, 24.I.2014, ster., Randrianaivo et al. 2451 (BR, G, MO, P); *ibid. loco*, 25.II.2021, fl., Randrianaivo & Andriamiadana 3675 (DBEV, MO, P, TAN, ZT); *ibid. loco*, fl., Randrianaivo & Andriamiadana 3676 (DBEV, MO, P, TAN, ZT); *ibid. loco*, 24.IX.2004, fr., Randrianarivelo et al. 138 (MO, P, TAN); Montagne d'Ambre NP, Antsampano, 31.X.2019, ster., Randrianaivo & Andriamiadana 3506 (DBEV, MO, P, TAN, ZT); Montagne d'Ambre NP, Sakaramy, 28.II.2021, fl., Randrianaivo & Andriamiadana 3682 (DBEV, MO, P, TAN, ZT); *ibid. loco*, fl., Randrianaivo & Andriamiadana 3683 (DBEV, MO, P, TAN, ZT); *ibid. loco*, fl., Randrianaivo & Andriamiadana 3684 (DBEV, MO, P, TAN, ZT); *ibid. loco*, fl., Randrianaivo & Andriamiadana 3685 (DBEV, MO, P, TAN, ZT); *ibid.*

loco, 29.IV.2021, fr., Razafitsalama 1504 (MO, P, TAN); Montagne des Français, 21.V.1951, fl., Service Forestier 3557 (P); Montagne d'Ambre, Sakaramy, 3.IV.1955, fl., Service Forestier 13215 (G, K, MO, P, TEF, WAG).

Dalbergia manongarivensis Bosser & R. Rabev. in *Adansonia* ser. 3, 27: 210. 2005 (Fig. 4).

Holotypus: MADAGASCAR. Reg. Sofia [Prov. Mahajanga]: Manongarivo SR, 3.VI.1996, fl., Totozafy Be 537 (G [G00011766] image!; iso-: K [K001351163]!, MO-4924628!, P [P00513688]!, TEF).

Trees or *shrubs* (or possibly lianescent shrubs) to c. 22 m tall; bole to 8 m high, DBH to c. 25 cm. *Branches* glabrous, green to olive-green *in vivo* (brown *in sicco*) when young, becoming pale grey-brown when old, lenticels present. *Leaves* alternate, c. 16–20.5 cm long, with 7–11(–12) alternate leaflets; petiole and rachis pale green *in vivo*, dark brown *in sicco*, glabrous except for a fine, scattered, white, puberulous indument on the entire surface of the rachis; petiole 2.5–4.5 cm long; stipules caducous (none seen on available specimens), leaving a visible scar; leaflets (1.5–)4–8.5 × (1–)1.5–3 cm, the proximal 2 or 3 leaflets often smaller than the rest, the distal 2 or 3 often larger; petiolule 2–3 mm long, pale green *in vivo*, dark brown *in sicco*, with a fine, scattered, white, puberulous indument on the upper surface; lamina elliptic, membranous, base rounded to obtuse, margin slightly revolute, apex acute to obtuse, shortly acuminate, venation brochidodromous, with c. 10 principal lateral veins per side; upper and lower surface bright mid-green *in vivo*, mid to dark brown *in sicco*, upper

Table 1. – Morphological comparison between *Dalbergia antsirananae* Phillipson, Cramer & N. Wilding, *D. manongarivensis* Bosser & R. Rabev., and related species occurring in northern Madagascar.

		<i>D. antsirananae</i>	<i>D. madagascariensis</i>	<i>D. manongarivensis</i>	<i>D. viguieri</i>
Leaflets	number	(5–)7–9	5–7(–9)	7–11(–12)	5–7
	lamina shape	ovate-triangular	ovate-oblong	elliptic	elliptic-suborbicular
	lamina texture	membranous	subcoriaceous	membranous	membranous
	lamina apex	acute to obtuse, shortly acuminate	attenuate	acute to obtuse, shortly acuminate	apex acute to rounded
Inflorescences	position	terminal	terminal or axillary	axillary	axillary
	length	as long as or longer than leaves	as long as or longer than leaves	shorter than leaves	shorter than leaves
Flowers	length [mm]	5	6–7.5(–9)	5	(3.5–)4–5
	calyx length [mm]	3	3–5(–6.5)	4	2.5–3
Fruits	shape [cm]	oval, 5–6 × 1.9–2.1	elliptic-oblong, 5–10 × 1.5–3 or 13–15 × 1.5–3 (2-seeded fruits)	elliptic-oblong, 7.5–9 × 3.3 or c. 11.5 × 2.8 (2-seeded fruits)	elliptic, 3–4 × 1–1.3 or 5–6 × 1–1.3 (2-seeded fruits)
	stipe length [mm]	c. 4	c. 4	c. 8	5–8

surface slightly glossy, glabrous, the midrib forming a groove, with a fine, scattered, white, puberulous indument on the proximal portion, lower surface matt, with scattered appressed indument, higher-order veins forming a fine network, midrib prominent, with indument present along sides. *Inflorescences* axillary, a series of corymbs, sometimes appearing terminal due to damaged or aborted terminal growth, the successive corymbs of similar size (not noticeably decreasing towards the apex of the fertile branch), subtended by a well-developed pinnate leaf-like bract and with reduced, caducous, scale-like bracts present within the corymb, distal portions curved, subspicate, secundiflorous, axes glabrous to sparsely pubescent; peduncle c. 4–8 cm long. *Flowers* subtended by a caducous, triangular, ciliate bract, c. 0.5–2 × 0.5–2 mm; pedicel c. 1 mm long, glabrous to sparsely pubescent; bracteoles ovate, c. 1.5 × 1.5 mm, apex rounded, sparsely ciliate, brown *in sicco*, caducous; calyx pale green *in vivo* (Nusbaumer 2564), becoming dark brown *in sicco*, villous or glabrous except for sparsely and minutely ciliate margins, persisting on fruits, c. 4 mm long, fused in the lower half, the 2 upper lobes fused to form a single, rounded unit, c. 1.5 × 2 mm, apex shortly notched, the 2 lateral lobes rounded-triangular, c. 1.5 × 1 mm, the lowest lobe rounded-triangular, keeled, c. 2.2 × 1 mm, with a distinctly curved, apex attenuate; petals glabrous, white *in vivo*, becoming yellow-brown *in sicco*; standard petal pandurate, c. 5 × 3 mm, claw c. 1 mm long, apex notched; wing petals c. 5 × 1.4 mm, claw c. 1 mm long; keel petals c. 5 × 1.3 mm, claw c. 1.8 mm long; androecium glabrous, monadelphous, c. 4.5 mm long; stamens 10, filaments free for the upper $\frac{2}{3}$; gynoecium c. 4.8 mm long; stipe densely pubescent, c. 2.1 mm long; ovary glabrous, c. 1.8 mm long, with 4 ovules; style glabrous, c. 0.9 mm long. *Fruits* pale yellow-green *in vivo* (Karatra 159), dark brown *in sicco*, remnants of the petals and calyx sometimes persisting at base of fruits, the body narrowly elliptic-rhombic, c. 7.5–9 × 3.3 cm, when single-seeded, or narrowly elliptic-oblong, c. 11.5 × 2.8 cm, when multi-seeded, base acute, apex acute, surface smooth but with coarse network of fine, mostly longitudinal ribs over the seed, and extending to the edges, glabrous; stipe c. 8 mm long, glabrescent but sometimes with indument persisting at the base; style caducous; seeds (immature) 9 × 5 mm, sub-reniform, flattened, brown, smooth.

Vernacular names and uses. – “Faralabikesa” (Ammann *et al.* 391, Tabinarivony *et al.* 708); “Hazovola” (Randriatsivory 446, Reserves Naturelles 6911, Service Forestier 7710, Wohlhauser 60279); “Manary” (Perrier 15188); “Manary Bomby” (“Manai-bomby”) (Antilahimena 404, 805); “Manary Boraka” (Service Forestier 3100, 95R152 [Tsimihety dialect]).

Specific uses do not appear to have been recorded for any of the available herbarium specimens of *Dalbergia manongarivensis*, however wood apparently from trees of this

species from Manongarivo, wrongly determined and illustrated as *D. madagascariensis*, has been described as a valued source of timber (ANONYMOUS, 2012: 40–44, photo N° 12).

Distribution, ecology and phenology. – *Dalbergia manongarivensis* occurs in primary lowland moist evergreen forest and disturbed areas in the Sambirano biogeographic region of northwestern Madagascar, from near sea level to c. 700 m, on “rocky ground”, alluvial soils, and gneiss. It is frequently reported as occurring on the edge of rivers and streams and on “lower slopes”. Some of specimen labels for collections from Ankaramy indicate DIANA Region or Antsiranana Province, but the locality details and/or coordinates clearly indicate that these collections were in fact made within the Sofia Region (Mahajanga Province); the data have been corrected accordingly. *Dalbergia manongarivensis* has been collected in flower from March to July and from October to December, and in fruit from July to November and in January. This corresponds most closely to periods of drier and slightly cooler conditions within its known distribution range; precipitation is typically at its lowest from April to October.

Conservation status. – *Dalbergia manongarivensis* has an estimated EOO of c. 3900 km² and a minimum AOO of 104 km² (based on a 4 km² grid). The species occurs within four formally recognised protected areas: Manongarivo Special Reserve (category II), Tsaratanana Strict Nature Reserve (category I), and both the Ampasindava and Galoko-Kalobinono Sustainable Use Areas (category V), as well as in unprotected areas between these sites. In the latter, as well as in less well-managed protected areas, the species is subject to land clearance for agriculture resulting in a loss of suitable habitat, which we consider to be the most serious plausible threat. On this basis, *D. manongarivensis* occurs at 13 locations, and is assigned a preliminary conservation status of “Near Threatened” [NT] according to Criterion B of the IUCN Red List criteria (IUCN, 2012). In unprotected areas, as well as at Ampasindava and Galoko-Kalobinono, exploitation of timber resources is permitted and consequently *D. manongarivensis* is also subjected to logging. Based on the Criterion A approach outlined above, we suspect a population size reduction of 77% for *D. manongarivensis* over the period 1990–2089, based on IUCN Criterion A4(c), i.e. “a decline in habitat quality”, using a generation time of 33 years, and assuming no habitat loss within protected areas (IUCN Categories I–IV). *Dalbergia manongarivensis* is therefore assigned a preliminary conservation status of “Endangered” [EN A4(c)] following the IUCN Red List Categories and Criteria (IUCN, 2012). The assessment under Criterion A suggests a higher level of threat of extinction than the assessment under Criterion B and therefore it should be used in a formal assessment for this species.

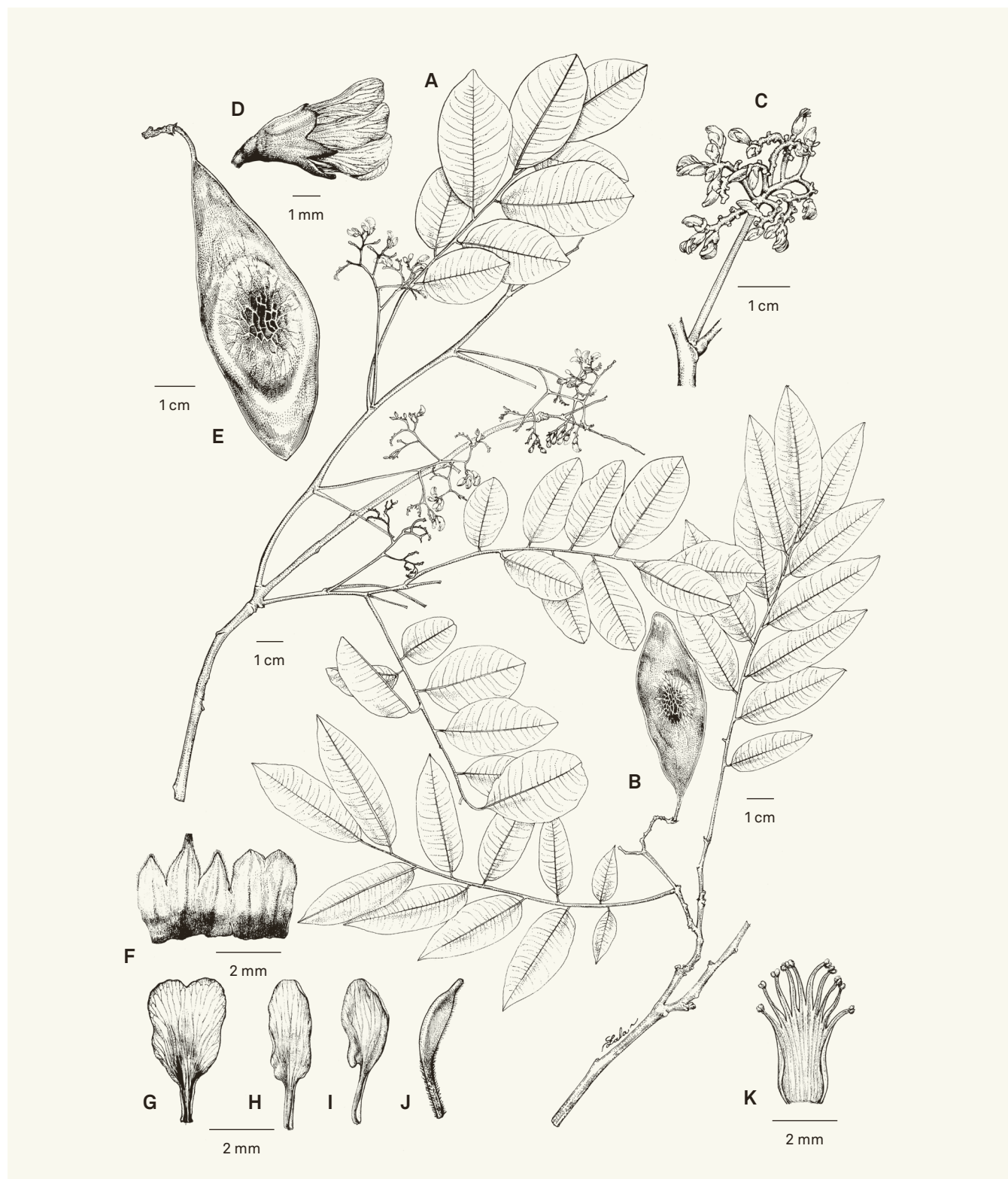


Fig. 4. – *Dalbergia manongarivensis* Bosser & R. Rabev. **A.** Flowering branch; **B.** Fruiting branch; **C.** Young inflorescence; **D.** Flower; **E.** Fruit; **F.** Calyx (outer surface; split open and flattened); **G.** Standard petal (adaxial surface); **H.** Wing petal (adaxial surface); **I.** Keel petal (adaxial surface); **J.** Gynoecium; **K.** Androecium (split open to show adaxial surface).
[A, F–K: Antilahimena 404, TAN; B: Birkinshaw 532 TAN; C–D: Randriatsivery 437 (ex photo); E: Randriatsivery 446, TAN] [Drawings: R.L. Andriamiarisoa]

Notes. – *Dalbergia manongarivensis* was described by BOSSER & RABEVOHITRA (2005) in their final published taxonomic contribution on the genus. It was based on a single collection from Manongarivo (*Totozafy Be 537*), which was described on the corresponding herbarium label in 1996 as a woody liana (“liane ligneuse”). Despite extensive inventory effort at Manongarivo and in its surroundings, and also at Galoko and Ampasindava, which has generated a wealth of new *Dalbergia* collections, no additional lianescent material has ever been recorded. Numerous specimens of arborescent *Dalbergia* from Manongarivo were identified by Bosser & Rabehohitra as *D. madagascariensis*, a species for which they adopted a very broad circumscription (BOSSER & RABEVOHITRA, 2002) that also included some of the material now assigned to the newly described *D. antsirananae* (see above). Phylogenomic and population genomic results (CRAMERI, 2020) support the recognition of arboreal forms (e.g. *Ammann et al. 391*, *Antilahimena 404*, *Randriatsivory et al. 437*, 446) and the single supposedly lianescent collection (*Totozafy Be 537*) as a coherent entity that is clearly differentiated from *D. madagascariensis*. This conclusion is supported by the morphological similarity of the leaves and inflorescences of arborescent specimens and those of the lianescent type collection. As circumscribed here, *D. manongarivensis* is clearly distinguished from related species (see Table 1). The observation of a lianescent habit on the label of *Totozafy Be 537* was possibly an error made in the field or when transcribing the field notes, but it is also possible that both lianescent and arborescent or shrubby forms of *D. manongarivensis* do exist. According to some accounts (KLITGAARD & LAVIN, 2005; LACHENAUD & VAN DER MAESEN, 2016), the growth form of individuals of certain species of *Dalbergia* may be influenced by environmental conditions. This observation is based on species from continental Africa and Asia, and further study is required to determine whether this phenomenon occurs in Madagascar.

Additional specimens examined. – MADAGASCAR Reg. DIANA [Prov. Antsiranana]: Ampasindava PA, 6.XII.2008, bud, fl., *Ammann et al. 147* (G, K, MO, P, TEF); *ibid. loco*, 26.II.2009, fl., *Ammann et al. 391* (G, K, MO, P, TEF); Tsaratanana RNI, 24.III.2000, bud, fl., *Antilahimena 404* (K, MO, P, TAN); *ibid. loco*, 14.XI.2001, fr., *Antilahimena et al. 805* (P); *ibid. loco*, 8.X.1998, fr., *Birkinshaw et al. 532* (MO, P, TAN); Massif du Manongarivo, 14.V.1995, fl., *Gautier 2653* (G, MO, P, TAN); Ampasindava, 29.VII.2019, fr., *Karatra et al. 157* (MO, P, TAN); *ibid. loco*, 29.VII.2019, fr., *Karatra et al. 158* (DBEV, MO, P); *ibid. loco*, 29.VII.2019, fr., *Karatra et al. 159* (P); *ibid. loco*, 29.VII.2019, y.fr., *Karatra et al. 161* (DBEV, MO, P); *ibid. loco*, 29.VII.2019, st., *Karatra et al. 162* (P); *ibid. loco*, 30.VII.2019, fl., *Karatra et al. 166* (DBEV, MO, P); *ibid. loco*, 27.II.2007, fl., *Nusbaumer 2564* (G, K, MO, P, TAN, TEF, WAG); vallée du Sambirano, 1.IX.1908, fr., *Perrier de la Bâthie 4107* (P); *ibid. loco*, *Perrier de la Bâthie 4115* (P); Massif du Manongarivo, 1.IV.1909, fl., *Perrier de la Bâthie 4137* (P); vallée du Sambirano, 1.XII.1922, fr., *Perrier de la Bâthie 15140* (P); *ibid. loco*, XII.1922–I.1923, fl., y.fr., *Perrier de la Bâthie 15188* (P); Ampasindava PA, 23.VII.2019, ster., *Ramanitrinazaka et al. 94* (DBEV, P); *ibid. loco*, 24.VII.2019, y.fr., *Ramanitrinazaka et al. 99* (DBEV, P, TAN); Galoko-Kalobinono PA, 23.III.2009, bud, fl., *Briggs et al. 284* (K, MO, P, TAN); *ibid. loco*, 7.X.2013, bud, fl., *Randriatsivory et al. 437* (G, MO, P, TAN); *ibid. loco*, y.fr., *Randriatsivory*

et al. 446 (G, MO, P, TAN); *ibid. loco*, 14.IV.2000, bud, fl., *Ravelonarivo et al. 1176* (MO, P, TAN); Massif du Manongarivo, 18.XII.2019, bud, fl., *Razakamalala et al. 8586* (DBEV, MO, P, TAN); Massif Marovato Ambanja, 19.XII.1954, fl., *Réserves Naturelles 6911* (K, MO, P, TEF); Galoko-Kalobinono PA, 26.X.1952, y.fr., *Service Forestier 6115* (K, P, TEF); *ibid. loco*, 2.X.1953, fl., *Service Forestier 7710* (K, P, TEF); Massif du Manongarivo, 10–16.XII.1954, fl., *Service Forestier 11480* (BR, G, K, MO, P, TEF, WAG); Ampasindava PA, 23.I.2009, bud, *Tabinarivony et al. 252* (G, K, MO, P); Massif du Manongarivo, 31.V.2000, fl., *Wohlhauser 60279* (G, K, MO, P, TAN). **Reg. Sofia [Prov. Mahajanga]:** Ankaramy (district de Maromandia), 11.VI.1923, fl., *Decary 2168* (P); *ibid. loco*, 31.VIII.1950, fl., *Service Forestier 3100* (K, P, TAN, TEF); Massif de Maromiandra, 9–11.XI.1952, ster., *Service Forestier 95–R-152* (P, TEF).

***Dalbergia obcordata* N. Wilding, Phillipson & Crameri, sp. nov.** (Fig. 5, 6).

Holotypus: MADAGASCAR. Reg. SAVA [Prov. Antsiranana]: Daraina, forêt de Solaniampilana-Maroadabo, 13°05'19"S 49°35'05"E, 140 m, 6.III.2004, fl., *Gautier, Wohlhauser, Nusbaumer & Ranirison 4567* (G [G0006697] image!; iso-: P [P02890651]!, TEF).

Dalbergia obcordata N. Wilding, Phillipson & Crameri most closely resembles *D. gautieri* Bosser & R. Rabev. from northern Madagascar in possessing leaflets of a similar size, shape and number per leaf, but differs by having inflorescences that are lax, sparsely-branched panicles (vs. short, dense, corymbiform panicles with secundiflorous terminal axes in *D. gautieri*).

Shrubs or sprawling shrubs to 6 m tall. Branches pubescent, reddish-brown *in vivo* (grey *in sicco*) when young, becoming glabrous, pale grey-brown when old, lenticels present. Leaves alternate, (4–)5–9(–10.5) cm long, with 5–8 alternate leaflets; petiole and rachis pale yellow-green *in vivo*, dark brown to black *in sicco*, sparsely white to yellowish-pubescent, glabrescent; petiole 9–15 mm long; stipules early caducous (none seen on available specimens), leaving a visible scar; leaflets (14–)20–41 × 8–18 mm, the proximal leaflets smaller than the rest, the distal leaflet equal to or slightly larger; petiolule 1.5–2.5 mm long, pale yellow-green *in vivo*, dark brown to black *in sicco*, sparsely white to yellowish-pubescent, glabrescent; lamina obcordate, rarely obovate or oblong-obovate, coriaceous, base cuneate or rounded in smaller leaflets, margin plane to slightly revolute, apex weakly to strongly retuse or less often rounded, venation eucamptodromous, with 6–10 principal lateral veins per side; upper and lower surface mid-green *in vivo*, red-brown to dark brown *in sicco*, upper surface glossy, glabrous to weakly pubescent along the proximal half of the midrib, midrib forming a groove, lower surface matt, glabrous, higher-order veins forming a fine network, midrib prominent. Inflorescences terminal or axillary, a panicle, 5.5–13 cm long, composed of sparsely-branched paniculate units decreasing in size towards the apex, the basal and apical units with oblong, scale-like bracts, 3.5–4 × 1 mm, distal portions racemose, axes glabrous; peduncle to 2 cm long. Flowers subtended by a caducous bract (none seen), leaving visible scar; pedicel



Fig. 5. – *Dalbergia obcordata* N. Wilding, Phillipson & Crameri. **A.** Flowering branch; **B–C.** Flower; **D.** Flower (with petals removed); **E.** Standard petal (adaxial surface); **F.** Wing petal (adaxial surface); **G.** Keel petal (adaxial surface); **H.** Calyx (outer surface; split open and flattened); **I.** Androecium (split open to show adaxial surface); **J.** Gynoecium. [Gautier et al. 4567, P] [Drawings: M. Lanas]

1.6–2.6 mm long, glabrous or weakly puberulous; bracteoles obovate, 1.5–1.7 × 7–8 mm, apex rounded, glabrous, red-brown *in sicco*, caducous; calyx pale yellow-green *in vivo*, becoming black to orange or yellow *in sicco*, glabrous except for minutely ciliate apices of lower three lobes, possibly persisting on fruits, 4–4.5 mm long, fused in the lower $\frac{2}{3}$, the 2 upper lobes fused to form a single, rounded unit, c. 1.5 × 3 mm, apex deeply notched, the 2 lateral lobes obtuse, c. 2 × 1.3 mm, the lowest lobe acute, keeled, c. 2 × 1.5 mm; petals glabrous, white (with green tints near the base) to yellow-cream *in vivo* (Gautier *et al.* 4567; Fig. 6), becoming yellow to orange *in sicco*; standard petal orbicular, 3.8–4.2 × 3–3.3 mm, claw c. 1 mm long, apex notched; wing petals 3.6–3.9 × 1.7 mm, claw c. 1.5 mm long; keel petals 3.6–3.9 × 2 mm, claw c. 1 mm long; androecium glabrous, monadelphous, 3.5–4 mm long; stamens 9 or 10, filaments free for upper $\frac{1}{2}$ – $\frac{3}{5}$; gynoecium 3–4 mm long, glabrous; stipe 1–1.5 mm long; ovary c. 1 mm long, with 1 or 2 ovules; style 1–1.3 mm long. Mature fruits unknown, young fruits green, margins and stipe red *in vivo*.

Etymology. – *Dalbergia obcordata* is named for its distinctive obcordate leaflet laminae, an unusual shape among Malagasy members of the genus.

Distribution, ecology and phenology. – *Dalbergia obcordata* is restricted to a small area in extreme northeastern Madagascar. It is known from only two localities, the Antsahabe and Solianampilana-Maroadabo forests, about 10.5 km apart, in the surroundings of Daraina in the SAVA region. It occurs at low elevation in dry forest.

Flowering has been recorded in March and May.

Conservation status. – *Dalbergia obcordata* is only known from two recent collections, from sites 10.5 km apart, each in a separate forest patch within the Loky-Manambato Protected Landscape, resulting in an AOO of 8 km² (based on 4 km² grid). Its presence in a Protected Landscape (IUCN category V), where human activity is permitted, does not afford the same level of protection as in IUCN category I–IV protected areas, where exploitation is strictly prohibited or controlled. *Dalbergia obcordata* is therefore at risk locally from habitat loss linked to ongoing forest clearing for agriculture and wild fires. Each of the two known subpopulations represents a separate location with respect to the most serious plausible threat of habitat loss and therefore *D. obcordata* is assigned a preliminary conservation status of “Endangered” [EN B2ab(ii,iii,iv,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Phylogenomic and population genomic results (CRAMERI, 2020) support the recognition of *Dalbergia obcordata* as a distinct species and point to only a distant



Fig. 6. – *Dalbergia obcordata* N. Wilding, Phillipson & Crameri. Inflorescence and leaflets. [Gautier *et al.* 4567] [Photo: L. Gautier]

relationship with *D. gautieri* (a Group 2 species), with which it bears some similarity (see diagnosis above).

While only immature fruits of *Dalbergia obcordata* are known, members of species of Group 1 generally possess fruits with a smooth pericarp that are oblong-elliptical and reddish-brown. The species is suspected to be deciduous, like other members of Group 1.

Paratype. – MADAGASCAR. Reg. SAVA [Prov. Antsiranana]: Daraina, forêt d’Antsahabe, 13°10'51"S 49°33'13"E, 415 m, 1.V.2004, fl., y.fr., Ranirison 758 (G [G00028112], P [P02890655], TAN).

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References

- ANONYMOUS (2012). *Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction. Vingtième session du Comité pour les Plantes. Dublin (Irlande), 22–30 March 2012*. Report, CITES. [https://cites.org/sites/default/files/common/com/pc/20/inf_docs/F20-03i.pdf]
- APD [AFRICAN PLANTS DATABASE] (2021). Conservatoire et Jardin botaniques de Genève and South African National Biodiversity Institute, Pretoria. [<http://africanplantdatabase.ch>]
- BARETTA-KUIPERS, T. (1971). An investigation into the generic limits of *Dalbergia* and *Machaerium* (Papilionaceae). *Acta Bot. Neerl.* 20: 655–662.
- BOSSER, J., & R. RABEVOHITRA (1996). Taxa et noms nouveaux dans le genre *Dalbergia* (Papilionaceae) à Madagascar et aux Comores. *Bull. Mus. Natl. Hist. Nat., Sér. 4*, 18: 171–212.
- BOSSER, J., & R. RABEVOHITRA (2002). Tribe Dalbergieae. In: DU PUY, D.J. et al. (ed.), *The Leguminosae of Madagascar*: 321–361. Royal Botanic Gardens, Kew.
- BOSSER, J. & R. RABEVOHITRA (2005). Espèces nouvelles dans le genre *Dalbergia* (Fabaceae, Papilionoideae) à Madagascar. *Adansonia* ser. 3, 27: 209–216.
- CRAMERI, S. (2020). *Phylogenomics, Species Discovery and Integrative Taxonomy in Dalbergia (Fabaceae) Precious Woods from Madagascar*. Doctoral dissertation [Diss. ETH No. 27241]. ETH, Zurich.
- IUCN (2012). *IUCN Red List Categories and Criteria: Version 3.1*. Ed. 2. IUCN Species Survival Commission, Gland and Cambridge.
- KLITGAARD, B.B. & M. LAVIN. (2005). Dalbergieae sens. lat. In: LEWIS, G. et al. (ed.), *Legumes of the World*: 307–335. Royal Botanic Gardens, Kew.
- LACHENAUD, O. & L.J.G. VAN DER MAESEN (2016). Notes on African *Dalbergia* (Leguminosae – Papilionoideae) with the description of two new species from Atlantic Central Africa. *Symb. Bot. Upsal.* 38: 167–194.
- MADAGASCAR CATALOGUE (2021). *Catalogue of the Plants of Madagascar*. Missouri Botanical Garden, St. Louis & Antananarivo. [<http://www.tropicos.org/project/mada>]
- MASON, J., M. PARKER, L. VARY, P.P. LOWRY II, S. HASSOLD & G. RUTA (2016). *Malagasy precious hardwoods: Scientific and technical assessment to meet CITES objectives*. Report. World Resources Institute and the World Bank. [<https://www.scribd.com/document/318123493/WRI-WB-Malagasy-Precious-Woods-Assessment-1-pdf>]
- MORELLI, T.L., A.B. SMITH, A.N. MANCINI, E.A. BALKO, C. BORGERSON, R. DOLCH, Z. FARRIS, S. FEDERMAN, C.D. GOLDEN, S.M. HOLMES & M. IRWIN (2020). The fate of Madagascar's rainforest habitat. *Nat. Clim. Change* 10: 89–96.
- POWO (2021). Plants of the World Online. Royal Botanic Gardens, Kew. [<http://powo.science.kew.org>]
- SONNERAT (2021). Muséum national d'Histoire naturelle, Paris. [<https://science.mnhn.fr/all/search#botany>]
- SZABÓ, A.I., A. RAVELOSON & B. SZÉKELY (2015). Landscape evolution and climate in Madagascar: Lavakization in the light of archive precipitation data. *Cuadernos de Investigación Geográfica* 41: 181–204.
- TROPICOS (2021). Missouri Botanical Garden, Saint Louis, USA. [<http://www.tropicos.org>]
- UNODC (2016). World Wildlife Crime Report: Trafficking in protected species. [https://www.unodc.org/documents/data-and-analysis/wildlife/World_Wildlife_Crime_Report_2016_final.pdf]
- VIEILLEDENT, G., C. GRINAND & R. VAUDRY (2013). Forecasting deforestation and carbon emissions in tropical developing countries facing demographic expansion: a case study in Madagascar. *Ecol. Evol.* 3: 1702–1716.
- VIEILLEDENT, G., C. GRINAND, F.A. RAKOTOMALALA, R. RANAIVOSOA, J.R. RAKOTOARIJAONA, T.F. ALLNUTT & F. ACHARD (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* 222: 189–197.