

# Two further new species in the highly-diverse Malagasy endemic genus *Capurodendron* (Sapotaceae)

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## Abstract

GAUTIER, L., C.G. BOLUDA, R. RANDRIANAIVO & Y. NACIRI (2022). Two further new species in the highly-diverse Malagasy endemic genus *Capurodendron* (Sapotaceae). *Candollea* 77: 119–126. In English, English and French abstracts. DOI: <http://dx.doi.org/10.15553/c2022v771a9>

During the course of a revision of the Malagasy species of the family *Sapotaceae*, two new species from the dry forest belonging to the highly-diverse endemic genus *Capurodendron* Aubrév. were discovered. The first one, *C. miquearum* L. Gaut. & Boluda, earlier hypothesised to be a hybrid, emerged as a valid species without any hybrid signal, based on a combination of genetic and morphological analyses of a species complex from the southwestern region. The second species, *C. namorokense* L. Gaut. & Boluda, occupies a basal position in the same species clade. It is clearly morphologically distinct and geographically distant, so far only being known from northwestern Madagascar. Both species are described and illustrated by line drawings and field photographs. Preliminary conservation assessments using the IUCN Red List criteria indicate that both species are threatened (EN and CR, respectively).

## Résumé

GAUTIER, L., C. G. BOLUDA, R. RANDRIANAIVO & Y. NACIRI (2022). Deux nouvelles espèces supplémentaires dans le genre endémique malgache hautement diversifié *Capurodendron* (Sapotaceae). *Candollea* 77: 119–126. En anglais, résumés anglais et français. DOI: <http://dx.doi.org/10.15553/c2022v771a9>

A la faveur d'une révision des espèces de Madagascar de la famille des Sapotacées, deux nouvelles espèces de forêt sèche ont été mises en évidence dans *Capurodendron* Aubrév., un genre endémique malgache hautement diversifié. La première, *C. miquearum* L. Gaut. & Boluda, qu'on croyait d'abord être un hybride, a été mise en évidence par la résolution d'un complexe d'espèces du Sud-ouest. Sur la base de données génétiques et d'une étude morphologique approfondie, il a pu être démontré qu'elle n'était pas d'origine hybride, comme supposé précédemment. La seconde, *C. namorokense* L. Gaut. & Boluda, occupe une position basale dans le même clade d'espèces. Elle est morphologiquement clairement distincte et, venant du Nord-ouest, également éloignée géographiquement. Les deux espèces sont décrites et illustrées par des dessins au trait et des photos de terrain. Une évaluation préliminaire de leur risque d'extinction selon les critères de la liste rouge de l'IUCN révèle que les deux espèces sont menacées (EN et CR, respectivement).

## Keywords

SAPOTACEAE – *Capurodendron* – Madagascar – New species – Species delimitation

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## Introduction

*Capurodendron* Aubrév. is a genus that was described by AUBRÉVILLE (1962) to accommodate seven Malagasy species of *Sapotaceae* originally described within *Sideroxylon* L. In the *Sapotaceae* treatment for the *Flore de Madagascar et des Comores* (AUBRÉVILLE, 1974) 16 additional species and three varieties were described. With a total of 23 species, it was ranked as the third richest endemic plant genus on Madagascar (CALLMANDER et al., 2011). Since then, three new species have been described (GAUTIER & NACIRI, 2018).

As part of a systematic study of the family *Sapotaceae* in Madagascar, a molecular analysis of the genus *Capurodendron* has been conducted, involving gene capture and next generation sequencing (see methodology in CHRISTE et al., 2021). Based on a survey of all specimens available in the herbaria G, K, MO, P, TAN and TEF, the c. 900 collections of *Capurodendron* were classified in morphospecies following a splitting approach. These species candidates were then sampled for molecular study, including adequate geographic representation of widespread and disjunct morphospecies. The analysis of 638 genes (CHRISTE et al., 2021; BOLUDA et al., 2022) confirmed the placement of the genus in the tribe *Tseboneae* (GAUTIER et al., 2013) and showed a massive radiation with numerous new species, upgrading *Capurodendron* as the richest endemic Malagasy genus with 33 described species so far.

BOLUDA et al. (2021) characterized the so-called “Arid Complex”, comprising *Capurodendron androyense* Aubrév., *C. mandrarensis* Aubrév., and some specimens collected north of the city of Toliara which were morphologically hypothesized to be hybrids between *C. mandrarensis* and *C. greveanum* Aubrév. This complex was part of a lineage containing also *C. microphyllum* (Scott-Elliott) Aubrév., *C. nanophyllum* L. Gaut. & Naciri, and an undescribed taxon (“*C. sp. 20*” of BOLUDA et al., 2021) recently collected in the Tsingy de Namoroka.

In the study focused on the “Arid Complex” by BOLUDA et al. (2021), 381 collections were morphologically analysed, and 85 samples were selected for a molecular study including highly variable markers able to detect population structure. This confirmed “*C. sp. 20*” as a distinct undescribed species (hereafter *Capurodendron namorokense* L. Gaut. & Boluda) and revealed that the suspected hybrids between *C. mandrarensis* and *C. greveanum* actually represent another undescribed species nested within the “Arid Complex” (hereafter *C. miquearum* L. Gaut. & Boluda). While genetic introgression was detected between *C. androyense* and *C. mandrarensis*, including hybridization, *C. miquearum* displayed no hybridization signals with the two former closely related species, and was morphologically, geographically and ecologically differentiated. It was only distantly related to *C. greveanum*, which was retrieved in a clade sister to that of the “Arid Complex”.

Here we formally describe these two new species and provide conservation assessments following the IUCN Red List Categories and Criteria (IUCN, 2012), with the Extent of Occurrence [EOO] and Area of Occupancy [AOO] calculated using GEOCAT (2022). The descriptions are accompanied by two line drawings and field photographs. Specimen records can be accessed for each species via the *Catalogue of the Plants of Madagascar* (MADAGASCAR CATALOGUE, 2022).

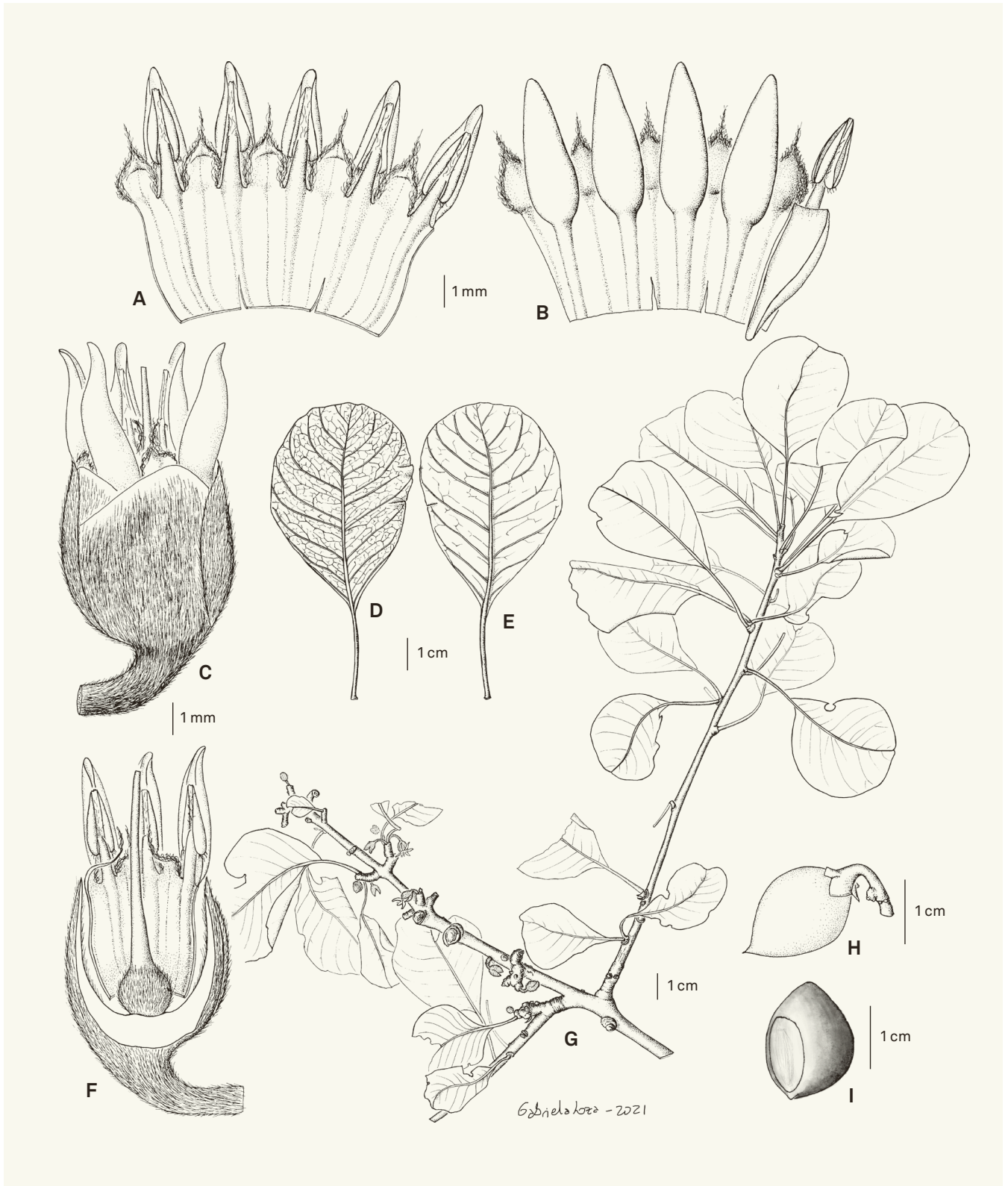
## Systematics

*Capurodendron miquearum* L. Gaut. & Boluda, **sp. nov.** (Fig. 1, 2A–E).

**Holotypus:** MADAGASCAR. **Reg. Atsimo-Andrefana [Prov. Toliara]:** Tuléar II, Belalanda, Ranobe, forêt de Ranobe PK32, 23°00'46"S 43°39'02"E, 101 m, 25.XI.2006, fl., *Razafindraibe et al. 165* (G [G00390469]!, iso-: MO-6427623!, P, TAN!)

*Capurodendron miquearum* L. Gaut. & Boluda differs from its closest relative *C. mandrarensis* Aubrév. by its glabrous lower leaf surface (vs. pubescent), with secondary nerves that are slightly raised (vs. conspicuously raised). It differs from the morphologically similar *C. greveanum* Aubrév. by its greyish pubescent young shoots (vs. green and glabrous), petioles with scattered trichomes (vs. glabrous), the presence of brachyblasts, and the very dense calyx indumentum (vs. sparse).

*Tree*, sometimes shrub, up to 18 m tall, 60 cm DBH, bark greyish, profoundly fissured longitudinally, outer wood pinkish, with white latex, inner wood light yellow; terminal twigs 2 mm in diam., at first densely brown-whitish curly pubescent, later glabrous, 2-year twigs pale to dark grey, longitudinally wrinkled, lenticels inconspicuous; brachyblasts present, 0.5–1(–3) cm long; stipules soon caducous, ovato-triangular, 1.5–2 mm long, densely pubescent on outer side. *Leaves* probably caducous; petioles 1.1–2.8 cm long, 0.8 mm in diam., with scattered thin whitish trichomes; blade oblanceolate to elliptical, rarely rounded, 2.2–5.5 × 1.4–3.2 cm, base cuneate to attenuate, apex rounded, sometimes acute, margin entire, with pubescent indumentum initially, soon becoming almost glabrous on both surfaces, except on the midrib of the lower surface that retains scattered yellowish to whitish trichomes, slightly discoloured in living plants (upper surface shiny, lower paler); midrib slightly prominent below, flat or slightly raised above, 8–13 pairs of camptodromous secondary veins spreading at 30–45°, straight or arching towards the leaf apex, slightly raised on both surfaces, pale green or yellowish, intersecondaries absent or when present similar to the tertiaries, tertiary veins sparse, slightly raised on dried specimens, forming irregular cells that contains a quaternary venation forming isodiametric polygons. *Flowers* solitary to 6-fasciculate, 6–9 × 5–7 mm, on last year shoots and brachyblasts, flowering sometimes profuse and packed;



**Fig. 1.** – *Capurodendron miquearum* L. Gaut. & Boluda. **A.** Corolla, seen from inside; **B.** Corolla, seen from outside; **C.** Flower; **D.** Leaf, abaxial side; **E.** Leaf, adaxial side; **F.** Flower, dissected laterally; **G.** Flowering branch; **H.** Fruit; **I.** Seed. [A–G: Gautier 6339; H–I: Andrianjafy 1679] [Drawing: G. Loza]

pedicels 3–6 × 0.7–1 mm, enlarging distally below calyx, densely pubescent; sepals 5, quincuncial, ovate-lanceolate, apex slightly acute, two outers 4–6.5 × 3.2–3.9 mm (at base), densely golden pubescent inside and outside, three inners 3.4–5 × 2.9–5.3 mm (at base), with scattered trichomes inside and densely pubescent outside except the margin; corolla gamopetalous, 5-lobed, pale yellowish or white, tube c. 3 mm long, lobes lanceolate, 3.5–5.3 × 1.1–1.9 mm, glabrous, erect, convex and enfolding the anther. *Stamens* 5, filaments cylindrical, 1.1–1.6 × 0.3–0.5 mm, same colour as the petals, glabrous, attached to the top of the corolla tube; anthers cream-coloured, lanceolate, 1.9–2.4 × 0.8–1 mm, medifixed, cordate at the base, extrorse, each theca lanceolate, 1.9–2.4 × c. 0.3 mm; connective hairy, prolonged into a 0.3 mm long mucro. *Staminodes* 5, alternate with respect to petals and stamens, ovate-triangular, same colour as the petals, 2.9–4.2 × 1–1.5 mm, with an arista 1.6–2.7 mm long, carnos, glabrous except on the margins which are densely hirsute with trichomes that may bend and cover the complete outer surface, connivent and concealing the ovary at least during part of anthesis. *Ovary* slightly pentagonal, 1.4 × 1.4 mm, with 5 uniovulate locules, densely hirsute; style 5–7.5 × 0.4 mm, glabrous; stigma with 5 minute papillae. *Fruit* on a thickened pedicel 3 mm in diam., globose to ovoid, 14–22 × 11–15 mm, apiculate, glabrescent, with a persistent enlarged (c. 2 ×) calyx; seeds one per fruit, 15–19 × 13 × 11 mm, testa shiny, scar basiventral, 11–13 × 6–8 mm.

*Etymology.* – This species is named after the Mikea ethnic group which inhabits the forests where the species is found.

*Distribution, ecology and phenology.* – *Capurodendron mikearum* is endemic to Madagascar where it is found in the Atsimo Andrefana region (part of the former Toliara Province) from Morombe southward to Toliara, at elevations between 10–135 m, never more than 20 km away from the coast. It occurs in forests on laterite sands in a transition zone between dry deciduous forest and dry spiny thicket. The flowering period extends from November to March and fruits were recorded in November and from February to April.

*Conservation status.* – The estimated EOO calculated with all available herbarium specimen data is 1,755 km<sup>2</sup>, and the minimum AOO is 76 km<sup>2</sup> (both qualifying for EN under criterion B). The species thrives at only five locations with respect to the most important threat, which is habitat transformation for large scale agriculture. Other important threats include uncontrolled forest fires and very probably selective logging. It is known from 26 herbarium collections. Although the five locations are in protected areas or in their close vicinity, the pressures encountered by the dry forests in the southwestern Madagascar are so high that a projected continuing decline is inferred and justifies the assignment of this species to the

category “Endangered” [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2012).

*Notes.* – Specimens attributed to this species have alternatively been identified as *Capurodendron mandrarensense* or *C. greveanum*, as they share character states with both. The new species differs from its closest relative *C. mandrarensense* by its glabrous lower leaf surface (vs. pubescent), with secondary nerves that are slightly raised (vs. conspicuously raised). It differs from the morphologically similar *C. greveanum* by its greyish pubescent young shoots (vs. green and glabrous), petioles with scattered trichomes (vs. glabrous), the presence of brachyblasts, and the very dense calyx indumentum (vs. sparse).

The three species occur in southwestern Madagascar and *Capurodendron greveanum* is even sympatric in the northernmost part of *C. mikearum* distribution. The hypothesised hybrid origin of this taxon has not been validated by the genetic studies we conducted, which indeed revealed that the new species was quite far from *C. greveanum*. It is however closely related to *C. mandrarensense*. Together with the very distinctive *C. androyense*, these three species form the core of what has been referred as the “Arid Complex” (BOLUDA et al., 2021, 2022).

*Additional specimens examined* – MADAGASCAR. Reg. Atsimo-Andrefana [Prov. Toliara]: Belalanda, Ranobe, 23°04'S 43°42'E, 110 m, 16.III.2006, fl. & old fl., *Andrianjafy 1669* (G, MO, P, TAN); ibid. loco, 23°01'S 43°39'E, 100 m, 16.III.2006, fr. & old fl., *Andrianjafy et al. 1679* (G, MO, P, TAN); Belakana, embouchure sur Fiherenana, [23°18'S 43°39'E], XI.1956, bud, *Bosser 10408* (P, TEF); 12 km N of Tulear on road to Morombe, [23°15'S 43°38'E], c. 0 m, 5.II.1975, *Croat 30799* (MO, TAN); 16–18 km N of Tulear along road to Morombe, [23°12'S 43°37'E], c. 0 m, 6.II.1975, *Croat 30885* (MO, TAN); Ranobe PK 32, partie W, 15 km à l'ESE d'Ankilimalinika, 23°01'S 43°42'E, 130 m, 17.II.2017, old fl. & imm. fr., *Gautier et al. 6329* (G, MO, P, TAN); ibid. loco, bud, *Gautier et al. 6331* (G, TAN); ibid. loco, old fl., *Gautier et al. 6332* (G, MO, P, TAN), *6333* (G, K, MO, P, S, TAN); Mikea, partie sud, 11 km à l'W d'Ankililoloaka, 22°47'S 43°31'E, 120 m, 18.II.2017, old fl., *Gautier et al. 6336* (G, MO, P, TAN); ibid. loco, 120 m, 18.II.2017, ster., *Gautier et al. 6337* (G, TAN); ibid. loco, 13.5 km à l'W d'Ankililoloaka, 22°47'S 43°29'E, 130 m, 18.II.2017, fl., *Gautier et al. 6339* (G, K, MO, P, S, TAN); ibid. loco, ster., *Gautier et al. 6340* (G, TAN); Ifaty, dans l'arboretum, 23°07'S 43°37'E, 10 m, 18.II.2017, ster., *Gautier et al. 6341* (G, MO, P, TAN); Songaritelo, [23°14'S 43°37'E], 23.IX.1967, ster., *Koechlin 44* (P); N of Toliara, forêt de Mikea, c. 18 road-km W of Vorehe, [22°16'S 43°26'E], 50 m, 8.II.1998, old fl., *McPherson et al. 17358* (G, MO); Mikea Forest, 22°47'S 43°31'E, 130 m, 20.XI.2002, fl., *Phillipson 5603* (G, MO, P); Ifaty, 23°09'S 43°37'E, 14.I.1994, old fl. & fl., *Rabesandratanana 4192* (P); Tulear II, Belalanda, forêt de Ranobe, 23°18'S 43°39'E, 35 m, 18.XI.2002, fr., *Ranaivojoana 459* (G, MO, P, TAN); Toliara II, Ankilimalinika, forêt de Ranobe, 23°00'S 43°41'E, 100 m, 24.IV.2005, fr., *Randrianarivo & Randrianarivo 1187* (G, MO, P, TAN); 35 km N of Toliara, along coast road, 23°4'S 43°35'E, 20 m, 12.XII.1988, fl. & old fl., *Schatz & Miller 2477* (MO, P, S, TAN); au bord d'un chemin qui mène vers Mambo, Ankazomanga Tosimitro, [23°16'S 43°43'E], 19.VI.1954, old fl., *Service Forestier 10220* (P); rte de Tuléar à Sarodrano, au pied des falaises du plateau calcaire, [23°29'S 43°46'E], 16.III.1961, fr., *Service Forestier 20178* (P, TEF); Sarodrano et environs, [23°32'S 43°45'E], XII.1961, fl., *Service Forestier 20831* (MO, P, TEF); sables littoraux au S de Morombe, [21°48'S 43°21'E], 1.XII.1969, fl., *Service Forestier 28965* (MO, P, TEF).



Fig. 2. – *Capurodendron miquearum* L. Gaut. & Boluda: A. Habit; B. Twig; C. Slashed bark; D. Fascicles of flowers; E. Flowers. *Capurodendron namorokense* L. Gaut. & Boluda: F. Slashed bark; G. Twig with two old flowers in an early fruit development stage. [A: Gautier 6329; B–E: Gautier 6339; F–G: Gautier et al. 6276] [Photos: L. Gautier]

*Capurodendron namorokense* L. Gaut. & Boluda, **sp. nov.** (Fig. 2F–G, 3).

**Holotypus:** MADAGASCAR. **Reg. Melaky [Prov. Mahajanga]:** Tsingy de Namoroka, sur Tsingy, 16°27'39"S 45°16'35"E, 146 m, 25.X.2016, old fl., *Gautier et al. 6276* (G [G0419383]!; iso-: P [P00947295]!, MO!, S!, TAN!)

*Capurodendron namorokense* L. Gaut. & Boluda resembles *C. antongilense* Aubrév., *C. birkinshawii* L. Gaut. & Boluda and *C. nodosum* Aubrév. in its medium-sized leaves (blade 5.5–12 cm long) with 10–15 straight secondary veins that are regularly spaced and clearly raised on lower surface. It however differs from the latter three species by the lack of an obvious Aubréville branching pattern in terminal shoots and by its smaller outer calyx lobes (5.5 mm vs. 9–11 mm long). It further differs from *C. birkinshawii* by the acute leaf base (vs. broadly rounded to subcordate) and from both *C. birkinshawii* and *C. antongilense* by its smaller stipules (< 5 mm vs. > 6 mm long).

*Tree*, 11 m tall, 30 cm DBH, outer bark greyish, deeply fissured longitudinally, slash pink, with white latex; terminal twigs 2.5–4 mm in diam., glabrescent, with leaves clustered at the distal 1–2 cm, twig bark pale to medium grey, smooth to longitudinally wrinkled, profusely warted by the attachment of previous years' leaves, later with short transversal cracks; brachyblasts absent; stipules triangular, 4 × 2 mm at base, felted outside, glabrous inside. *Leaves* chartaceous, caducous; petiole 9–17 × c. 1 mm, tomentose, terete proximally and semi-terete distally; leaf blade elliptic, 5.5–12 × 2.2–3.7 cm, base acute, apex obtuse, margin entire to slightly sinuous, frequently revolute, glabrous adaxially, whitish-tomentose abaxially, slightly bullate; midrib slightly prominent adaxially, very prominent abaxially, tomentose, 10–15 pairs of craspedodromous raised secondary veins spreading at 60–80°, straight, arching in the last millimetres to form a marginal vein, intersecondaries present, similar to the secondary veins but dissolving half-way to the margin, tertiary veins slightly conspicuous adaxially, inconspicuous abaxially, irregular, not forming well-delimited cells. *Flowers* solitary or in pairs, at the base of the current years' shoots; pedicels 9–12 × 0.5–1 mm, tomentose. *Sepals* (old flowers) 5, quincuncial, two outers sub-triangular to ovato-lanceolate, 5.5 × 4 mm, apex subacute, sparsely tomentose inside except in the central portion, tomentose outside, three inners lanceolate, 4.8 × 4 mm, apex subacute, glabrous inside and densely pubescent with adpressed trichomes outside except at the overlapping margins. *Corolla*, *stamens* and *staminodes* unknown. *Ovary* (in late flowering state) with 5 uniovulate locules, densely hirsute with beige trichomes. *Fruit* unknown.

*Etymology.* – The specific epithet refers to the Tsingy de Namoroka, where the species was found.

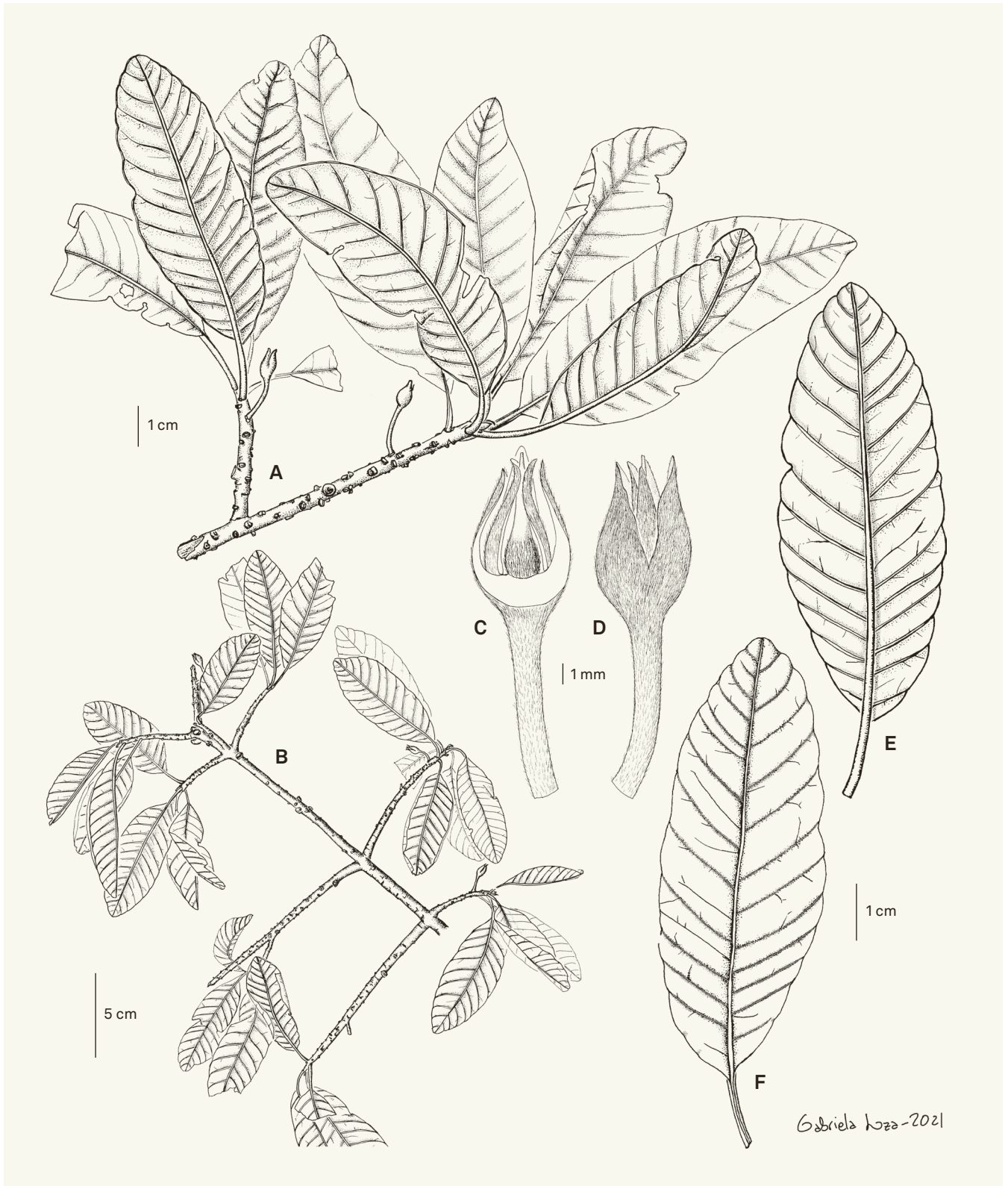
*Distribution, ecology and phenology.* – *Capurodendron namorokense* is known only from northwestern Madagascar, thriving in dry deciduous forest on limestone outcrops (tsingy). The single known specimen has been collected in October, with old flowers.

*Conservation status.* – *Capurodendron namorokense* is known only from a single locality within the Tsingy de Namoroka Protected Area, only 800 m from its border. Its AOO is 4 km<sup>2</sup> and its EOO is estimated to be less than 100 km<sup>2</sup> (both qualifying for CR under criterion B). The species is documented in only one location with respect to the most probable threat which is selective logging. As most *Capurodendron* species are actively logged for their valuable timber, it has to be considered as threatened by selective logging despite the natural protection that the tsingy environment provides, and a population decline is projected. On this basis, the species is assessed as “Critically Endangered” [CR B1ab(i,ii,iii,v)+2ab(i,ii,iii,v)] (IUCN, 2012).

*Notes.* – *Capurodendron namorokense* can be recognised by the characteristic venation pattern of its leaves, which is only slightly reminiscent of *C. antongilense*, *C. birkinshawii*, and *C. nodosum*. Genetically, it is retrieved with *C. nanophyllum* at the base of the “Arid Complex”, comprised of *C. androyense*, *C. mandrarensis*, *C. microphyllum*, and *C. miquearum* (BOLUDA et al., 2021). The species of this clade are restricted to the southern half of the island whereas *C. namorokense* is known only from northwestern Madagascar.

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**Fig. 3.** – *Capurodendron namorokense* L. Gaut. & Boluda. **A.** Apex of branch; **B.** Branch; **C.** Old flower lacking corolla, dissected laterally; **D.** Old flower lacking corolla; **E.** Leaf, abaxial side; **F.** Leaf, adaxial side. [Gautier et al. 6276] [Drawing: G. Loza]

## References

- AUBRÉVILLE, A. (1962). *Capurodendron*, genre nouveau de Sapotacées de Madagascar. *Adansonia*, sér. 2, 2: 92–98.
- AUBRÉVILLE, A. (1974). Sapotacées. In: HUMBERT, H. (ed.), *Fl. Madagascar Comores* 164.
- BOLUDA, C.G., C. CHRISTE, A. RANDRIARISOA, L. GAUTIER & Y. NACIRI (2021). Species delimitation and conservation in taxonomically challenging lineages: the case of two clades of *Capurodendron* (Sapotaceae) in Madagascar. *Plants* 10: 1072. DOI: <https://doi.org/10.3390/plants10081702>
- BOLUDA C.G., C. CHRISTE, Y. NACIRI & L. GAUTIER (2022). A 638-gene phylogeny supports the recognition of twice as many species in the Malagasy endemic genus *Capurodendron* (Sapotaceae). *Taxon* 71: 360–395. DOI: <https://doi.org/10.1002/tax.12676>
- CALLMANDER, M.W., P.B. PHILLIPSON, G.E. SCHATZ, S. ANDRIAMBOLOLONERA, M. RABARIMANARIVO, N. RAKOTONIRINA, J. RAHARIMAMPIONONA, C. CHATELAIN, L. GAUTIER & P.P. LOWRY II (2011). The endemic and non-endemic vascular flora of Madagascar updated. *Pl. Ecol. Evol.* 144: 121–125. DOI: <https://doi.org/10.5091/plecevo.2011.513>
- CHRISTE, C., C.G. BOLUDA, D. KOUBÍNOVÁ, L. GAUTIER & Y. NACIRI (2021). New genetic markers for Sapotaceae phylogenomics: More than 600 nuclear genes applicable from family to population levels. *Molec. Phylogen. Evol.* 160: 107123. DOI: <https://doi.org/10.1016/j.ympev.2021.107123>
- GAUTIER, L. & Y. NACIRI (2018). Three critically endangered new species of *Capurodendron* (Sapotaceae) from Madagascar. *Candollea* 73: 121–129. DOI: <https://doi.org/10.15553/c2018v731a13>
- GEOCAT (2022). *Geospatial Conservation Assessment Tool*. Royal Botanic Gardens, Kew. [<http://geocat.kew.org>]
- IUCN (2012). *IUCN Red List Categories and Criteria: Version 3.1*. Ed. 2. IUCN Species Survival Commission, Gland and Cambridge.
- MADAGASCAR CATALOGUE (2022). *Catalogue of the Plants of Madagascar*. Missouri Botanical Garden, St. Louis and Antananarivo. [<http://www.tropicos.org/Project/Madagascar>]