EDINBURGH JOURNAL OF BOTANY 80, Article 1996:
1–17 (2023). https://doi.org/10.24823/EJB.2023.1996

Published by the Royal Botanic Garden Edinburgh
ISSN (online): 1474-0036, ISSN (print): 0960-4286

A TAXONOMIC REVISION OF THE MADAGASCAR-ENDEMIC GENUS *BEMANGIDIA* (SAPOTACEAE), WITH DESCRIPTION OF A SECOND SPECIES

C. G. Boluda*, A. Randriarisoa, Y. Naciri & L. Gautier

Bemangidia L.Gaut. (Sapotaceae) is a genus endemic to a restricted area in the southeastern lowland moist evergreen forests of Madagascar. It was published in 2013 to accommodate an undescribed species, *Bemangidia lowryi* L.Gaut., which showed a combination of characters unique in the family Sapotaceae. At the time of description, three atypical collections from the same locality but growing on a ridge, slightly higher in altitude, were already known. Although matching well with the *Bemangidia* genus, they were phenotypically different from *B. lowryi* and were therefore not included in the species description. In the present study, we evaluate whether these specimens correspond to a new species, using a combination of morphological and genetic data based on 638 nuclear genes. The results show that *Bemangidia* contains two lineages, each one corresponding to a different morphology, with a genetic branch length similar to those observed among species pairs in other genera of Sapotaceae. We conclude that the genetic and morphological differences are sufficient to consider the two lineages as two distinct species. Consequently, the genus is here revised and a second species described.

Keywords. *Bemangidia*, Critically Endangered, Madagascar, new species, Sapotaceae.
Received 12 April 2023 Accepted 12 September 2023 Published 19 December 2023

Introduction

The monotypic genus *Bermangidia* L.Gaut. and its type species, *B. lowryi* L.Gaut., were described by Gautier *et al.* (2013) from the Bemangidy forest, in the Tsitongambarika Protected Area, Southeast Madagascar. In that publication, it was considered different from *Tsebona* Capuron based on molecular data as well as on morphological characters such as seed scar area, venation pattern, and number of stamens. During a field trip in 2011, a specimen was collected in bud only 600 m away from the type locality of *Bemangidia lowryi* but at higher elevation (c.650 m) on a secondary summit at the top of a ridge. It was obvious that this collection belonged to the same genus, although being reduced in habit and leaf size compared with the lower-altitude *Bemangidia lowryi*.

Based on research carried out in the MO and P herbaria (herbarium codes follow Thiers, continuously updated), the new collection was rapidly associated with two additional specimens collected from the same locality in 2007 (in submature flowering stage) and 2008 (in early fruiting stage), both of which were identified as an unknown species of the

PhyloLab, Conservatoire et Jardin botaniques de Genève and Department of Plant Sciences, University of Geneva, Chemin de l'Impératrice 1, C.P. 71, 1292 Chambésy, Switzerland.
* Author for correspondence. E-mail: carlos.boluda@ville-ge.ch.

genus *Labourdonnaisia* Bojer. Because these specimens were all collected on ridges, a windier and sunnier habitat than the slopes and valleys in which *Bemangidia lowryi* grows, it was possible that the three collections were merely the result of the phenotypic plasticity of that species. However, the names of the specimens from the mountain ridge were retained as *Bemangidia* sp. aff. *lowryi*, in anticipation of more specimens becoming available for examination and for molecular analysis, and the consequent building of a more robust phylogeny.

In the present study, we investigated whether the previously undescribed morphological characters of the *Bemangidia* sp. aff. *lowryi* specimens could be attributed to the phenotypic plasticity of *Bemangidia lowryi* in response to local environmental conditions, or if they would warrant description of a new taxon at either the specific or infraspecific level. This research is completed by a taxonomic revision of the genus.

Materials and methods

Taxon sampling

All Malagasy Sapotaceae collections deposited in G, K, MO, P, TAN and TEF herbaria were examined, representing a total of c.3500 collections. Each specimen was identified to genus, resulting in nine collections attributed to *Bemangidia*. Six of these could be confidently assigned to *Bemangidia lowryi*, the remaining three being morphologically different and hereafter named *Bemangidia* sp.

Phylogenetic reconstruction

Two collections of *Bemangidia lowryi*, including the type, and the three *Bemangidia* sp., were selected for molecular analysis. As outgroups, we added the 131 specimens analysed by Boluda *et al.* (2022), comprising all described tribes of Sapotaceae and 35 species of *Capurodendron* Aubrév., a genus related to *Bemangidia* and *Tsebona*. Additionally, we included a recent Malagasy accession (*Andriamiarisoa* 2582) of a disjunct collection of *Tsebona* situated at a latitude of 23°S (all the remaining known collections were growing between 14°S and 19°S), as well as a specimen (*Bernardi* 14641) of *Northia seychellana* Hook.f., from the Seychelles, a genus of uncertain position (Gautier *et al.*, 2013) but hypothesised as being the closest relative to the tribe Tseboneae.

The DNA was extracted using the CTAB method with chloroform (Russell *et al.*, 2010; Souza *et al.*, 2012), either from fragments of dry leaves sampled from herbarium specimens or from silica gel–dried leaves harvested simultaneously for recently collected specimens. DNA fragment sizes for each extraction were estimated using a 2200 TapeStation (Agilent, Santa Clara, CA, USA).

A genomic library was prepared for each specimen, using the KAPA HyperPrep Kit (Roche, Basel, Switzerland), with a Bst Polymerase for Large Fragments (New England

Biolabs, Ipswich, MA, USA) and labelling each specimen with dual-indexed primers (Microsynth, Balgach, Switzerland; Christe *et al.*, 2021). The constructed libraries were pooled in equimolar proportions, and 794 protein-coding genes were captured following the protocol of Christe *et al.* (2021), with a hybridisation step using specific biotinylated oligonucleotide probes complementary to the targeted loci. Hybridised sequences were retained on streptavidin-covered magnetic beads while all non-target DNA was washed away. Captured DNA was amplified in an 11-cycle PCR using Illumina (San Diego, CA, USA) primers provided by the KAPA HyperPrep Kit and sequenced in an Illumina HiSeq 4000 machine (2 × 100 bp paired-end). For more information about the laboratory and the bioinformatic pipeline, see Christe *et al.* (2021).

From the 794 protein-coding genes obtained, we excluded those with putative signals of paralogy according to the pipeline of Christe *et al.* (2021), using HybPiper (Johnson *et al.*, 2016), and retained 638 genes for the phylogeny. DNA sequences were aligned using MAFFT version 7 (Katoh & Standley, 2013), and positions with > 20% missing data were removed using trimAl version 1.4 (Capella-Gutiérrez *et al.*, 2009).

The phylogenetic reconstruction was created, generating one maximum-likelihood gene tree for each of the 638 loci, using RAxML verson 8.2.4 (Stamatakis, 2014), and then inferring the species tree using Astral-II, a method based on the multispecies coalescence (Mirarab *et al.*, 2014; Mirarab & Warnow, 2015).

Potential distribution

The potential distribution of the genus was determined using Maxent version 3.3.3a (Phillips *et al.*, 2006). This was done at the generic level because both species taken separately did not reach the minimum number of occurrences required for computation. The 19 environmental variable layers BIO1 to BIO19, with a spatial resolution of 30 arcsec (about 1 km^2), were obtained from the WordClim database (Hijmans *et al.*, 2005), using the raster package in R (R Core Team, 2014; https://cran.r-project.org/web/packages/raster/raster.pdf). Each analysis was run 10 times, and the median value of all runs was plotted.

Results

The phylogenetic reconstruction (**Figure 1**) shows all members of the Malagasy-endemic tribe Tseboneae (*Bemangidia*, *Capurodendron* and *Tsebona*) clustered in a highly supported clade with a posterior probability (PP) of 1. This clade is sister to the monotypic genus *Northia* Hook.f., from the Seychelles archipelago, and together they form a monophyletic group (PP = 1). The relationships between *Bemangidia*, *Capurodendron* and *Tsebona* are not fully resolved (PP = 0.93); however, each of the three genera is highly supported as monophyletic and is therefore confirmed to be different from the others, both genetically and morphologically (Gautier *et al.*, 2013). The *Tsebona* sp. specimen (*Andriamiarisoa* 2582),

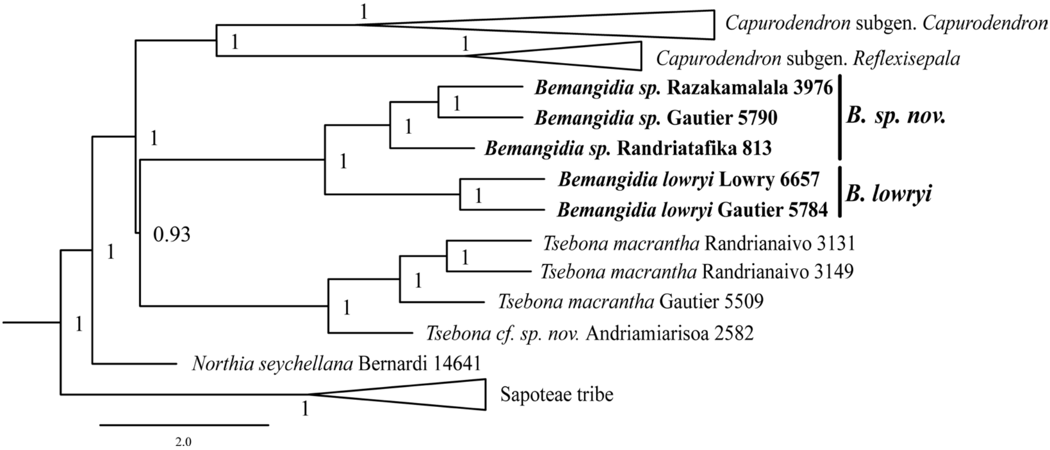

Figure 1. Phylogenetic tree reconstruction from ASTRAL, using 638 protein-coding genes. Note that ASTRAL calculates only internal branch lengths, and that tip lines are artificially fixed at the same length for all the specimens. The node labels represent ASTRAL support values given as posterior probabilities (PP). Specimen collector's numbers are indicated after the species name, except for *Capurodendron* and Sapoteae, which appear in Boluda *et al.* (2022). BioSample numbers for sequence accessions are given in Boluda *et al.* (2022), except for *Bemangidia* sp. nov. *Randriatafika* 813 (BioSample no. SAMN35983425), *B. lowryi Gautier* 5784 (BioSample no. SAMN35982381), *B. lowryi Lowryi* et al. 6657 (BioSample no. SAMN35983092), *Northia seychellana Bernardi* 14641 (BioSample no. SAMN35983402) and *Tsebona* sp. *Andriamiarisoa* 2582 (BioSample no. SAMN35983419).

collected far beyond the current southern limits of the genus, is here retrieved as sister to specimens identified as *Tsebona macrantha* Capuron.

In the genus *Bemangidia*, the three medium-altitude collections identified as *Bemangidia* sp. form a highly supported clade (PP = 1) that is sister to *B. lowryi*. Both clades are separated in the phylogenetic tree by branch lengths similar to those observed among *Capurodendron* species. The *Bemangidia* sp. specimens differ from *B. lowryi* by the smaller size of the vegetative and fertile organs, as well as by the characteristics of the leaf apex, midrib and lateral veins (see below, under *Taxonomic treatment*).

Discussion

The Malagasy-endemic Tseboneae tribe comprises three genera, *Bemangidia*, *Capurodendron* and *Tsebona*; however, their relationships are not well resolved, and the three genera may have diverged almost simultaneously, as suggested by the topology retrieved here and in other studies (Gautier *et al.*, 2013; Christe *et al.*, 2021). Additionally, the results of the node-age estimation performed by Boluda *et al.* (2022) suggest that these three genera split around 45 (± 6) million years ago (although they did not enable a conclusion to be reached regarding which of these genera diverged first).

An outgroup specimen, *Andriamiarisoa* 2582 (*Tsebona* sp.), which is known by only a leaf fragment and two field photographs, is reported to have a seed scar covering < 40% of the seed surface, leaving a dorsal and lateral smooth testa. However, in *Tsebona macrantha* the scar covers > 60% of the surface, leaving only a dorsal segment of smooth testa. The seed characteristics, together with the disjunct distribution and the phylogenetic tree topology, suggest that *Andriamiarisoa* 2582 may belong to an undescribed species. However, a more detailed morphological study is needed before it can be described as a new species.

The genus *Bemangidia* is divided into two main clades corresponding to the two different phenotypes collected in different ecologies (slopes below 450 m vs ridges above 600 m). This suggests that *Bemangidia* is either a single taxon with a wide phenotypic plasticity depending on the environment, or that it consists of two distinct taxa.

Under the scenario of a single plastic species, the smaller size of the leaves, stipules and flowers, coupled with the more pointed leaf apex of *Bemangidia* sp., would be the consequence of different ecological conditions, especially those related to the windier and more exposed habitat on ridges. However, differences in other morphological characters have also been observed that are more difficult to associate with phenotypic plasticity, such as the raised midrib on the adaxial surface of *Bemangidia* sp. (vs nearly flat to depressed in *B. lowryi*), the midrib on the abaxial surface depressed or rarely slightly raised (vs strongly raised), the smaller number and less obvious lateral veins (the lateral vein is used to include secondaries and intersecondaries, because these are hardly distinguishable) 70–145 (vs 175–330 pairs per leaf), and the angle the lateral veins form with the midrib (45°–60° vs 70°–90°) and their almost evenness with blade surface (vs raised and forming a conspicuous striate surface). By comparison with some other species of Sapotaceae for which the availability of more specimens allows a better understanding of variability within the family, the latter differences in character states may indeed be better explained by a genetic component rather than by phenotypic plasticity.

Furthermore, if *Bemangidia* sp. is conspecific to *B. lowryi*, then the populations would be expected to interbreed because of their geographical proximity and overlapping flowering period. However, no morphological intermediates have so far been collected. This could be attributed to either a lack of hybridisation, or the suppression, by natural selection, of any hybrids that do occur, both explanations reinforcing the two-species hypothesis (Christe *et al.*, 2016; Naciri & Linder, 2020).

A further argument for the two-species hypothesis is the restricted distribution of *Bemangidia* (< 10 km^2) but relatively high genetic diversity observed across all specimens, as revealed by the branch lengths in **Figure 1**. Fieldwork has shown that *Bemangidia* trees are rare in the forest, suggesting that populations are small. Such small populations usually harbour a reduced genetic variability (Khatri *et al.*, 2019), thus a monotypic concept of *Bemangidia* would conflict with the observed genetic diversity.

In conclusion, we propose the recognition of *Bemangidia* sp. as a new species.

Taxonomic treatment

Bemangidia L.Gaut., Taxon 62(5): 979 (2013) – Type species: *Bemangidia lowryi* L.Gaut., Taxon 62(5): 979 (2013).

Trees to 25 m tall, sparsely branched, all organs with white latex. *Leaves* alternate, clustered at apex of the twigs, leaving conspicuous scars when shed. *Stipules* present, broadly triangular, V-shaped in cross-section, rusty pubescent, early caducous. *Leaves* with long petioles (1/3 to 2/3 of blade length), elliptical, rusty pubescent when young, glabrescent or totally glabrous when mature; leaf venation brochidodromous with numerous straight parallel lateral veins (secondaries almost indistinguishable from intersecondaries). *Flowers* fasciculate inserted at twig apices above the previous flush of leaves or axillary among the leaves, pentamerous, large (sepals at least 12 mm long); pedicel rusty pubescent, pendulous. *Calyx* quincuncial; sepals broadly lanceolate, the two external thicker than the internal ones, with involute margins impressing a median groove on the internal sepals, rusty pubescent on the external surface, beige-pubescent on the internal surface; the three internal sepals pubescent on the external surface and glabrous on the internal surface. *Corolla* gamopetalous, tube shorter than the lobes, lobes broadly lanceolate, contorted in bud, overlapping to the right. *Stamens* isomerous, opposite to the corolla lobes; filaments short, glabrous, attached to the top of the corolla tube, attached at 1/3 to 1/4 from the base of the anthers. *Staminodes* alternipetalous, more or less cordate at base, margin ciliate. *Ovary* superior, with 5 uniovulate locules, 5-lobed, densely hirsute. *Fruit* a single-seeded berry. *Seed* ellipsoid, testa shiny; seed scar ovate basi-ventral.

Distribution. *Bemangidia* is endemic to Madagascar. It is so far known only from the Bemangidy forest, located approximately 55 km north-northeast of Tolagnaro (Fort Dauphin) within the Tsitongambarika Protected Area. This enigmatic genus has been reported only from a small area of few square kilometres. It may be present in the neighbouring areas, although recent explorations focused on Sapotaceae in Andohahela and Beampingaratra did not yield any collections. The potential distribution of *Bemangidia*, determined using the Maxent software and information on all available collections (Supplementary file), suggests that suitable habitats are only present in the southeast of the island, from the area where *Bemangidia* has been reported up to 230 km north. A second small disjunct area with a lower probability appears in the Fenoarivo area 1000 km northwards; this is a quite well-prospected area from which *Bemangidia* has never been reported.

Habitat and ecology. *Bemangidia* grows on moist evergreen lowland to lower montane forests of the southeast of the island. Individual plants grow sparsely, forming very low-density populations (the genus is known from only nine collections) on slopes as well as on mountain ridges up to 700 m a.s.l. *Bemangidia* fruits and seeds are larger than those observed for most other Sapotaceae from Madagascar; however, they overlap in size with the large fruits and seeds of some members of the genera *Capurodendron* and *Mimusops* L., and they are smaller than those of *Tsebona*.

Lemurs and large birds are known to disperse *Capurodendron* and *Mimusops* (Gautier *et al.*, 2022); therefore, it can be hypothesised that *Bemangidia* seeds may be dispersed, at least along the southeastern region, by the same animals. Because neighbouring regions are modelled as adequate habitats for *Bemangidia* and dispersal does not seem to be limited, the restricted known distribution of the genus could be simply the result of limited botanical exploration, because the two known species appear to be present at low densities. Alternatively, it could be explained by the extinction of populations in other regions due to natural factors, such as species competition, or anthropogenic factors, such as selective logging and massive deforestation.

Notes. As a member of the tribe Tsebonae within the subfamily Sapotoideae, *Bemangidia* has pentamerous flowers with a quincuncial calyx, lacks dorsal appendages in the corolla lobes, and has a contorted aestivation, villous staminodes, and seeds with plano-convex cotyledons without endosperm (the latter character only observed in *B. lowryi*). It has, however, a very distinct brochidodromous venation pattern with very numerous lateral veins (secondaries hardly distinct from intersecondaries), these characters separating it from *Capurodendron* and *Tsebona*. It is further distinguished from *Tsebona* by its isomerous androecium, and from *Capurodendron* by its external calyx lobes longer than 10 mm and impressing a median groove on the internal ones (Gautier *et al.*, 2013).

Key to *Bemangidia* species

1a. Leaves 4.3–14 × 1.4–3.5 cm, apex usually acute, 70–145 pairs of lateral veins forming an angle of 45°–60° with the midrib, not or only slightly raised in herbarium material, not forming a striated surface, external sepals c.12 mm long ________ **B. frankliniae**

1b. Leaves 18–22 × 6–6.5 cm, apex mostly rounded, 175–330 pairs of lateral veins forming an angle of 70°–90° with the midrib, slightly raised in herbarium material to form a striated surface, external sepals c.20 mm long ________________ *B. lowryi*

Species descriptions

Bemangidia frankliniae Boluda & L.Gaut., **sp. nov.**

Differs from the only other known species in the genus, *Bemangidia lowryi*, by its smaller stipules (1–3.5 mm vs c.8 mm), its smaller leaf lamina (4.3–14 × 1.4–3.5 cm vs 18–22 × 6–6.5 cm), the apex usually acute (vs mostly rounded), the midrib raised on the adaxial surface (vs nearly flat to depressed), depressed or rarely slightly raised on the abaxial surface (vs strongly raised), its faintly raised to flat lateral veins (vs raised and forming a conspicuous striate surface), the less numerous lateral veins (70–145 vs 175–330) forming an angle of 45°–60° with the midrib (vs 70°–90°), and its smaller sepals (12 mm vs > 20 mm). – Type: Madagascar, Anosy Region [formerly Toliara Province], Taolagnaro (Fort Dauphin), Iaboko, Antsotso Avaratra, Bemangidy Forest, 24°33'42"S, 047°12'02"E, 662 m, 11 xii 2007, submature flowers, *Razakamalala* et al. 3976 (holotype G [barcode G00379482!]; isotypes MO [registration number 3126491!], P [barcode P06242475!], TAN!). **Figures 2, 3.**

Small to medium-sized tree up to 13 m tall and 15 cm in diameter, sparsely branched, slash with white latex; ultimate twigs 4–10 mm in diameter, at first rusty pubescent, later glabrescent; growing twigs dark greyish brown drying black; mature twigs with a thin dark grey or greyish brown bark, longitudinally fissured; lenticels sparse to dense, raised, ellipsoid to fusiform, 0.5–1(–2) mm long. *Leaves* alternate, grouped at the end of the twigs, leaving conspicuous scars when shed; stipules broadly triangular, 1–3.5 × c.1 mm, V-shaped in cross-section, rusty pubescent, early caducous; petiole 15–60 mm long, 1–2 mm in diameter, longitudinally ridged on herbarium material, smooth when fresh, rusty pubescent when young, later with sparse persisting trichomes; blade elliptical, 43–140 × 14–35 mm, base cuneate, apex acute to acuminate, rarely rounded, chartaceous to coriaceous, covered by a rusty pubescence when young, glabrous or nearly glabrous when mature; midrib depressed, flat or slightly raised on the lower surface, sometimes with scattered trichomes on mature leaves, level to raised on the upper surface; leaf venation brochidodromous with 70–145 straight lateral veins (secondaries poorly distinguishable from intersecondaries), among which c.4–12 per cm are more conspicuous and very slightly raised on herbarium material; the veins diverging from the midrib at an angle of 45°–60°, and reaching an intramarginal vein. *Flowers* in fascicles of 2–6 inserted at twig apices, above the previous flush of leaves; pedicels rusty pubescent, pendulous, 18–23 × c.2 mm, thus placing the flowers below the petioles of the uppermost leaves. *Calyx* quincuncial with 5 sepals united at the base; sepals broadly lanceolate, the two external ones coriaceous, with involute margins, 12 × 7 mm, rusty pubescent externally, pubescent on internal surface except for a triangular centro-basal glabrous region occupying c.1/3 of the surface; the three internal sepals slightly smaller and less coriaceous, rusty pubescent externally, glabrous internally except on the distal portion of the margins. *Corolla* (developed but not opened) gamopetalous, tube 1.3–2 mm long, with 5 broadly lanceolate lobes 7 × 4 mm, contorted in bud, overlapping to the right. *Stamens* 5, opposite to the corolla lobes; filaments glabrous, attached to the top of the corolla tube, free part 1.5 mm long, 0.5 mm wide; anthers 5 mm long, filaments attached at 1/3 to 1/4 from their base; thecae glabrous on the external side, hairy on the internal side especially towards the base; connective nearly glabrous on the internal side, hairy on the external side, extending above the thecae in an acute 0.2 mm

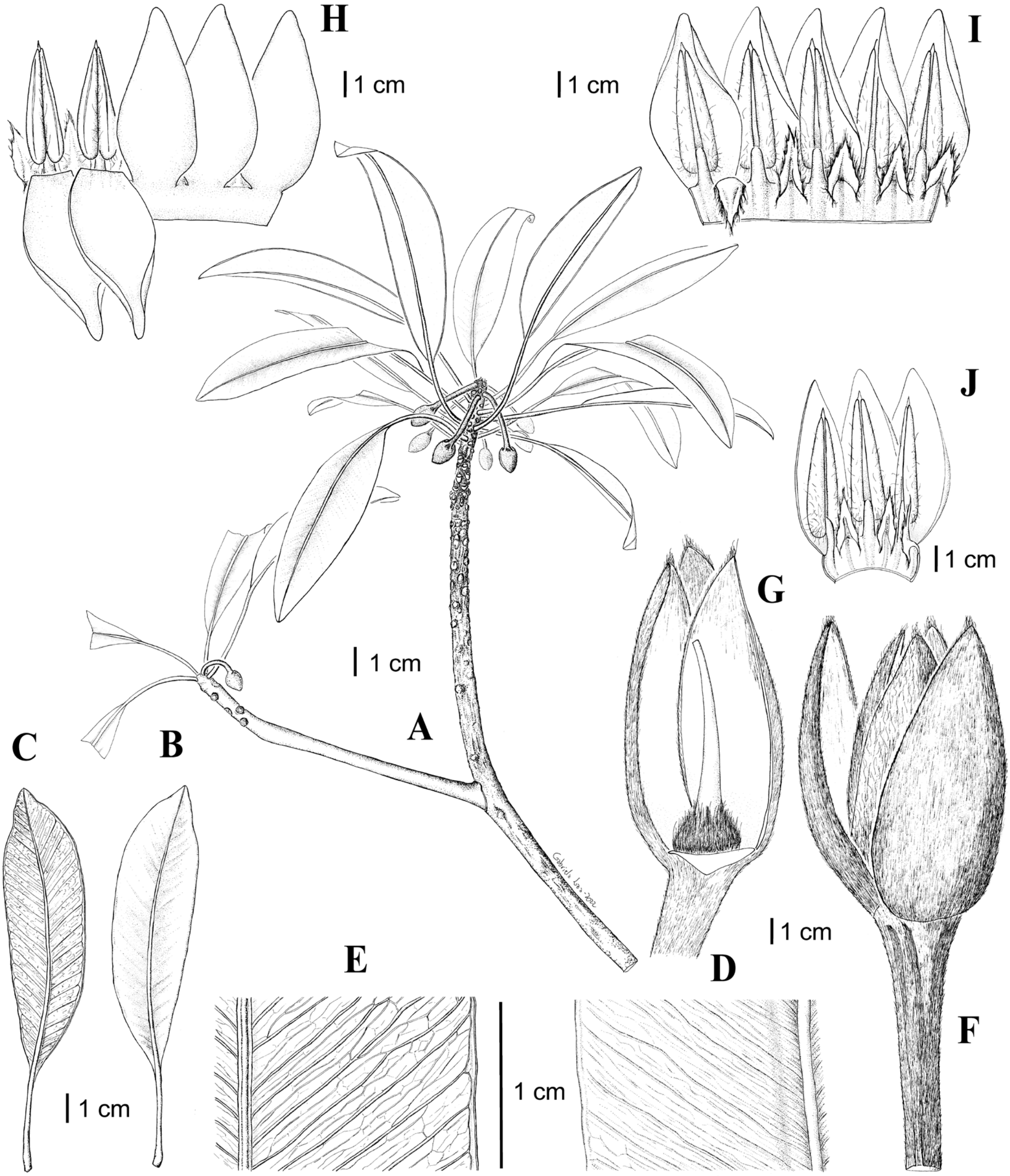

Figure 2. *Bemangidia frankliniae* Boluda & L.Gaut. A, Flowering branch; B, leaf (adaxial surface); C, leaf (abaxial surface); D, detail of leaf adaxial surface; E, detail of leaf abaxial surface; F, calyx; G, calyx (longitudinal section showing the ovary); H, corolla detached and spread, viewed from outside; I and J, corolla detached and spread, viewed from inside. Drawn from the type specimen, *Razakamalala* et al. 3976, by G. Loza.

Figure 3. *Bemangidia frankliniae* Boluda & L.Gaut. A, Detail of the abaxial surface of a dried leaf; B, tree upper branches; C, detail of a flowering branch; D, flower buds. Photographs: A (the type specimen, *Razakamalala* et al. 3976), Carlos G. Boluda; B–D (*Gautier* 5790), L. Gautier.

long appendage. *Staminodes* 5, alternipetalous, broadly lanceolate, 2 × 1 mm, basis cordate with auricles 0.7 mm long; apex entire, bifid or lacerate, margin irregular to lacerate, ciliate. *Ovary* superior, with 5 uniovulate locules, 5-lobed, 2.2 × 1.6 mm, densely hirsute; style 6.4–8 mm long, 0.7 mm in diameter, glabrous. *Fruit* observed only at very early stage of its development, with post-anthesis sepals becoming triangular, larger, 15 × 6–8 mm at the base, pedicel thickened, 3 mm in diameter.

Distribution. *Bemangidia frankliniae* is endemic to a small region of southeastern Madagascar, located approximately 55 km north-northeast of Taolagnaro (Fort Dauphin) and c.7 km from the sea, in the Tsitongambarika Protected Area.

Habitat and ecology. The three known specimens were collected on small mountain ridges and summits, in windy moist evergreen forests, between 600 and 700 m a.s.l. Flowers are reported as starting in December and very young fruits in April, indicating that flowering period may range from December to March.

Etymology. The specific epithet honours the Franklinia Foundation, a non-governmental organisation dedicated to the conservation of trees, which founded the project 'Understanding Malagasy Sapotaceae, a critical step towards conservation of a threatened group of prime importance trees', in the framework of which this species is described.

Proposed IUCN conservation category. The estimated extent of occurrence (EOO) calculated with all available herbarium specimen data is 8 km^2, and the area of occupancy (AOO) is estimated to be < 100 km^2, both qualifications for CR under criterion B. The species exists at a single location with respect to its most plausible threat, which is selective logging. It is known from three herbarium collections, the most recent dating back to 2011. Although the sole region where the species has been found is in a protected area, it is threatened by selective logging, even in the protected area of Tsitongambarika (Asity Madagascar & Rabarisoa, 2018) and a projected continuing decline in mature individuals is inferred, which justifies the assignment of this species to the category Critically Endangered [CR, B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v) (IUCN, 2012).

Notes. Measurements given for the corolla, stamens, staminodes and ovary are from developed but unopened flowers and can be expected to increase until anthesis.

Additional specimens examined. *Paratypes*. MADAGASCAR. **Anosy Region [formerly Toliara Province]**: Taolagnaro (Fort Dauphin), Iaboko, Antsotso Avaratra, Bemangidy Forest, summit of the Ivohibe mountain, 24°33'41"S, 047°12'01"E, 670 m, 11 xii 2011, flower buds, *Gautier* 5790 (G [barcode G00377561!], MO [registration number MO-3126554!], P [barcode P00932594!], TEF!); Bemangidy Forest, 24°34'10"S, 047°12'01"E, 651 m, 5 iv 2008, very early fruiting stage, *Randriatafika* et al. 813 (MO [registration number MO-3126554!], P [barcode P06242474!], TEF!).

Bemangidia lowryi L.Gaut. in Taxon 62(5): 979 (2013) – Type: Madagascar, Anosy Region [formerly Toliara Province], Taolagnaro (Fort Dauphin), Iaboko, Antsotso Avaratra, Bemangidy Forest, 7 ii 2006, flowers, *Lowry* et al. 6657 (holotype P [barcode P00568788!]; isotypes G [barcode G00340094!], MO [number 6141396!], TEF!). **Figures** 4, 5.

Medium to large tree up to 25 m tall and 55 cm in diameter, bark dark brown, oak-like fissured; inner bark tender, pink, with copious white latex, wood very hard, light yellow; ultimate twigs 8–10 mm in diameter, with rusty pubescence on growing shoots, growing twigs frequently green on fresh material, drying dark greyish brown to almost black. *Leaves* alternate, grouped at the end of the twigs, leaving conspicuous scars when shed; stipules narrowly triangular to sublinear, V-shaped in cross-section, 8 × 1.5 mm, rusty pubescent, early caducous; petiole 60–100 × 1.5–2 mm, channelled, rusty pubescent when growing, later with some persisting sparse trichomes especially inside the channel; blade elliptical, 180–300 × 60–65 mm, base cuneate, apex obtuse, sometimes shortly and broadly acuminate, chartaceous to coriaceous, with a caducous rusty pubescence on lower surface, glabrous on upper surface; midrib raised on lower surface, impressed above, in continuation with the channelled petiole; leaf venation brochidodromous with lateral veins dense and parallel, the secondaries almost indistinguishable from the intersecondaries, 175–330 on each side, diverging from the midrib at an angle of 70°–90°, looping very near the margin to constitute a faintly conspicuous intramarginal vein. *Flowers* grouped at the end of the twigs, 2- or 3-fascicled on leaf axils; pedicel rusty pubescent, pendulous, c.50 × 2 mm. *Calyx* quincuncial with 5 sepals united at the base; sepals broadly lanceolate, 20–2 × 10–12 mm, rusty pubescent externally; the two external sepals also pubescent internally, except for the middle 1/3, both margins involute and causing longitudinal grooves on the overlapped sepals; the intermediate sepal with only one involute margin, and 1/3 of the internal surface pubescent; the two most internal sepals glabrous internally. *Corolla* gamopetalous, pale greenish or cream; tube 7–8 mm long, with 5 broadly lanceolate lobes 18–20 × 10 mm, contorted in bud, overlapping to the right, basis cordate with auricles c.0.9 mm long; apex entire to lacerate. *Stamens* 5, opposite to the corolla lobes; filaments glabrous, attached for 1/2 of their length to the corolla tube, free part 7–8 mm long; anthers 10 mm long, attached to the filaments at 1/3 from base, sagittate; thecae ciliate; connective extending above thecae in an acute 1 mm long appendage. *Staminodes* 5, alternipetalous, broadly lanceolate, 8 × 5 mm, margin ciliate, connivent and forming a chamber over the ovary. *Ovary* superior, with 5 uniovulate locules, 5-lobed, 3.3 mm high by 6.5 mm broad, densely hirsute; style 27 mm long, with 5 weak longitudinal grooves; c.0.8 mm in diameter, glabrous. *Fruit* borne on 40–50 × c.3 mm pedicel gradually widening to 6 mm near the calyx; calyx partly persistent; fruit an obconic and asymmetrical berry, 40–50 × 30–35 mm, with copious white latex; seed solitary, ellipsoid, slightly laterally compressed, c.30 × 22 × 19 mm; testa shiny,

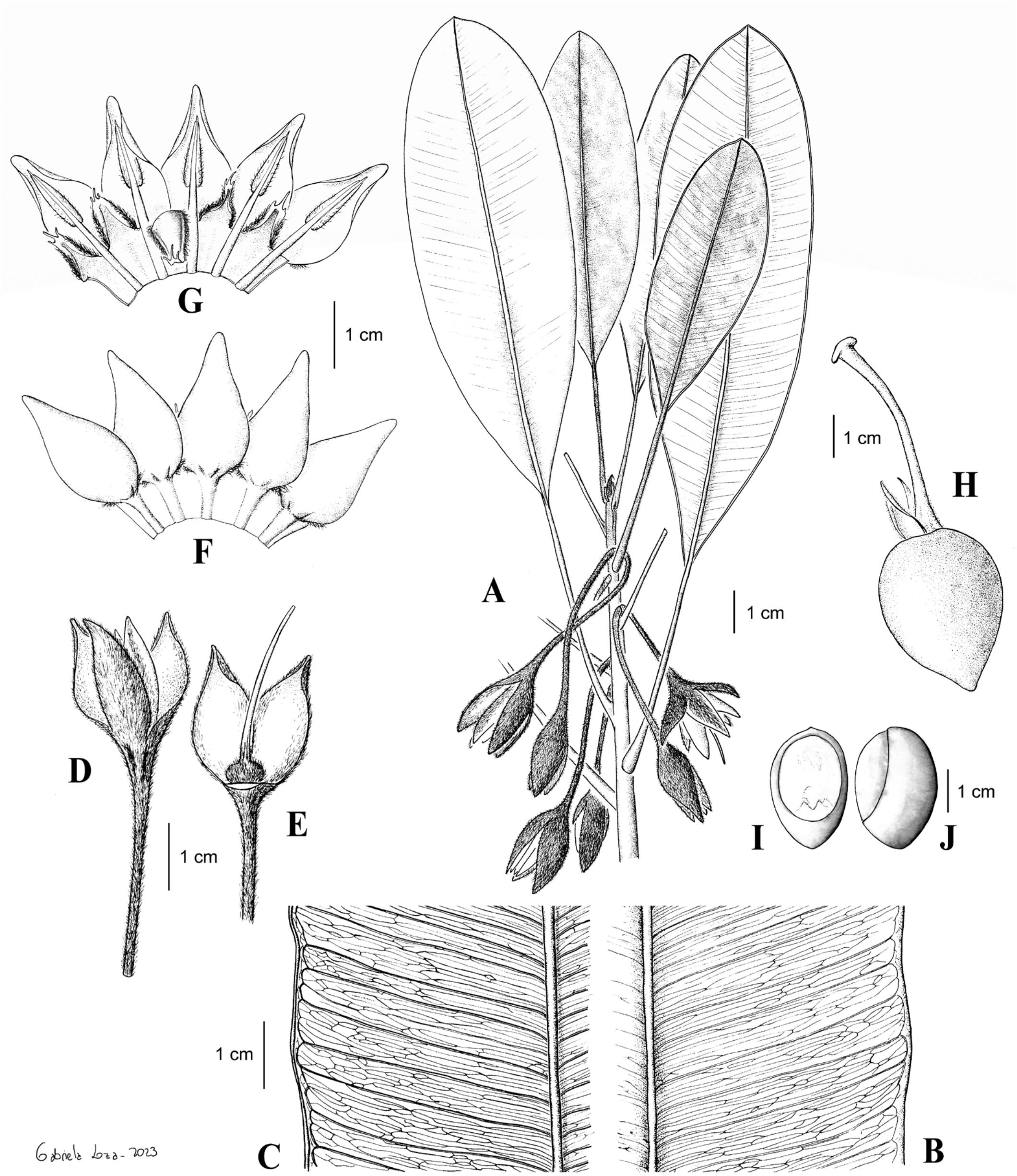

Figure 4. *Bemangidia lowryi* L.Gaut. A, Flowering branch; B, detail of leaf (adaxial surface); C, detail of leaf (abaxial surface); D, calyx; E, calyx (longitudinal section showing the ovary); F, corolla detached and spread, viewed from outside; G, corolla detached and spread, viewed from inside; H, fruit; I, seed (ventral side); J, seed (lateral side). Drawn from *Lowry* et al. 6657, the type specimen (A–G), *Gautier* et al. 5789 (H) and *Gautier* et al. 5786 (I and J), by G. Loza, based on original drawings by Cyrille Châtelain.

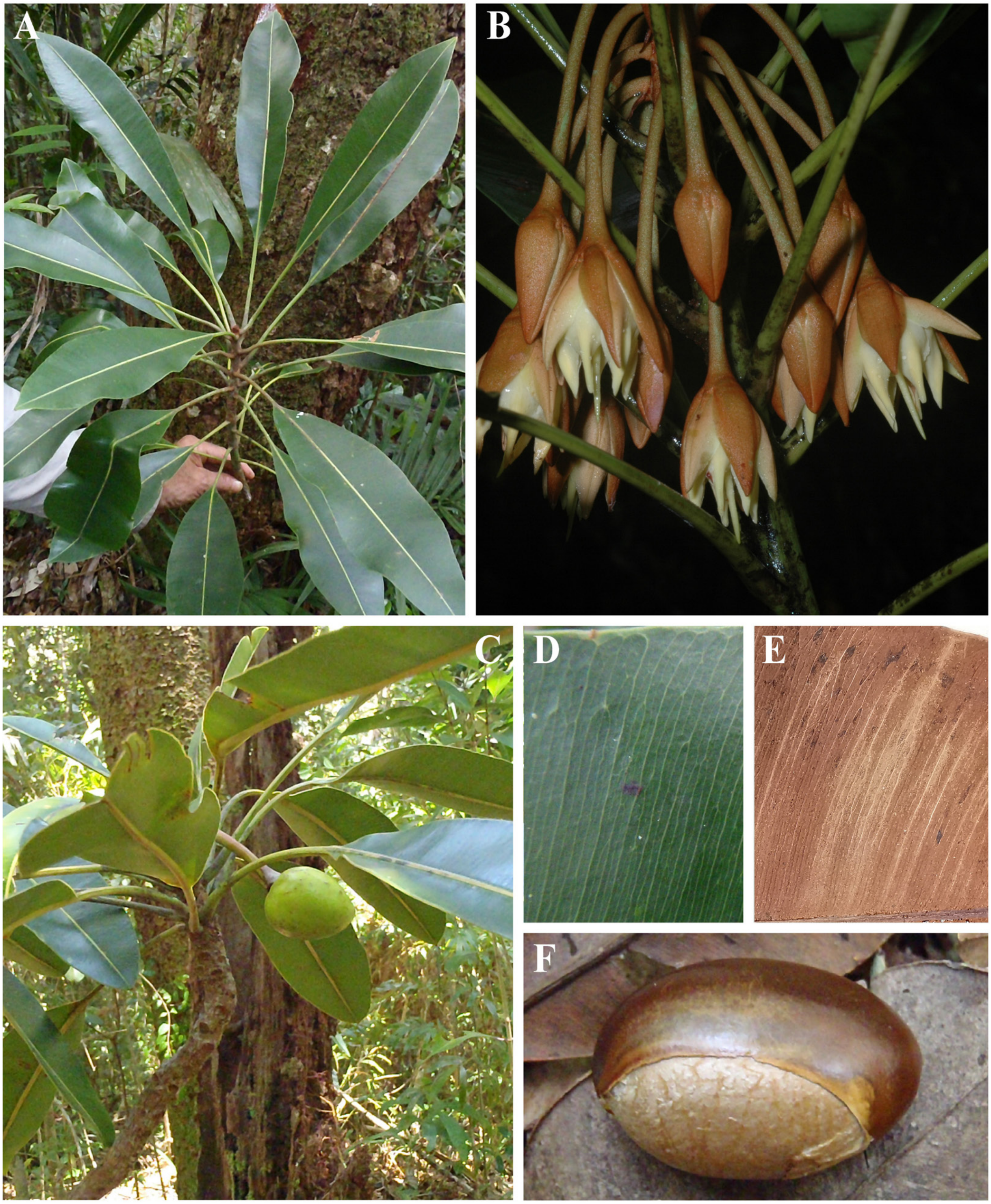

Figure 5. *Bemangidia lowryi* L.Gaut. A, Sterile branch (*Gautier* et al. 5784); B, flowering branch (*Lowry* et al. 6657); C, fruiting branch (*Gautier* et al. 5789); D, leaf detail showing the secondary nerves (*Gautier* et al. 5784); E, detail of the abaxial surface of a dried leaf (*Lowry* et al. 6657); D, seed (*Gautier* et al. 5789). Photographs: A, C and D, L. Gautier; B, P. Lowry; E, U. Swenson.

light brown; seed scar adaxial, covering 65% of the length and 40% of the circumference; embryo with plano-convex cotyledons; endosperm absent.

Distribution. *Bemangidia lowryi* is endemic to southeastern Madagascar and is so far known only from the Bemangidy forest, part of the Tsitongambarika Protected Area, approximately 55 km north-northeast of Taolagnaro (Fort Dauphin) and c.7 km from the sea.

Habitat and ecology. It is restricted to the lowland moist evergreen forest on slopes below 450 m a.s.l. Flowers are reported in February, and fruits in December.

Proposed IUCN conservation category. With an estimated EOO of < 100 km^2, and an AOO of 9 km^2 in a single location, *Bemangidia lowryi* has been assessed as Critically Endangered (CR B1ab(iii); B2ab(iii)) (Gautier & Rivers, 2019), following the *IUCN Red List Categories and Criteria* (IUCN, 2012). It is known from only seven collections, and although no logged trees have been observed, logging may constitute its main threat, together with deforestation. Its seeds have never been included in seedbanks, and no *ex situ* conservation measures have been applied to date.

Additional specimens examined. MADAGASCAR. **Anosy Region [formerly Toliara Province]**: Taolagnaro (Fort Dauphin), Iaboko, Antsotso Avaratra, Bemangidy Forest, 10 xii 2011, sterile, *Gautier* et al. 5784 (G, S, TAN); Bemangidy Forest, 11 xii 2011, sterile, *Gautier* et al. 5786 (G, S, TAN); Bemangidy Forest, 11 xii. 2011, fruit, *Gautier* et al. 5789 (G, K, MO, P, S, TAN); Bemangidy Forest, 5 iv 2008, fruits, *Ramison* et al. 578 (MO, P, TAN); Forêt Ivohibe, xi 2005, young fruits, *Razakamalala* et al. 2510 (MO, TAN); Bemangidy Forest, no date, sterile, *Service forestier* s.n. (P [P00568786, P00568787]).

Acknowledgements

This work was supported by a grant from the Franklinia Foundation given to L.G. (no. 2019-20), by a SNF grant to Y.N. (no. 31003A_166349/1) and by two grants from the Schmidheiny Foundation to Y.N. The field trip to the Bemangidy forest was funded jointly with the Swedish Museum of Natural History through a grant to Ulf Swenson. We thank the Malagasy Government for permits to conduct research, perform collections, and export specimens. We are also much grateful to the protected areas managers and local guides on-site for their kindness and assistance while we collected Sapotaceae specimens. Our thanks extend to herbarium managers and staff of the herbaria G, MO and P for authorisation to sample the DNA of herbarium specimens. We would like also to thank Gabriela Loza for her very accurate drawings.

ORCID iDs

C. G. Boluda https://orcid.org/0000-0001-7922-8718
A. Randriarisoa https://orcid.org/0000-0003-3990-507X
Y. Naciri https://orcid.org/0000-0001-6784-8565
L. Gautier https://orcid.org/0000-0003-4157-3713

Supplementary material

Supplementary material is available from the *Edinburgh Journal of Botany* online portal.

Supplementary file. Potential distribution of the genus *Bemangidia*, determined using Maxent. The numbers indicate the probability of *Bemangidia* being present.

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