RESEARCH ARTICLE

A 638-gene phylogeny supports the recognition of twice as many species in the Malagasy endemic genus *Capurodendron* (Sapotaceae)

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Abstract The Malagasy genus *Capurodendron* currently accommodates 26 described species and is the largest genus of the family Sapotaceae in Madagascar. These species are frequently logged because of their valued hardwood, which potentially puts them at risk of extinction. Species-level identifications are often problematic, and this hinders both an accurate assessment of their conservation status and the development of effective protection measures. We sorted all the material (ca. 860 collections) available in the herbaria with significant collections for Madagascar into 47 putative species based on morphology. On 41 of these, for which we were able to retrieve suitable DNA, we conducted a phylogenetic reconstruction based on molecular sequences of 638 loci from 108 *Capurodendron* specimens, performing a target capture approach combined with next-generation sequencing. Maximum likelihood (RAxML), pseudocoalescence (ASTRAL), and coalescence (STACEY) analyses showed that *Capurodendron* comprises two deeply divergent lineages. One, which includes a single species, is here newly described as *C.* subg. *Reflexisepala* based on its distinctive morphology. The second lineage contains all remaining species, which seem to have resulted from a rapid radiation event. The phylogenetic tree provides good support for most of the species hypothesized based on morphology, with the exception of two species-groups that we have named the Arid Complex and the Eastern Complex. As many as 20 species-level lineages genetically distinct from any of the currently recognized species were identified, 17 of which were morphologically well-characterized, representing strong candidates for new species. This would suggest that *Capurodendron* is the most species-rich endemic genus of plants in Madagascar. While 14 of these 20 clades are still under study, we here describe six species new to science: *Capurodendron andrafiamenae* (provisionally assessed as CR), *C. aubrevillei* (VU), *C. birkinshawii* (CR), *C. naciriae* (EN), *C. randrianaivoi* (CR), and *C. sakarivorum* (EN). *Capurodendron oblongifolium* comb. nov. (EN), previously regarded as a variety of *C. perrieri*, represents a distinct lineage that is here recognized at the species level. The newly described species are illustrated by line drawings and photographs from the field, and a preliminary threat assessment is provided. We discuss the evolutionary history of *Capurodendron* and also explore the question of node age estimates and their methodological limitations.

Keywords *Capurodendron*; Madagascar; NGS; new species; node age estimation; phylogenomics; Sapotaceae; target capture

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Madagascar provides one of the most striking examples of massive deforestation in a megadiverse area whose biodiversity is highly endemic and poorly studied (Myers & al., 2000; Ganzhorn & al., 2001). As such, it has been identified as a major biodiversity hotspot and has developed one of the densest networks of protected areas in the world (Goodman & al., 2018). However, because of very high international demand for precious woods, generating financial incentives for illegal trade, selective logging, together with indiscriminate deforestation, is still common, even in protected areas (Patel, 2007; Hassold & al., 2016). *Dalbergia* (rosewood) are among the tree species most heavily impacted by illegal exploitation (Schuurman & Lowry, 2009), but as they are becoming scarcer, *Diospyros* (ebonies) and species of the family Sapotaceae (generically referred to as "Nanto" in Madagascar) are being increasingly threatened. Most of the recently described species in the Sapotaceae and Ebenaceae have been assessed as endangered or critically endangered (Gautier & Naciri, 2018; Randriarisoa & al., 2020; Schatz & Lowry, 2020), and timber exploitation, as well as habitat reduction, is likely to drive many of them to extinction.

Until recently, the Malagasy Sapotaceae had mostly been exploited for the local market, but signs of illegal export-oriented logging have already been detected in protected areas

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(R. Randrianaivo, pers. comm.), and a dramatic increase is highly feared. While Malagasy *Dalbergia* and *Diospyros* are currently being studied in order to create a sound systematic foundation from which to establish protection measures (Hassold & al., 2016; Schatz & Lowry, 2020), the taxonomy of Sapotaceae was last revised 50 years ago for the *Flore de Madagascar et des Comores* (Aubréville, 1974). At that time, the number of available collections was only one-third of what we have today. Furthermore, that revision was based only on herbarium samples, and most species were known from a very restricted number of specimens, often lacking either flowers or fruits. Recent collections have revealed numerous undescribed morphospecies (a morphologically delimited group, described or not, which may or may not be determined to be a valid species) in lowland moist evergreen forest as well as in dry environments, and some of these have already been described (Gautier & al., 2013; Gautier & Naciri, 2018; Randriarisoa & al., 2020). In other cases, new material has been collected exhibiting morphologies intermediate between two described species, calling into question their distinctiveness. Additionally, a few described species are still only known from the type specimen collected in areas that are now completely deforested, and are thus possibly extinct (e.g., *Capurodendron antongiliense*, *C. nanophyllum*, *Faucherea longepedicellata*, and *Mimusops nossibeensis*; see Aubréville, 1974; Gautier & Naciri, 2018; Madagascar Catalogue, 2021).

Field identification of Sapotaceae is usually difficult or impossible due to the rarity of flowers and fruits, inaccessibility of such material high in the canopy, or the lack of recent taxonomic revisions with appropriate descriptions and up-to-date identification keys. In a conservation context, identification difficulties and unclear species-limits become a serious burden: conservation assessments cannot be conducted for 35% of the described species of Malagasy Sapotaceae, nor is it possible to conduct field inventories for logging management for most taxa. Consequently, taxonomic revisions of Malagasy Sapotaceae are urgently needed, and treatments must be oriented toward providing reliable characters for identification in the field.

The 91 currently accepted species of Sapotaceae in Madagascar are divided into 11 genera belonging to two main subfamilies, Chrysophylloideae (*Donella* Pierre ex Baill., *Gambeya* Pierre) and Sapotoideae as defined by Anderberg & Swenson (2003) and Swenson & Anderberg (2005). The subfamily Sapotoideae includes three tribes: Sapoteae (including *Faucherea* Lecomte, *Labourdonnaisia* Bojer, *Labramia* A.DC., *Manilkara* Adans., and *Mimusops* L.), Sideroxyleae (*Sideroxylon* L.), and the recently described endemic tribe Tseboneae (Gautier & al., 2013) (comprising *Bemangidia* L.Gaut, *Capurodendron* Aubrév., and *Tsebona* Capuron). The last three mentioned genera, together with *Faucherea* and *Labramia*, are endemic to Madagascar, as are 88 of the 91 currently accepted species (Gautier & al., in press).

Based on the 23 species accepted by Aubréville (1974) in his treatment of Sapotaceae for the *Flore de Madagascar et des Comores*, Callmander & al. (2011) listed *Capurodendron* as the third-largest endemic genus of plants on the island. Recently, three additional species were described (Gautier & Naciri, 2018). Morphologically, this genus has been characterized as "exceptionally stable in flower structure" across all 26 species (Aubréville, 1974; Gautier & Naciri, 2018), however, the size, shape and venation of the leaves vary greatly across species. *Capurodendron* was shown to be monophyletic on a selection of 10 species and, alongside the two monotypic genera *Tsebona* and *Bemangidia*, it forms a highly supported clade within the Malagasy endemic tribe Tseboneae (Gautier & al., 2013). These two monospecific genera are restricted to the humid evergreen forests of the Eastern Phytogeographical Domain (sensu Humbert, 1955). With only one-third of *Capurodendron*'s described species inhabiting that biome, the genus is remarkable for its exceptional diversification in seasonally dry and subarid climates, where the balance of its species is found (Aubréville, 1974). *Capurodendron* can be considered among the Madagascar endemic genera that have undergone rapid radiation on the island (Buerki & al., 2013). Whether the shift in habitat described above occurred once or several times is however unknown.

Unclear species limits can be the result of phenotypic plasticity, morphological convergence, or recent divergence, possibly with persisting gene flow. While phenotypic plasticity or convergence can be detected relatively easily with molecular study involving a restricted number of loci, rapid diversification and recent speciation often produce inconsistent phylogenies across loci (Cai & al., 2020; Dodsworth & al., 2020). Significantly increasing the number of loci might therefore help resolving these last two phenomena (Sass & al., 2016; Fernández-Mazuecos & al., 2018; Paetzold & al., 2019).

Standard barcoding sequences, such as ITS, *matK*, *RPB2*, or *rbcL* (Saddhe & Kumar, 2018), are time-consuming and expensive to obtain using Sanger methods, often provide inadequate resolution, and are susceptible to problems arising from paralogy, chloroplast capture, and/or incomplete lineage sorting (Spooner, 2009; Roy & al., 2010; Swenson & al., 2013; Naciri & Linder, 2015; Wyler & Naciri, 2016; Goncalves & al., 2020). Moreover, we have found that Sanger sequencing in Sapotaceae is often complicated by the presence of secondary metabolites (Christe & al., 2021) or repetitive sequences that block PCR reactions (Farias do Valle, 2019). The rapid development of massive sequencing methods has facilitated a leap from single-loci to genomic sequencing, though genomes contain a high percentage of DNA that is uninformative for phylogenetic reconstruction. Gene capture is a more efficient and cost-effective methodology in that it allows restricting sequencing to target loci across many specimens for the price of sequencing a single genome.

In the present study, we performed a target capture combined with next-generation sequencing on 638 loci across 131 samples including 108 *Capurodendron* to: (1) elucidate the evolutionary history of the genus, (2) propose a revised classification, and (3) establish clear species limits, enabling us to describe species new to science and to assess their risk of extinction.

■ MATERIALS AND METHODS

Taxon sampling and DNA quality. — All *Capurodendron* specimens available at six key herbaria for the Malagasy flora, G, K, MO, P TAN and TEF (representing ca. 860 collections), were assembled first into morphospecies (putative species, described or not, based on morphological characters alone). We based our approach first and primarily on vegetative characters, in order to group specimens independently of their phenological state, but used floral and fruiting characters, when available, to check afterward the consistency of our groups. We reached a total of 47 morphospecies. Those including a type specimen were assigned the associated name, and the others were given provisional names consisting of "sp." followed by a number.

The sampling for molecular analysis involved 2–3 representative specimens for each morphospecies. For morphospecies that showed a geographical disjunction in the assigned material, the sampling was increased so that each geographical area would be represented.

DNA was obtained either from fragments of dry leaves sampled from herbarium specimens (51%) or from silica-gel dried leaves harvested simultaneously from recently collected specimens (49%). DNA was extracted using the CTAB method with chloroform, including previous sorbitol washes in order to remove mucilaginous substances (Russell & al., 2010; Souza & al., 2012). Prior to final sampling, DNA fragmentation was analyzed using a 2200 TapeStation (Agilent, Santa Clara, California, U.S.A.). Only specimens with an average fragment size above ~75 bp were chosen for sequencing. We were able to obtain DNA fragments larger than 75 bp for 131 specimens, representing 23 of the 28 described species and 16 of the undescribed morphospecies for the tribe Tseboneae (*Bemangidia*, *Capurodendron*, *Tsebona*). Two of the undescribed morphospecies included described varieties of *C. perrieri* and *C. tampinense*. Eighteen specimens representing the main lineages of Sapotaceae were added as outgroups (Appendix 1).

Sequencing. — We obtained sequences following the methodology described by Christe & al. (2021). Briefly, a genomic library of each specimen was constructed and labelled with dual indexing. Then the libraries of specimens with similar DNA sizes were pooled in equimolar proportions, and 794 protein coding genes were captured using a hybridization step with specific biotinylated oligonucleotide probes complementary to the loci of interest. Hybridized sequences were retained on streptavidin-covered magnetic beads while all non-target DNA was washed away. Finally, captured DNA was sequenced using an Illumina HiSeq 4000 machine (2×100 bp paired-end). From the 794 genes obtained, 638 displayed no signal of paralogy, and their consensus sequences were used for phylogenetic tree reconstruction after removing positions with over 20% missing data, using trimAl v.1.4 (Capella-Gutierrez & al., 2009).

Phylogenetic reconstruction. — We used three different methods: Maximum likelihood (ML) using single nucleotide polymorphisms (SNPs), ML combined with pseudocoalescence (ASTRAL), and coalescence (STACEY), the last two on unlinked sequences.

SNPs were obtained from a concatenated supermatrix of the 638 genes using SNP-sites software (Page & al., 2016), ignoring indels and ambiguous sites. The dataset contained 254,292 positions and was run in RAxML v.8.2.4 (Stamatakis, 2014) under an ASC_GTRGAMMA substitution model, with a Lewis ascertainment bias correction, and 100 rapid bootstrap replicates. Clades with bootstrap values higher than 70 were considered supported.

To avoid sequence concatenation, which may not be an appropriate method when topological conflicts or incomplete lineage sorting exist, we generated one gene tree for each locus using RAxML v.8.2.4 (Stamatakis, 2014). Then we used ASTRAL-II (Mirarab & al., 2014; Mirarab & Warnow, 2015), a method based on the multispecies coalescence (MSC), to infer the species tree from the 638 gene trees. We considered clades with posterior probability above 0.7 as moderately supported and above 0.95 as strongly supported. However, because ASTRAL cannot be considered a true coalescent method, in part because gene trees and species trees are constructed independently, we also performed a MSC tree associated with a species delimitation analysis (see below).

Species delimitation analysis. — STACEY v.1.2.2 (Jones & al., 2015; Jones, 2017) implemented in BEAST v.2.4.5 (Bouckaert & al., 2014) combined with the Species Delimitation Analyzer tool (Jones & al., 2015; Jones, 2017) was used to estimate the number of distinct species-level entities that would best fit the molecular data. Due to the long computing times, we reduced the dataset to 20 genes to run the analysis. The proportion of parsimony-informative sites for all markers longer than 500 bp and including all the 131 samples was calculated using AMAS software (Borowiec, 2016). Three datasets including only material from the tribe Tseboneae were selected, the first one containing the 20 most variable loci (23,175 bp, 53% of parsimony-informative sites, viz. genes 34, 90, 97, 132, 189, 221, 244, 293, 356, 362, 398, 403, 445, 465, 484, 489, 507, 518, 571, 724); the second with the 20 loci closest to the average variability value (31,296 bp, 36% of parsimony-informative sites, viz. genes 8, 12, 42, 56, 111, 151, 163, 213, 252, 262, 290, 302, 311, 330, 333, 338, 395, 680, 684, 776); and the third containing the 20 least variable markers (23,845 bp, 21% of parsimony-informative sites, viz. genes 54, 80, 444, 481, 544, 545, 559, 582, 586, 596, 611, 667, 677, 705, 729, 743, 752, 761, 768, 770). The STACEY input was prepared using BEAUTI2 v.2.4.5 (Bouckaert & al., 2014). The most variable gene of each dataset was set in the first position, and site, clock and trees were kept unlinked. All substitution models for each analysis were set as GTR with estimated substitution rates (gamma categories = 4, shape = estimated, invariant sites = 0, Kappa = estimated, frequencies = estimated) and relaxed lognormal clocks. Each sample was encoded as belonging to a distinct species, and the species tree prior was set under the birth-death model, with a collapse height of 0.0001 and all other parameters

estimated. The species tree growth rate (bdcGrowthRate) and popPriorScale were set to a lognormal distribution with default parameters. The collapse weight, a parameter related to the number of species, was set to a beta distribution, with alpha = 1 and beta = 1 to keep it under a uniform probability. Three independent files for each dataset (nine data files in total) were run in BEAST v.2.4.5 (Bouckaert & al., 2014) with 10^9 MCMC iterations, sampling every 10,000th iteration. Trees were generated at the Genetic Diversity Centre (GDC, ETH Zurich) and at the Baobab cluster of the University of Geneva. The resulting phylogenies were visualized with FigTree v.1.4 (Rambaut, 2009).

Tracer v.1.6 (Rambaut & al., 2014) was used to ensure that all runs reached an equilibrium of the log-likelihood values for the sample points and that effective sample size (ESS) values were above 200 (with few exceptions). The three MCMC outputs of each dataset were combined in a single file with Log Combiner (BEAST v.2.5.2 package), discarding the first 25% of the trees as burn-in. Tree Annotator (BEAST v.2.5.2 package), with the maximum clade credibility (MCC), was used to obtain the species tree, and its topology was checked with FigTree v.1.4 (Rambaut, 2009). Combined MCMC outputs were processed with Species Delimitation Analyzer (SDA; Jones & al., 2015; Jones, 2017) with a collapse height from 0.01 to 0.05, a similarity cut off of 1.0, and a burn-in of 0, as the first 25% of the trees had been removed in the previous steps. To visualize the SDA output, the script of Jones & al. (2015), modified by Simon Crameri (https://github.com/scrameri/smtools/tree/master/SpeciesDelimitation), was run in R v.2.15.1 (R Core Team, 2014). Clades with posterior probabilities above 0.95 were considered as highly supported.

Node age estimation. — To estimate divergence times of the main Tseboneae lineages, various analyses were conducted using different datasets and calibration points. As no Tseboneae fossils are presently known, we expanded the tree to the family level in order to use fossil-calibrated nodes and/or secondary calibration points. The outgroup taxa samples shown in Appendix 2, obtained from Christe & al. (2021) and Randriarisoa & al. (in prep.), were used together with a selection of 22 Tseboneae samples.

The input was prepared with BEAUTI2 (Bouckaert & al., 2014) using the three different datasets of 20 genes used for the species delimitation analyses, along with sequences from 52 samples representing the main lineages of interest. The most variable gene in each dataset was set in the first position, and site models were kept unlinked, while the clocks and tree models were linked. Substitution models for each locus in each dataset were set as GTR with a gamma category account of 4, estimating neither the substitution rate nor the proportion of invariants (set to 0), nor fixing the mean substitution rate, but estimating gamma shape and rate frequencies of nucleotides (except for CT rates). A relaxed clock log normal was used to allow rate heterogeneity among lineages while estimating the clock rate. Results from the ASTRAL and STACEY analyses, as well as unpublished phylogenetic reconstructions for members of the tribes Sapoteae and Gluemeae, helped to constrain the major clades known to be monophyletic (Appendix 1) in order to improve the speed of reaching the most probable tree topology.

First, two fossils were used to calibrate the tree, following Armstrong & al. (2014). *Tetracolporpollenites* pollen from 37.2–48.6 mya from England was used to constrain the crown of the tribe Sapoteae (off-set: 42.9, mean 0.095; Harley, 1991; Armstrong & al., 2014), and a group of fossil leaves of a putative *Manilkara* sp. from 23–33.9 mya from Ethiopia was used to constrain *Manilkara* s.l. (off-set: 28.0, mean 0.1; Jacobs & al., 2005; Armstrong & al., 2014).

Second, three secondary calibrations points from Armstrong & al. (2014) were used independently from the former analyses to calibrate the tree under a normal distribution: The *Vitellaria* + *Baillonella* clade (mean 31.0 mya, off-set: 0, sigma 3.0), the *Mimusops* + *Tieghemella* clade (mean 35.0 mya, off-set: 0, sigma 1.9), and the Indo-Pacific *Manilkara* + *Faucherea* + *Labourdonnaisia* clade (mean 28.0 mya, off-set: 0, sigma 2.15). A third node age estimation was performed only for tribe Tseboneae, selecting the two most divergent samples per species. In this case, secondary calibration was performed using a normal distribution of the ages estimated in the previous analyses for the stem nodes for *Tsebona*, *Bemangidia* and *Capurodendron madagascariense*.

Node age estimations were performed with the priors for gammaShape, nucleotide rates, and ucldStdev set with a gamma distribution, while the proportionInvariant prior was set as uniform. Prior distribution of the calibration points was set as lognormal for fossils and normal for secondary calibration. Three independent files for each dataset were executed in BEAST v.2.4.5 (Bouckaert & al., 2014) with up to 300 million MCMC iterations to ensure data stabilization, sampling every 10,000th iteration. Outputs were processed with the BEAST v.2.5.2 package as explained above in the species delimitation analysis section. Tracer v.1.6 (Rambaut & al., 2014) was used to ensure that the log-likelihood values of the sample points reached an equilibrium with ESS values above 200.

At this point, each dataset was run modifying selected parameters to test output variability depending on the assumptions made for the dating. These modifications included: (1) replacing the GTR substitution model by those predicted by jModelTest v.2.0 (Darriba & al., 2012), (2) calculating the proportion of invariable sites, (3) replacing the birth-death model with the Yule one, and (4) testing a gamma and a uniform distribution for each.

Clade ages were also estimated using treePL (Smith & O'Meara, 2012) with the same datasets and calibration points as described above. Parameters were selected following the suggestions of Maurin (2020), setting the smooth value to 1,000,000.

■ RESULTS

Phylogenetic reconstructions. — All 131 samples analyzed yielded DNA sequences for 638 protein-coding genes

without paralogy signals and with no more than 5% of missing data (BioSample accession numbers in Appendix 1, alignments in suppl. Appendix S1). The three phylogenetic reconstruction methods used (SNP with RAXML, ASTRAL and STACEY) produced trees with very similar topologies, with only minor differences for the unsupported branches (Fig. 1). Tribe Chrysophylleae (represented by *Donella*) appears as the most external outgroup, followed by the tribe Sideroxyleae, and then a clade comprising *Lecomtedoxa* and *Neolemonniera*, which is sister to a lineage that includes the nested clades *Inhambanella*, Isonandreae, Sapoteae, and the Malagasy tribe Tseboneae. *Inhambanella* is found sister to Sapoteae + Isonandreae in ASTRAL (posterior probability 0.91), separated by a very short branch (Fig. 1), but sister to Tseboneae (bootstrap = 99) in the SNPs tree.

Within tribe Tseboneae, all three genera are well-supported and they split nearly at the same point, with the following topology: (*Tsebona* (*Capurodendron* + *Bemangidia*)). *Capurodendron* is divided into two main lineages with branch-lengths as long as those observed at the generic level in other parts of the tree. The first lineage comprises the three samples of *C. madagascariense* included in our study, the second one contains all the remaining collections. This second clade shows a huge radiation of species groups and species, but while each of these clades is supported, there is limited support for the relationships among them (Fig. 1). The first

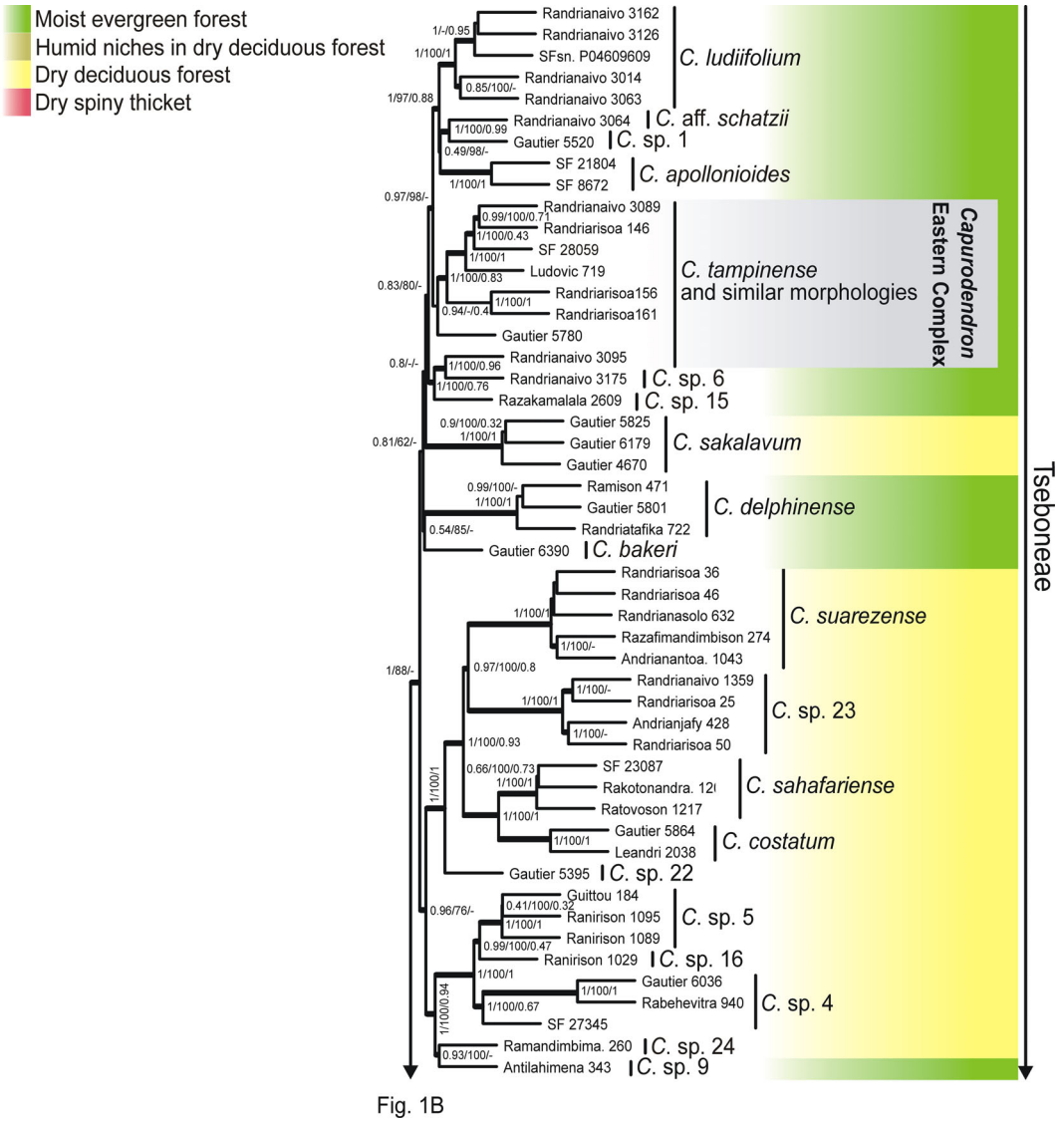

Fig. 1B

Fig. 1. Phylogenetic tree reconstruction topology from ASTRAL using 638 protein-coding genes and 131 specimens with support values from ASTRAL, RAxML with SNPs and STACEY indicated in the tree following the mentioned order. Clades without values were considered unsupported (<0.7/<70/<0.95 respectively). Note that ASTRAL only calculates internal branch lengths and that tip lines are artificially fixed with the same length for all the specimens. Tribes are shown on the right side of the tree, with "Gluemeae" and "*Inhambanella*" suggested as two undescribed tribes. *Capurodendron* undescribed morphospecies are indicated by "*C.* sp." followed by a number.

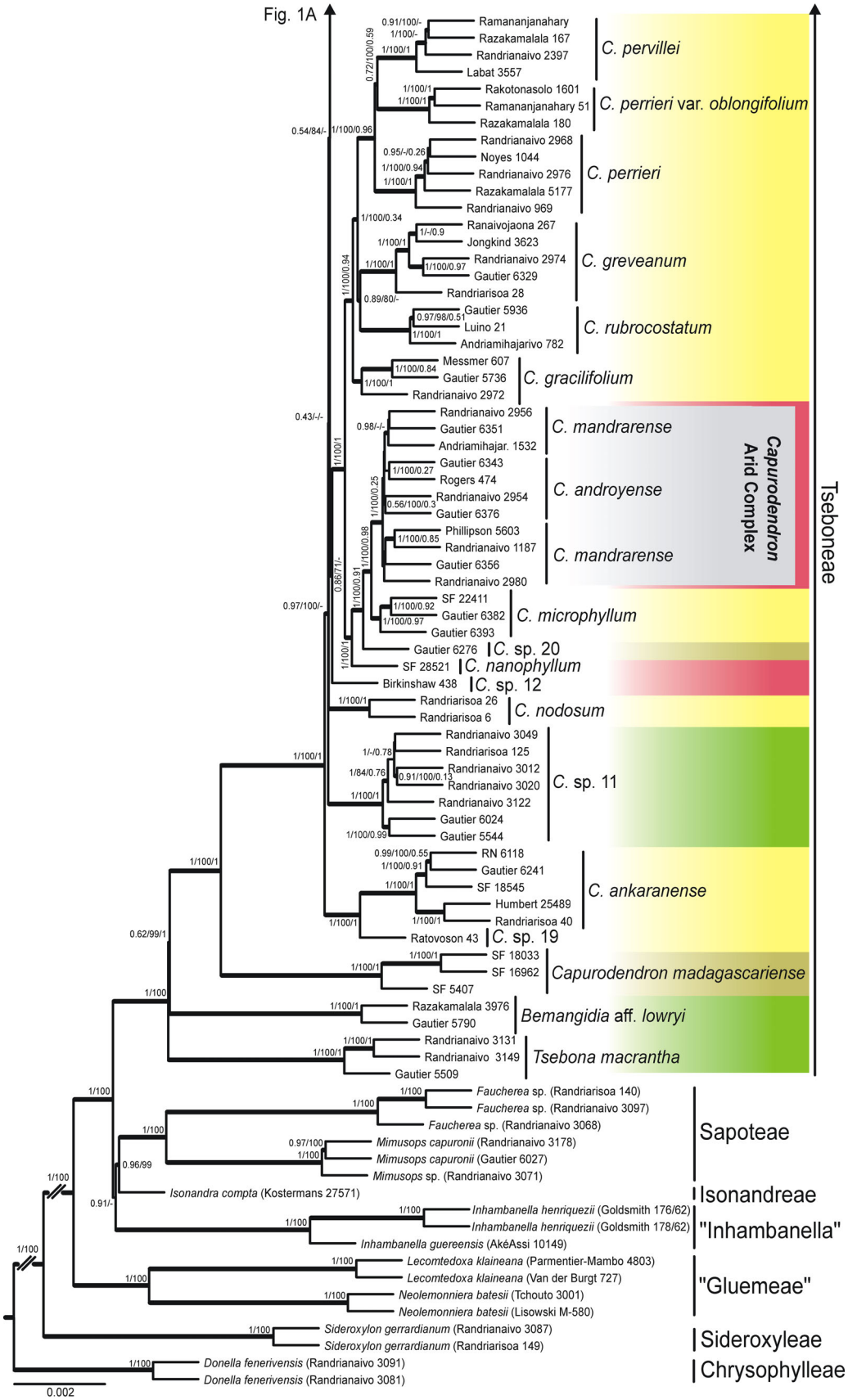

Fig. 1. Continued.

two lineages appearing in the radiation are supported and composed respectively of a clade with *C. ankaranense* (five samples) and *C.* sp. 19 (one sample), and a clade with *C.* sp. 11 (seven samples). Each of the clades comprising two or more samples assigned to a given species-level entity (including undescribed morphospecies) were well-supported, with the exception of *C. mandrarense* and *C. androyense*, whose relationships were poorly resolved, and of *C. tampinense*, which is polyphyletic with one sample closer to *C.* sp. 6 than to the other *C. tampinense* specimens.

Dated tree. — The different methodologies used provided the tree topologies and estimated node ages shown in Fig. 2A. The topologies are very similar in all the trees, even when none of the clades are constrained. The Yule and the birth-death branching process priors gave similar estimated ages regardless of the distribution used (uniform or gamma), and the recorded differences could be attributed to the MCMC process itself. Estimated ages for the Sapoteae lineages are similar to those reported by Armstrong & al. (2014), although the topology is slightly different and better supported in our analyses, with the confirmed polyphyly of *Manilkara*, and *Labramia* placed as sister to *Manilkara* s.str. The origin of the tribe Tseboneae is estimated at 45.7 mya (51.3–39.5 mya), that of *Capurodendron* at 40.2 mya (34.7–45.8 mya), and the main *Capurodendron* radiation beginning around 29.9 mya (25.7–34.4 mya; Fig. 2B). Species crown ages were unexpectedly old for *Capurodendron*, ranging from 11 to 16 mya, older than the estimates obtained for the crown of the genera *Labramia*, *Labourdonnaisia*, and *Faucherea*. The age estimation using a dataset restricted to the tribe Tseboneae with secondary calibration provided similar ages at the species level (data not shown).

TreePL produced age estimates 9.5–4.4 million years older than those obtained in BEAST. The origin of tribe Tseboneae was estimated at 55.2 mya rather than 45.7 mya, that of *Capurodendron* at 47.2 mya instead of 40.2 mya, and the main *Capurodendron* radiation around 34.3 mya instead of 29.9 mya. Species estimated crown ages were usually 1 million years older than in BEAST.

Species complexes. — The phylogenetic reconstructions of *Capurodendron* confirmed a finding based on the preliminary grouping of specimens in morphospecies, that is, the presence of two species complexes. The first one contains samples assigned to *C. androyense* and *C. mandrarense*, two partially sympatric species that occur in the dry spiny thicket of southern Madagascar. Although morphologically distinct, they are not retrieved as monophyletic (Fig. 1B). Furthermore, specimens that have not been sequenced show intermediate morphologies between *C. mandrarense* and the genetically distant *C. greveanum*, as well as intermediate morphologies between *C. androyense* and the closely related *C. microphyllum*. We refer to this informal group as the "Arid Complex".

The second species complex occurs throughout the Eastern moist evergreen forest of Madagascar, including littoral, lowland and medium-altitude situations up to ca. 1000 m elevation. It has thus been named the "Eastern Complex" (Fig. 1A). It is composed of specimens with morphologies corresponding to *Capurodendron tampinense* var. *tampinense*, *C. tampinense* var. *analamazaotrense*, and *C. bakeri* var. *antalahaense*, together with intermediate morphologies. The morphological variability of leaves is relatively high. However, there is a continuum of variation and none of the extreme morphotypes appear to represent a discrete entity. The majority of the collections were sterile, further complicating the group refinement. The morphology of the sterile specimen *Randrianaivo 3095* suggests a *C. tampinense* with rather large leaves and red petioles, but the phylogenetic analyses did not place it within the *C. tampinense* clade. However, we could not observe clear morphological or ecological differences to support its placement in a different species. Two other specimens previously identified as belonging to *C. tampinense* similarly fell outside the *C. tampinense* clade, *Antilahimena 343*, collected in the Sambirano phytogeographical domain and *Ramandimbimanana 260*, collected in the Western domain, both in dryer habitats than the specimens of the Eastern Complex. These specimens turned out to display subtle yet distinct morphological characters, suggesting they represent distinct entities that may merit recognition at the species level. They are provisionally named here *Capurodendron* sp. 9 and *Capurodendron* sp. 24, respectively.

Undescribed morphospecies. — Within tribe Tseboneae there are up to 20 species-level lineages that are genetically isolated from any of the currently recognized species (Fig. 1). Of these, 17 show morphological characters that allow their clear distinction at the specific level (*Capurodendron perrieri* var. *oblongifolium*, *C.* aff. *schatzii*, *C. tampinense* var. *analamazaotrense*, *C.* sp. 1, *C.* sp. 4, *C.* sp. 5, *C.* sp. 6, *C.* sp. 9, *C.* sp. 11, *C.* sp. 12, *C.* sp. 15, *C.* sp. 16, *C.* sp. 19, *C.* sp. 20, *C.* sp. 22, *C.* sp. 23, and *C.* sp. 24; Fig. 1). The remaining three comprise material initially identified as *Bemangidia* aff. *lowryi* (*Gautier 5790*, *Razakamalala 3976*), *Capurodendron* aff. *tampinense* (*Gautier 5780*), and *C.* cf. *tampinense* (*Randrianaivo 3095*). Both *Bemangidia* aff. *lowryi* collections are in bud stage, showing a similar morphology to material of *B. lowryi*, but the trees were described on the collection labels as having a shorter habit, and the specimens have distinctly smaller leaves. They were collected at higher altitudes in the same forest. As the morphological variability of *B. lowryi* is still not well understood, more specimens are needed to determine whether the plants growing at higher elevation fall within the normal variation of *B. lowryi* or represent a distinct taxon. With regard to the remaining two collections, the specimen *Gautier 5780* is sister to two clades each containing a variety that could possibly be elevated to species rank, and the specimen *Randrianaivo 3095* is more closely related to *C.* sp. 6 than to *C. tampinense*.

The level of genetic distinctiveness indicated by the STACEY analysis (Fig. 3) for each recognized morphospecies, described or not, is generally consistent with a possible recognition at the level of species. Exceptions include cases in which the analysis lumps distinctive morphospecies, particularly the Arid Complex, the clade comprising *Capurodendron* sp. 4 + *C.* sp. 5 + *C.* sp. 16, and the clade with *C.* aff.

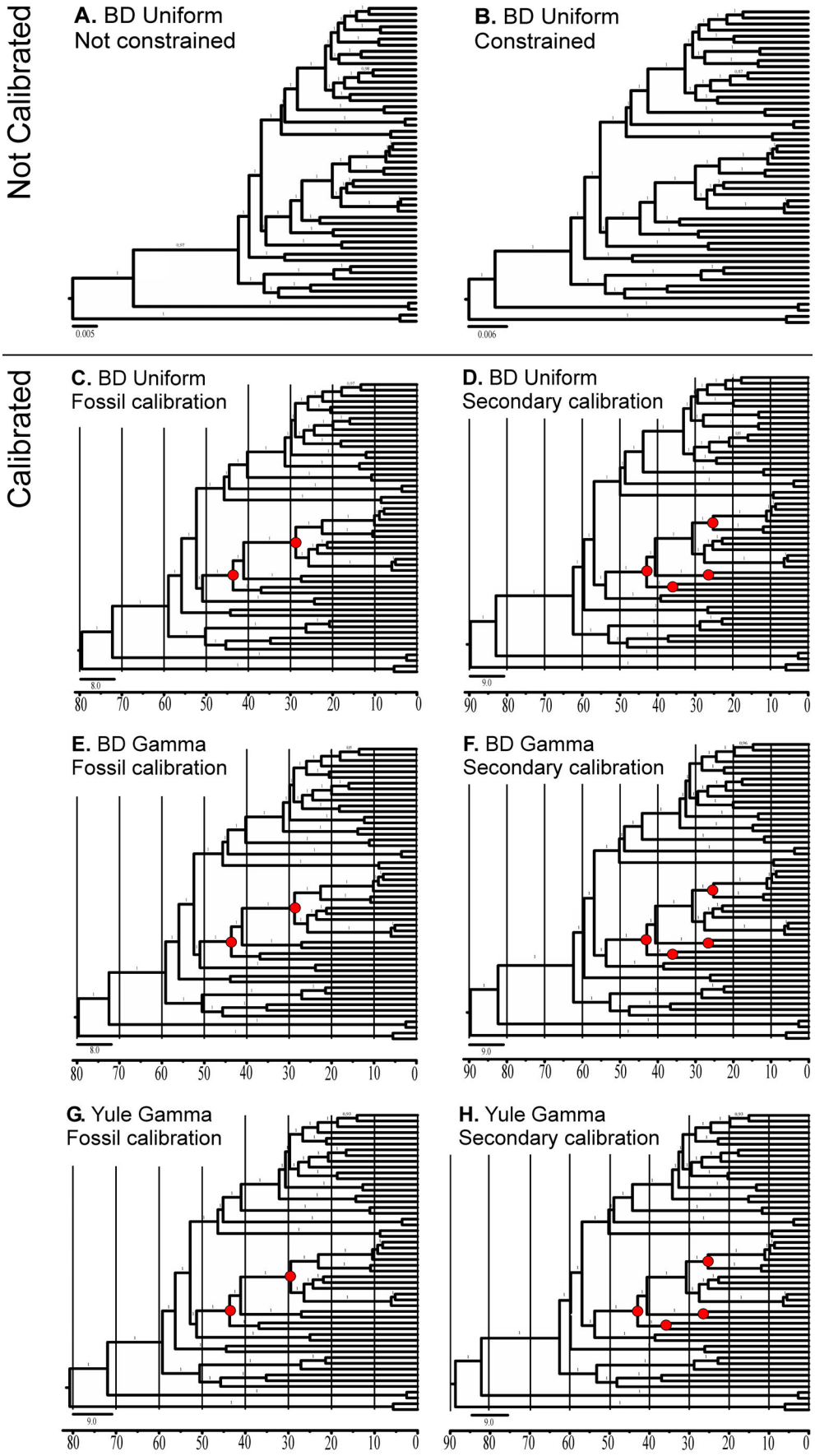

Fig. 2A. Maximum clade credibility phylogenetic trees from BEAST using the 20 average-variable genes dataset and different prior assumptions indicated at the top of the corresponding tree. The scale below each tree indicates million years before present, and red circles represent the calibration points. BD: birth-death model.

schatzii + *C.* sp. 1. The reverse is found for *C. ludiifolium*, which appears morphologically homogenous (based on sterile specimens) and geographically delimited, yet for which 2–3 different species are suggested in STACEY.

■ DISCUSSION

Evolutionary and speciation patterns. — The *Capurodendron* lineage is estimated to have originated some 40 mya (Fig. 2B), a period in which the then-extensive dry spiny thicket slowly contracted, resulting in an expansion of humid and dry forests in Madagascar (Buerki & al., 2013). Other endemic genera of trees from Madagascar are known to have originated during this period, such as *Quivisianthe* Baill. (Meliaceae) and *Tetrapterocarpon* Humbert (Fabaceae) from the dry forests, and *Baudouinia* Baill. (Fabaceae) and *Malagasia* L.A.S.Johnson & B.G.Briggs (Proteaceae) from humid forests (Buerki & al., 2013).

Capurodendron is divided into two main clades, one restricted to a single extant species, *C. madagascariense*, inhabiting humid habitats in dry areas (clade A in Fig. 4), and

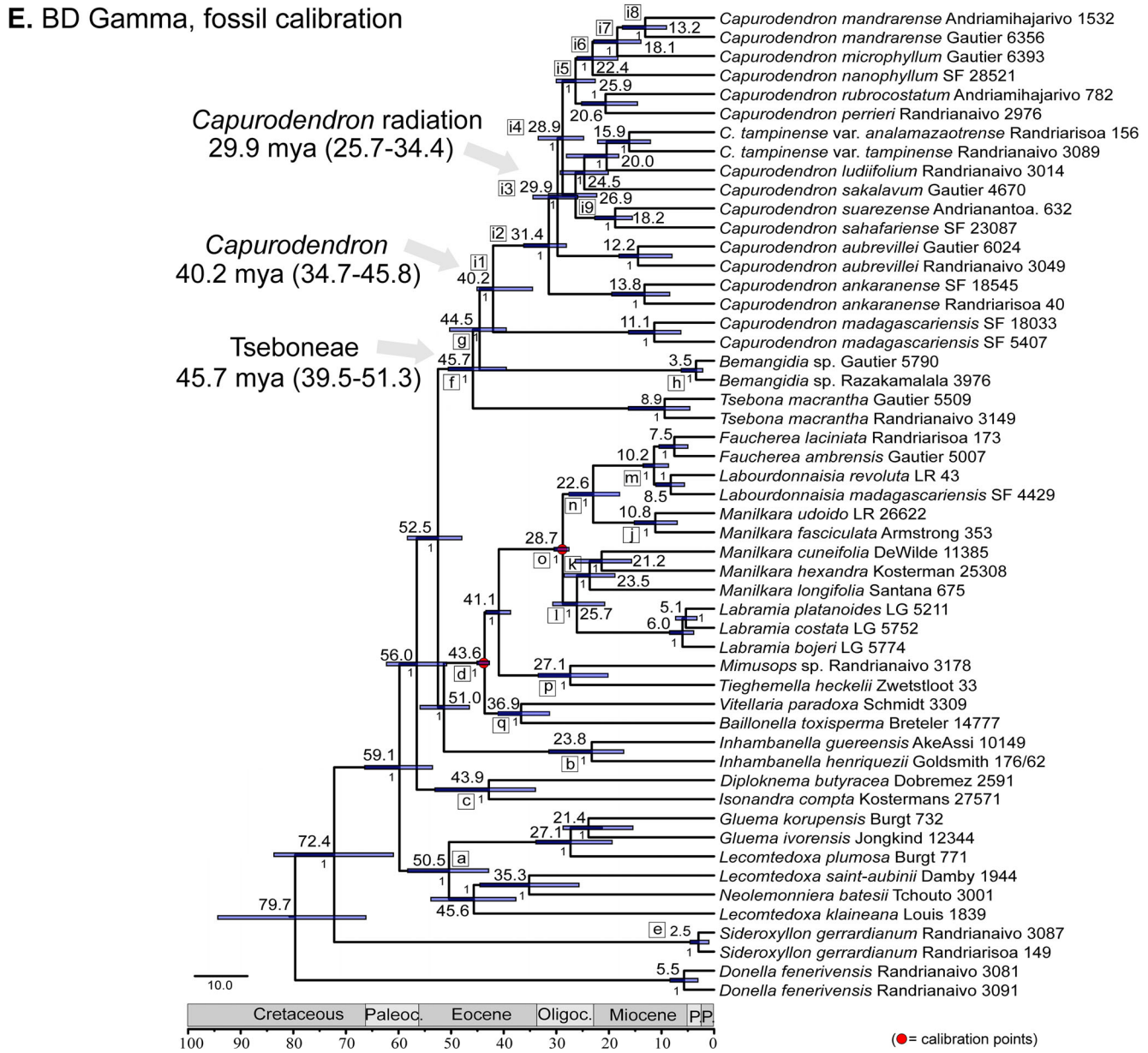

Fig. 2B. Maximum clade credibility phylogenetic tree from BEAST using the 20 average-variable genes dataset, with fossil calibration and a birth-death model with a gamma distribution. The scale below the tree indicates million years before present together with the different geological epoch, and red circles represent the calibration points. Constrained clades are specified by the letters a to q inside a square (Table 1), with node ages indicated and the 95% HPD age ranges shown by grey bars. For information on specimens, see Appendices 1 & 2.

the other containing all the remaining taxa (clades B to G) and found from the most arid to the most humid regions. The phylogenetic branch lengths of these two lineages are comparable to those separating the currently recognized genera of Sapotaceae (Fig. 1). The single species of clade A additionally shows distinctive morphological characters: (1) Seeds of *Capurodendron* have a basiventral scar, which is much more basal in *C. madagascariense* than in all other species; (2) the staminodes of *C. madagascariense* are glabrous and petaloid, erect or spreading, as opposed to those of all other members of the genus, which are hirsute, convergent and conceal the ovary; (3) the sepals of *C. madagascariense* are much narrower and acuminate, their apical half is relatively soft and reflexed after anthesis, not adpressed as in all the other species. However, following the general principles of Backlund & Bremer (1998) and the current generic concept in tribe Sapotoideae, in which genera are distinguished using more obvious and discrete characters, we consider that this lineage is not sufficiently morphologically different to justify its recognition as a separate genus. We therefore prefer to describe a new subgenus to accommodate its single species, *C. madagascariense* (see taxonomic section).

The main *Capurodendron* lineage shows a radiation-like topology (Glor, 2010), in which clades B to G (Fig. 4) diverged over a relatively short time span. The previous phylogeny of *Capurodendron* (Gautier & al., 2013) showed a slightly different topology, with a less pronounced radiation-like pattern. This may be explained by the use of far fewer specimens and species, omitting some of the main lineages, but also by the use of only two loci, which are less informative than our 638 loci. As expected for a radiation, clade relationships are less supported than in other regions of the phylogenetic tree, presumably because of the estimated short period of time during which they differentiated (Glor, 2010; Cai & al., 2020). During such a rapid process, most mutations are specific to one of the many emerging lineages but not shared among them, resulting in short bifurcations but well-supported clades. Moreover, extensive incomplete lineage sorting might have occurred, the effect of which is still discernable due to the many genes used in this study (Naciri & Linder, 2015, 2020). Most species-level clades nonetheless are well-enough supported to deem these as good species. *Capurodendron* appears to have experienced a series of rapid diversification events leading to the high level of clade diversity observed today. This radiation most probably started around 31 mya, when global temperatures stabilized and while forest biomes expanded in Madagascar (Buerki & al., 2013). However, the age estimates for diversification events that took place after this initial radiation should be taken with caution, as they may be strongly biased (see dating analysis section).

From the least to the most divergent clades in the radiation, the first includes *Capurodendron ankaranense* and *C.* sp. 19, both of which are adapted to dry environments (clade B; Fig. 4). It is followed by *C.* sp. 11 (recognized hereafter as *C. aubrevillei* sp. nov.; clade C), from humid rainforest areas, and then by three sister lineages containing taxa from dry to arid regions (clades D, E, and F; Fig. 4), except for *C.* sp. 9 (nested in clade F), which probably underwent a secondary back-adaptation to rainforest habitats. Finally, the most diverging lineage (clade G) contains humid-adapted species, with the exception of *C. sakalavum*. This pattern suggests several successive habitat-shifts from dry to humid environments and back, which may point to climate adaptation as a key factor in *Capurodendron* radiation. After the evolutionary events associated with these environmental changes, incipient species may have diversified into species groups, each containing species adapted to the environment of their parental species. Unlike all the other genera of Sapotaceae in Madagascar, which are largely or entirely restricted to humid areas, *Capurodendron* has diversified extensively in dry regions, and, most likely, in a few instances, went back to humid environments.

As mentioned by Naciri & Linder (2020), "radiations are a product of the right genetic material and the right genomic structure, in the right environment". Interestingly, two of the most species-rich genera of angiosperms, *Carex* and *Euphorbia*, are sister to monotypic genera (Horn & al., 2012; Léveillé-Bourret & al., 2018), and the two sister lineages of *Capurodendron*, *Bemangidia* and *Tsebona*, similarly appear to be monospecific. Understanding what led *Capurodendron* to be so different from the other Malagasy genera of Tseboneae, therefore, deserves consideration. Whereas *Bemangidia*

Table 1. Lineages constrained in the clade age estimation analysis in BEAST.

Clade	Node in Fig. 2
Baillonella + *Vitellaria*	q
Bemangidia	h
Bemangidia + *Capurodendron*	g
Capurodendron subgeneric clades	i1 to i9
Faucherea + *Labourdonnaisia*	m
"Gluemeae"	a
Inhambanella	b
Indo-Pacific *Manilkara* (*Manilkara fasciculata* + *M. udoido*)	j
Indo-Pacific *Manilkara* + *Faucherea* + *Labourdonnaisia*	n
Isonandreae	c
Manilkara sensu stricto (*M. cuneifolia* + *M. hexandra* + *M. longifolia*)	k
Manilkara sensu stricto + *Labramia*	l
Manilkarinae (*Manilkara* + *Faucherea* + *Labourdonnaisia* + *Labramia*)	o
Mimusops + *Tieghemella*	p
Sapoteae	d
Sideroxyleae	e
Tseboneae	f

and *Tsebona* are restricted to humid and mature forests, *Capurodendron* has colonized the entire island except high-altitude areas (above 1800 m). The members of the genus *Capurodendron* exhibit a particularly high level of diversity in their niches, expressed as multiple adaptations to different climate and soil conditions. Interestingly, *Capurodendron madagascariense*, the first diverged species of the genus, is found in humid habitats within dry areas, and it can be expected to behave as a species adapted to dry environments in its first years of life, and as a species adapted to humid environments when the roots go deep into permanently moist soils. We hypothesize that a potential broad ecological niche of the ancestral species may be the key factor that led to the diversification of the genus.

Among the many other factors that consequently fueled this radiation, three were identified that might have contributed to the observed pattern: (1) fragmented distribution of soil types (2) limited dispersal ability, and/or (3) genetic drift in environments with recurrent disturbances. We briefly discuss each of these three factors below.

(1) Soil adaptation seems particularly important in the species radiation within *Capurodendron*. The main soil types found on the island can be grouped roughly into three categories: nutrient-poor, sandy substrates (including sand and sandstone); laterite and other siliceous soils with low pH; and calcareous soils with high pH. Calcareous and sandy soils appear to be more or less isolated on the island (Du Puy & Moat, 1996) and are frequently surrounded by areas with other soil types. Fragmented distribution of soils may therefore have favored speciation through localized soil adaptation, as in *C. ankaranense*, *C. costatum*, *C. sakalavum*, *C. suarezense*, and *C.* sp. 20, all of which occur only on limestone and are sister to species adapted to siliceous or sandy soils (*C.* sp. 19, *C. sahafariense*, *C.* sp. 15 – *C. ludiifolium* clade, *C. randrianaivoi*, and *C. microphyllum*, respectively). Adaptation to the sandy soils of littoral forests might also have resulted in speciation events, for example with *C. delphinense*, *C. naciriae* and *C. randrianaivoi*, which are sister to one or more non-littoral species (*C. bakeri*, *C. sakarivorum* + *C.* sp. 16, and *C. suarezense*, respectively).

(2) Diversification in *Capurodendron* may have also been enhanced by intrinsic seed dispersal limitations combined with physical barriers that together favor allopatric speciation. Although *Capurodendron* seeds have been observed to be dispersed not only by terrestrial and arboreal mammals, but also by bats and birds (Gautier & al., in press), Fig. 4 shows that many clades are geographically restricted. In some cases, geographical restriction is linked to a given environment, as in the arid south, which presents a set of environmental conditions not found elsewhere on the island. Other lineages, however,

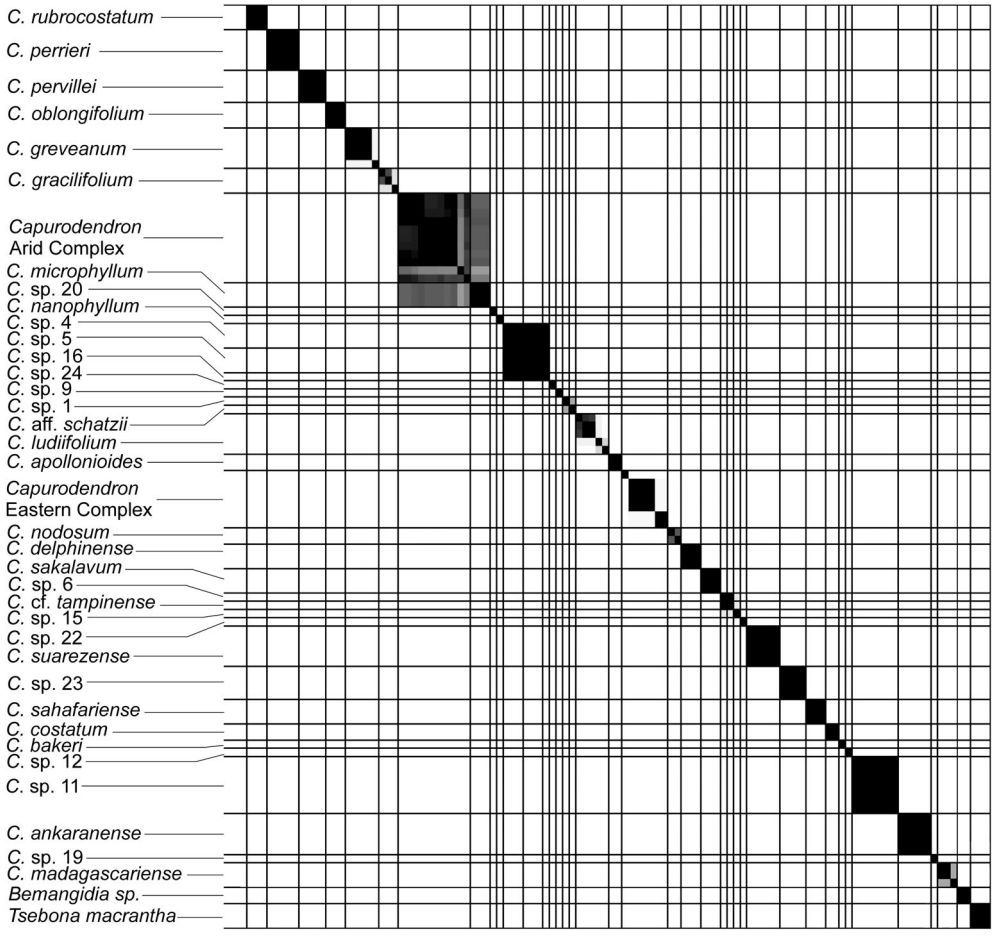

Fig. 3. Similarity matrix based on STACEY analysis using 20 average-variable genes showing the posterior probability of two individuals belonging to the same multi-species coalescent cluster (MSCC). A black square indicates a posterior probability of 1, while no color indicates a posterior probability of 0. The lines delimit the morphospecies.

appear to be surrounded by geographical barriers. This is the case of the clade comprising the species from *C.* sp. 9 to *C. suarezense*, nearly entirely endemic to the extreme north of Madagascar (*C. costatum* is the one exception; Fig. 4). All these species (except *C.* sp. 9) are restricted to deciduous forests, an environment that is common in all western Madagascar. Here, however, the relatively small Sambirano humid area seems to have acted as an effective dispersal barrier, impeding this northern clade from colonizing the western deciduous forests. *Capurodendron costatum*, the only species of the northern clade occurring in the West, may be the result of allopatric speciation following an ancient migration that crossed the Sambirano barrier. *Capurodendron* sp. 9, although included in the northern deciduous lineage (clade F in Fig. 4),

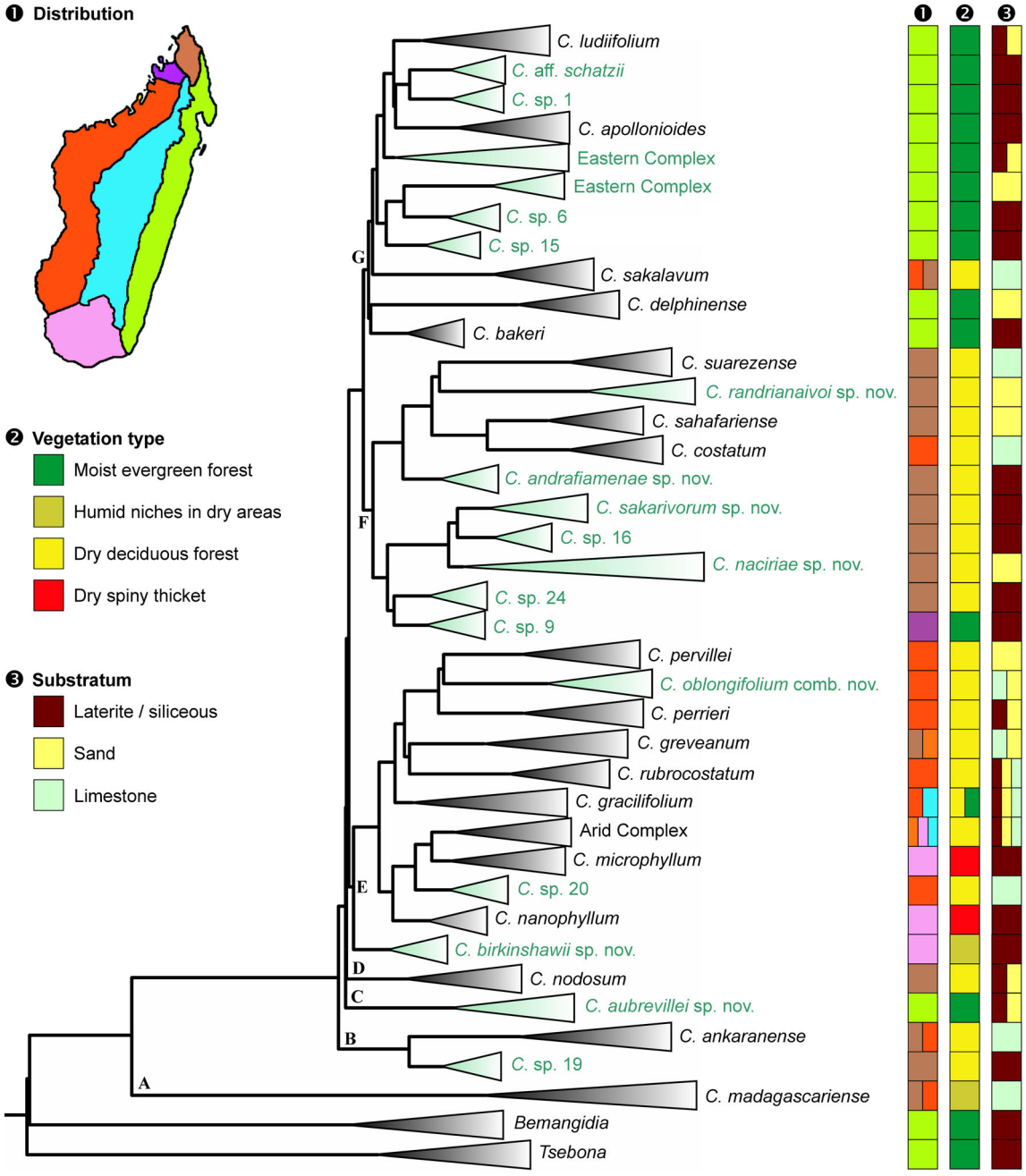

Fig. 4. Phylogenetic tree topology from ASTRAL using 638 protein-coding genes and 111 specimens collapsed at species level with chorological and ecological information shown in the colored squares on the right. Letters A–G indicate the main clades of *Capurodendron*, and new species are in green. For distribution, Madagascar map divisions are derived from Humbert (1955) and based on climatic and phytogeographic data, with color code as follows: green (east) and purple (Sambirano) colors represent hot and perhumid areas with a climax of low-altitude moist evergreen forests, cyan: temperate humid areas with a climax of medium-altitude moist evergreen forests, brown (north) and orange (west): hot seasonally humid areas with a climax of dry deciduous forest and pink (south) subarid areas with dry spiny thicket.

is adapted to Sambirano's moist evergreen forests, but it apparently never dispersed to the Eastern Domain, nor did any close relative succeed in colonizing the moist evergreen forests. The central mountain range, despite being only 70 km wide and rarely exceeding 2000 m elevation, seems to act as an effective dispersal barrier between the two homologous lowland moist evergreen forests of Sambirano and the East, considered as distinct phytogeographic entities (Humbert, 1955; D'Amico & Gautier, 2000; Gautier & Goodman, 2003). Symmetrically, the eastern rainforest is inhabited by species such as *C. antongiliense*, *C. apollonioides*, *C. ludiifolium*, and *C. tampinense* that have long fusiform seeds, which could be adapted to large-bird dispersal following ingestion without preliminary mastication. If large birds are really involved in the dispersal of these species, it is striking that none of them colonized the lowland moist-evergreen rainforests of Sambirano. However, these four species inhabit the perhumid climatic zone and could possibly not settle in the less humid and slightly seasonal climate of the Sambirano.

(3) Environmental instability might be an additional factor driving radiation within *Capurodendron*. According to Naciri & Linder (2020), a radiation can occur when genetic drift is high with repeated colonization events and founding effects. The East and North of Madagascar are frequently affected by cyclones that heavily impact parts of the forests. This phenomenon opens up spaces for recolonization by surrounding old-growth tree species, leading to a patchy geographical distribution of "extinction-recolonization" events highly influenced by genetic drift. For a tree species genus like *Capurodendron*, in which flowering begins late in development, this furthermore creates a longer interval during the first years of development where selection can operate on vegetative characters. Accordingly, at least in some species, the leaves of the young trees are different from those of the adult ones. A combination of genetic drift and selection of vegetative features might explain, for instance, the very high diversity of leaf morphology observed in *Capurodendron*.

Species complexes. — Two species complexes have been found in *Capurodendron*, one restricted to dry southern Madagascar (the Arid Complex) and the other to the eastern rainforests (the Eastern Complex). A preliminary study of the Arid Complex using 50 specimens and the same 638 genes recovered three main genetic groups, one composed of *C. androyense*, a second containing *C. androyense* and *C. mandrarense*, and a third one only comprising material assigned to *C. mandrarense* but sharing phenotypic characteristics with *C. greveanum*. These data suggest the possibility of reticulate evolution highly influenced by recurrent hybridization between the three taxa, which present overlapping distribution ranges (Christe & al., 2021). A more detailed revision of the complex has been presented in a separate study using additional samples and more variable genetic markers (Boluda & al., 2021).

The Eastern Complex is composed of *Capurodendron tampinense* var. *tampinense*, *C. tampinense* var. *analamazaotrense*, *C. bakeri* var. *antalahaense* (as for *C. bakeri* var. *bakeri*, our results show it to be a distinct, unrelated species), and a number of specimens morphologically similar to *C. tampinense*. This group is found throughout the humid east of Madagascar, from north to south. Genetic and morphological data suggest that the group may comprise several species, albeit with morphological limits not well delineated. *Capurodendron tampinense* var. *analamazaotrense* is perhaps morphologically and ecologically the best-defined candidate species. It forms a clade nested within the complex, indicating that if considered a distinct species, it would also be necessary to consider all the other clades within the complex as distinct species too, in order to avoid paraphyly with respect to the entity currently called *C. tampinense* var. *analamazaotrense*. Since only limited fertile material is available for the entities contained in the Eastern Complex, the group will have to be studied further, with improved sampling.

Dating analyses. — Dating analyses (Fig. 2A,B) resulted in estimated node ages similar to those obtained by Armstrong & al. (2014), something expected as we used the same calibration points. According to our analysis and the sampling used, the endemic Madagascar genera *Labramia* and *Faucherea* + *Labourdonnaisia*, yielded crown ages estimated to be within the late Miocene, whereas the *Capurodendron* crown age is estimated to be much older, in the Eocene, around 40 mya. The older origin of *Capurodendron* might be expected, as it contains more species and is morphologically and ecologically more variable. At the species level, however, ages recovered for the genus were unexpectedly old. Crown/stem ages for the lineages of *C. ankaranense* (13.8/31.4 mya), *C. aubrevillei* (12.2/29.9 mya), and *C. mandrarense* (13.2/18.1 mya) are older than the ages estimated for some genera in the family (e.g., *Labramia*, *Faucherea* and *Labourdonnaisia*). Species with most recent common ancestors (MRCA) older than 10 million years are rather rare in flowering plants in general (Meseguer & al., 2015; Rockinger & al., 2017; Hipp & al., 2019; Thornhill & al., 2019), and in particular in Sapotaceae (Armstrong & al., 2014; Stride & al., 2014; Terra-Araujo & al., 2015). The aforementioned species are morphologically well delimited and are tightly clustered in the ASTRAL analyses (Fig. 1). Below we will discuss why, on this basis, we suspect that node ages may be overestimated, especially for those subsequent to the principal radiation taking place around 31 mya.

The node age in an ultrametric tree is proportional to the distance from the node to the tips, and hence depends on branch length estimation under the assumption that substitution rates have a constant value across time (although different for each clade). In Bayesian phylogenetic trees, branch lengths are related to lineage extinction and speciation rates (Morlon, 2014). The most common branching process priors (BPP) used for node age estimation are the Yule process, which uses a rate of speciation, and the birth-death (BD) process, which includes both a speciation and an extinction rate. Usually, either of the BPP priors can be used, yielding very similar results (Kergoat & al., 2014; Meseguer & al., 2015; Toussaint & al., 2015), but in some cases BPP priors selection is crucial.

The extinction rate in the BD model produces shorter branches toward the tips, with respect to the backbone, because extinction has a lower effect on recent nodes. This phenomenon is known as the "pull of the present", as it moves the nodes toward the tree tips (Gernhard, 2008). For example, in recently evolved groups such as the family Brassicaceae, where extinction is expected to have played a minor role in producing the topology of phylogenetic trees, the Yule and BD models give similar branch lengths (Couvreur & al., 2010). Conversely, in Zamiaceae, an old family of gymnosperms strongly affected by extinctions, the Yule model overestimates the terminal branch lengths, providing estimates of the genus crown ages that are three times older than those obtained with the BD model (Condamine & al., 2015). The terminal branch lengths observed in Fig. 2A for *Capurodendron* are not significantly longer under the Yule model compared to the BD model, indicating that here the "pull of the present" phenomenon has a limited effect on lineage ages. Accordingly, the treePL results, which use a maximum likelihood approach, also estimate similar ages from branch lengths.

Phylogenetic analysis performed in sparsely sampled groups violates the basic assumptions for most of the tree priors used in Bayesian dating (Condamine & al., 2015; Drummond & Bouckaert, 2015: 98). In our case, we are attempting to estimate node ages in a highly incomplete and variable dataset that ranges from family to species level, and the only known calibration points are in the outgroups. In this type of situation, it is difficult to find appropriate priors describing the entire tree, and neither the Yule nor the BD model is designed to handle situations where parts of the tree are densely sampled while others are not (Condamine & al., 2015). BEAST software computes the most appropriate extinction and speciation rates for the dataset, but unfortunately the program assumes a constant rate across time and clades. However, in the context of a radiation such as that found in *Capurodendron*, it is not reasonable to assume a constant rate, which could produce a severe bias in age estimation (Rabosky, 2010; Morlon & al., 2011). Given the morphology and ecology of the group, the elevated number of species, and the radiation-like topology seen in Fig. 1, we hypothesize that *Capurodendron* might have experienced successive ancient radiations throughout Madagascar. If this is indeed the case, high speciation and low extinction rates would be expected for *Capurodendron*, but not necessarily for the outgroups. Because these rates have been estimated using calibration points and topologies from external groups, they may well be inappropriate for *Capurodendron*. In the case of treePL, the program does not estimate extinction and speciation rates. However, during the *Capurodendron* radiation, substitution rates may have been higher than for the outgroup species, thereby producing longer branches resulting in overestimated ages.

Recent studies suggest that the pipeline used here, HybPiper (Johnson & al., 2016), may not effectively detect paralogous genes (Zhou & al., 2020), which artificially increase the number of sites that appear to be phylogenetically informative. Although this has little impact on the reconstructed topology, it increases branch lengths, and hence estimated divergence times. Putative false phylogenetically informative sites would be expected to be more frequent in the most variable gene set, but estimated ages were similar in the most variable and the least variable datasets. Moreover, estimated ages in tribe Sapoteae (clades c + d in Fig. 2B) match well with previous estimates (Armstrong & al., 2014). If paralogs are indeed present, internal calibration points could correct the resulting bias in tribe Sapoteae, but perhaps not in external lineages lacking calibration points, as in *Capurodendron*. To solve these problems, a fossil calibration point inside Tseboneae would be required, and until this becomes available, node ages after the main radiation of *Capurodendron* should be considered overestimated or at least treated with caution.

Species concept and conservation assessments. — Among the new species described below and in a previous contribution (Gautier & Naciri, 2018), four are based on specimens previously identified as *Capurodendron ludiifolium* (*C. sahafariense*, *C. naciriae* sp. nov., *C. sakarivorum* sp. nov., *C. randrianaivoi* sp. nov). These species do not form a closely related species complex, but rather had reached a similar morphology by convergence, sharing the same thin, parallel and anastomosing leaf venation. A conservation assessment was recently published for *C. ludiifolium* (Faranirina & al., 2019) including these misidentified specimens, which led to an assessment of VU (Vulnerable). When the material assigned to the four species mentioned above is removed, a revised assessment of *C. ludiifolium* yields a status of EN (Endangered), while two of the segregated species are similarly assessed as EN (see below) and two as CR (Critically Endangered). A similar situation is found in *Capurodendron andrafiamenae* sp. nov, provisionally assessed as CR, which includes material previously confounded with the genetically distant species *C. greveanum*, which is classified as LC (Least Concern) (Faranirina & Rabarimanarivo, 2019a). The only known specimen of *C. birkinshawii* sp. nov. (CR) was previously identified as *C.* aff. *nodosum*, a species assessed as VU (Faranirina & Rabarimanarivo, 2019b). While *C. nodosum* is restricted to the extreme north of Madagascar, the only known specimen of *C. birkinshawii* was collected in the extreme south. If the latter specimen had been included in the conservation assessment of *C. nodosum*, its extent of occurrence would have been incorrectly increased by far. This highlights the importance of a solid taxonomy that produces a clear species concept for the group under study, which is in turn essential for formulating accurate conservation assessments.

Considerations about species description. — Based on the currently available morphological, geographical and genetic data, *Capurodendron* may contain as many as 20 undescribed species. That would make it the largest endemic genus of plants in Madagascar, far exceeding *Aspidostemon* Rohwer & H.G.Richt. (Lauraceae) and *Microsteira* Baker (Malpighiaceae), each with 28 species (Callmander & al., 2011). Additional material currently under examination appears to

contain other morphologically distinct entities that may also represent new species, further highlighting the richness of this genus.

In this contribution, we have chosen to be conservative and describe only the new taxa that: (1) are morphologically well differentiated from any other taxa or from the two species-complexes; and (2) are known by two or more specimens, of which at least one is fertile. However, in response to urgent conservation needs, we had to make two notable exceptions to these rules. In one case (*Capurodendron* sp. 12, described here as *C. birkinshawii*), only one specimen is known, collected around 25 years ago with flowers in the dry spiny thicket in SE Madagascar, and for which GPS coordinates are available. Recent fieldwork revealed that the original vegetation at the locality has been cleared. Although the vicinity was scrutinized for similar habitats, the species was not recovered, and discussions with the local population based on herbarium specimen photographs made clear that the species was not familiar, even to elderly farmers and loggers, and therefore probably very rare. As it is unlikely that any further specimens will be collected in the near future, the decision was made to describe it. The second exception (*C.* sp. 11, described here as *C. aubrevillei*) corresponds to a rather different case: a species with relatively frequent collections (12 collections, most from the last 10 years), and displaying a rather broad distribution in the eastern lowland moist evergreen forest, but which has never been collected in flower nor in fruit. As it appears to be a very clear species, both morphologically and genetically, and as its habitat is under major threat, we decided to describe it based on vegetative characters in order to ascertain and publish its conservation status under a valid name.

The remaining likely new species are currently under study, with the expectation of additional collections in the future.

■ TAXONOMIC TREATMENT

Capurodendron Aubrév. in Adansonia, sér. 2, 2: 92. 1962.

Capurodendron subg. ***Reflexisepala*** Boluda & L.Gaut., **subg. nov.** – Type: *Capurodendron madagascariense* (Lecomte) Aubrév. (≡ *Sideroxylon madagascariense* Lecomte).

Capurodendron subg. *Reflectosepala* differs from the nominal subgenus by the lack of Aubréville's branching pattern in the twigs, the longer and narrower (ratio 3–6) triangular sepal lobes with an acuminate apex (vs. lanceolate to ovate; ratio <2.5, with an obtuse to acute apex), with a membranaceous (vs. chartaceous to coriaceous) distal half, reflexed at anthesis and remaining so after the loss of the corolla (vs. adpressed to the post-anthesis ovary), the glabrous staminodes that do not conceal the ovary, and the basiventral seed scar that never extends further than 1/3 of seed length (vs. extending from 1/2 to almost the whole length).

Capurodendron subg. *Reflectosepala* contains only one species. It grows on limestone soils along riverbanks in deciduous forests of the Western Domain in Madagascar. Its name derives from the shape of its sepals.

Capurodendron Aubrév. subg. ***Capurodendron***

Capurodendron andrafiamenae L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Antsiranana: Reg. DIANA, Andrafiamena, forêts aux alentours d'Anjahankely, forêt dense humide semi-décidue dégradée, 12°55′42″S, 049°19′21″E, 360 m, 10 Nov 2010, fl., fr., *Gautier & Ranirison 5395* (G barcode G00304201!; isotypes: MO No. 6606097!, P barcode P00783278!, S No. S13-21927!, TEF!).

Figs. 5A,B, 6

Diagnosis. – *Capurodendron andrafiamenae* differs from the vegetatively most similar species *C. greveanum* by the young shoots and petioles covered by rusty trichomes (vs. green and glabrous in *C. greveanum*), the longer pedicels (7–11 vs. 5 mm), the longer sepals (4.5 vs. 3.5 mm), the longer corolla lobes (5.4 vs. 3 mm), and the glabrous (vs. pubescent) ovary.

Description. – *Tree*, small to medium, to 5 m in height in the collected specimens (but certainly much more), up to 35 cm DBH on a fallen individual, with white latex. Terminal twigs 2–3 mm in diam., broadening to 4 mm distally, with leaves clustered at the tip, at first pubescent with a dense rusty indumentum of T-shaped trichomes, soon becoming glabrous. Twigs with grey bark, smooth, but with numerous pale circular lenticels. Stipules inconspicuous, hidden in the indumentum at the apex of the shoot, early caducous, narrowly lanceolate, quite swollen at base, densely villous outside, glabrous inside, ca. 3.5 mm long. *Leaves* probably caducous; petiole relatively long, 1/3 the length of the blade, 15–30 mm long, to 1.5 mm wide, terete, but opening distally in the 2–3 mm below the lamina, exposing the midrib, densely villous at proximal end, glabrescent distally; leaf blade coriaceous, more or less concolorous, upper surface of mature leaves shiny when dry, ovate to obovate, 4.5–9.5 × 2.0–4.3 cm, soon glabrous but sometimes with a few scattered trichomes near the midvein on the lower surface, base obtuse to acute, sometimes slightly asymmetrical, apex acute or broadly acuminate to sharply acuminate, margin entire, faintly thickened; primary vein reaching apex, distinctly prominent below, slightly prominent within a median depression above, glabrous or sometimes with scattered trichomes, especially on lower surface near the base; 14–22 pairs of brochidodromous secondary veins forming an angle of 30°–50° with midrib, straight, branched in the last millimeters before the margin to join the adjacent secondaries; intersecondaries sometimes present, extending halfway to the margin; tertiary venation reticulate, forming large polygons, with smaller open reticulations inside, raised on both surfaces on dry specimens, especially on mature leaves. *Flowers* solitary or in pairs, on previous or current year's shoots; flowering pedicels 7–11 × 1.0 mm,

Fig. 5. *Capurodendron andrafiamenae*: **A**, Flower fascicles (*Gautier 5395*); **B**, Flower detail (*Burivalova 138*). *C. aubrevillei*: **C**, Twig showing Aubréville's branching pattern and thickened apices (*Gautier 5544*); **D**, Detail of the stipules among the petioles (*Randriarisoa 125*); **E**, Young leaves (*Randriarisoa 125*); **F**, Bark with a slash showing some latex and the external wood color (*Gautier 6024*). — Photos: A, C & F by Laurent Gautier; B by Zuzana Burivalova; D & E by Carlos G. Boluda.

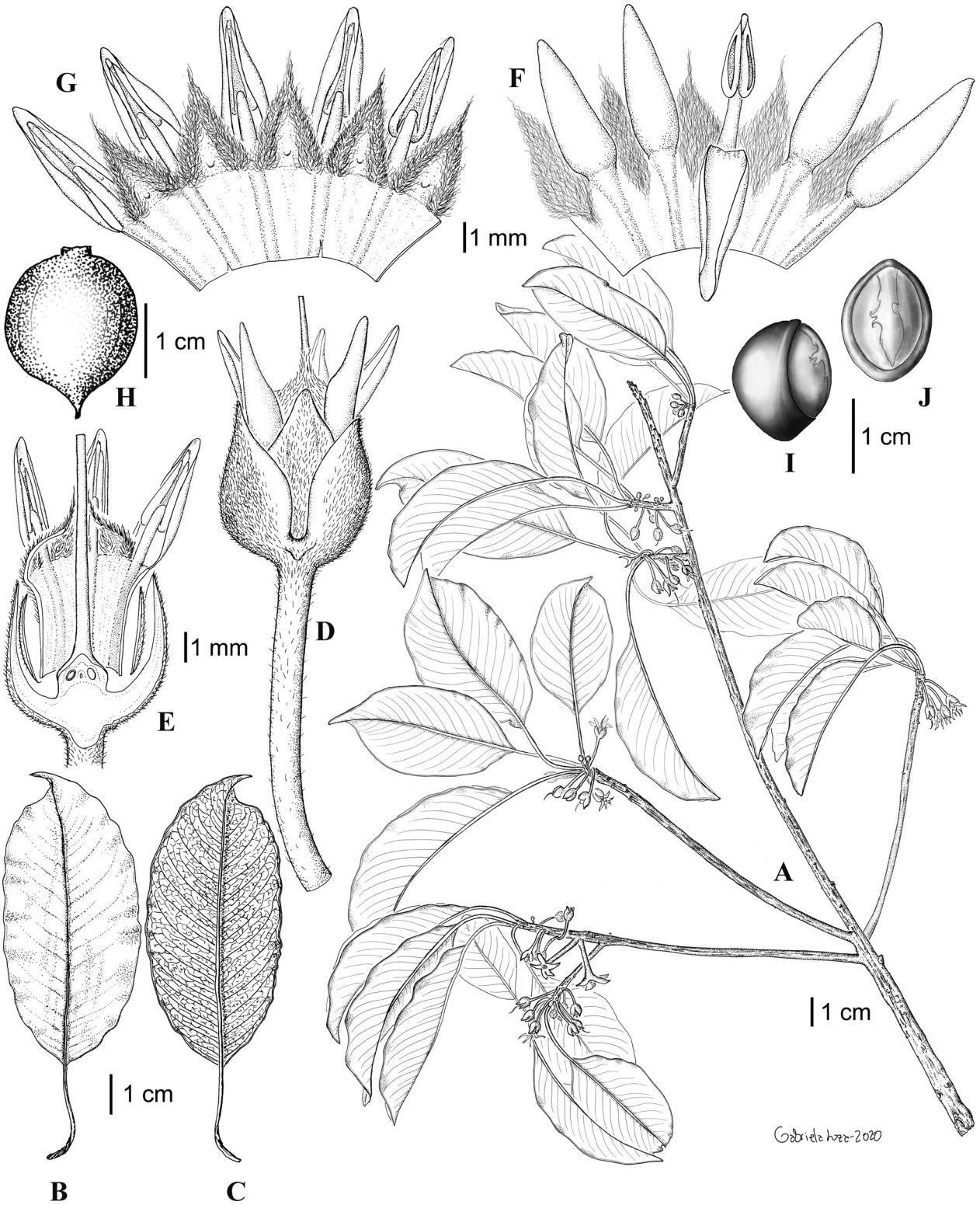

Fig. 6. *Capurodendron andrafiamenae*. **A**, Flowering branch; **B**, Leaf (upper surface); **C**, Leaf (lower surface); **D**, Flower; **E**, Flower in longitudinal section; **F**, Outer side of a detached corolla spread and opened, with a lobe folded down showing a stamen; **G**, Inner side of a detached corolla spread and opened; **H**, Fruit; **I**, Lateral view of a seed; **J**, Ventral view of a seed. — Drawing: Gabriela Loza.

nearly glabrous, becoming villous towards calyx. *Sepals* 5, quincuncial, ovate, with an obtuse apex, 4.5 × 3.5 mm, convex, glabrous inside, densely pubescent outside except for the glabrous margin, which is much broader in the three inner sepals. *Corolla* gamopetalous, with 5 lobes; whitish, tube glabrous, except below the staminodes on the outer side, 2.5 mm long, lobes lanceolate, glabrous, 5.4 × 2.1 mm, widest 1/3 from the base, erect to spreading at anthesis. *Stamens* 5, filaments terete, villous on the outer side, 2.2 × 0.3 mm, attached at the top of the corolla tube; anthers medifixed, extrorse, 1.9 × 0.5 mm at the broadest, connective glabrous, prolonged in a 0.3 mm mucro. *Staminodes* 5, whitish to pinkish, alternate with respect to petals and stamens, cream to pink when fresh, ovate–triangular, 1.7 × 2.5 mm, densely villous on outer side, mostly glabrous on the inner side, except for a densely hirsute margin, crustaceous at base, connivent and completely concealing the ovary. *Ovary* 5-lobed, 2.8 mm high, 2.3 mm wide, glabrous, with 5 uniovulate locules; style 6.2 mm long, 0.4 mm diameter, slightly broader near the base, 5-fluted halfway to the apex, glabrous, stigma indistinct. *Fruit* on a slightly elongated pedicel 15 mm long, with an enlarged persistent calyx with lobes 6.0 × 4.5 mm; the fruit ovate, 20 × 19 mm when dry, with a persistent style. Seeds circular in outline but slightly laterally compressed, 16 × 14 × 11 mm, testa shiny, scar basiventral, broadly ellipsoid, 13 × 11 mm, extending from the bottom to 3/4 of the height.

Etymology. – The specific epithet refers to the Andrafiamena forest, where the new species was found, now part of the Andrafiamena-Andavakoera protected area, managed by the NGO Fanamby.

Distribution, ecology and phenology. – *Capurodendron andrafiamenae* is only known from the type locality in the north of Madagascar, in dense humid semi-deciduous forest on sandstone from 360 to 540 m asl (Fig. 7). The two collections have flowers and were collected in November and December, the earlier one also bearing fruit from the previous season's flowering.

Conservation status. – Only known from two collections, *Capurodendron andrafiamenae* has an area of occupancy (AOO) of 8 km^2, and its extent of occurrence (EOO) is estimated to be less than 100 km^2, both values qualifying for a CR status under criterion B. The two occurrences are ca. 350 m apart and represent the entire known population. They are from the same location with respect to threat, which is

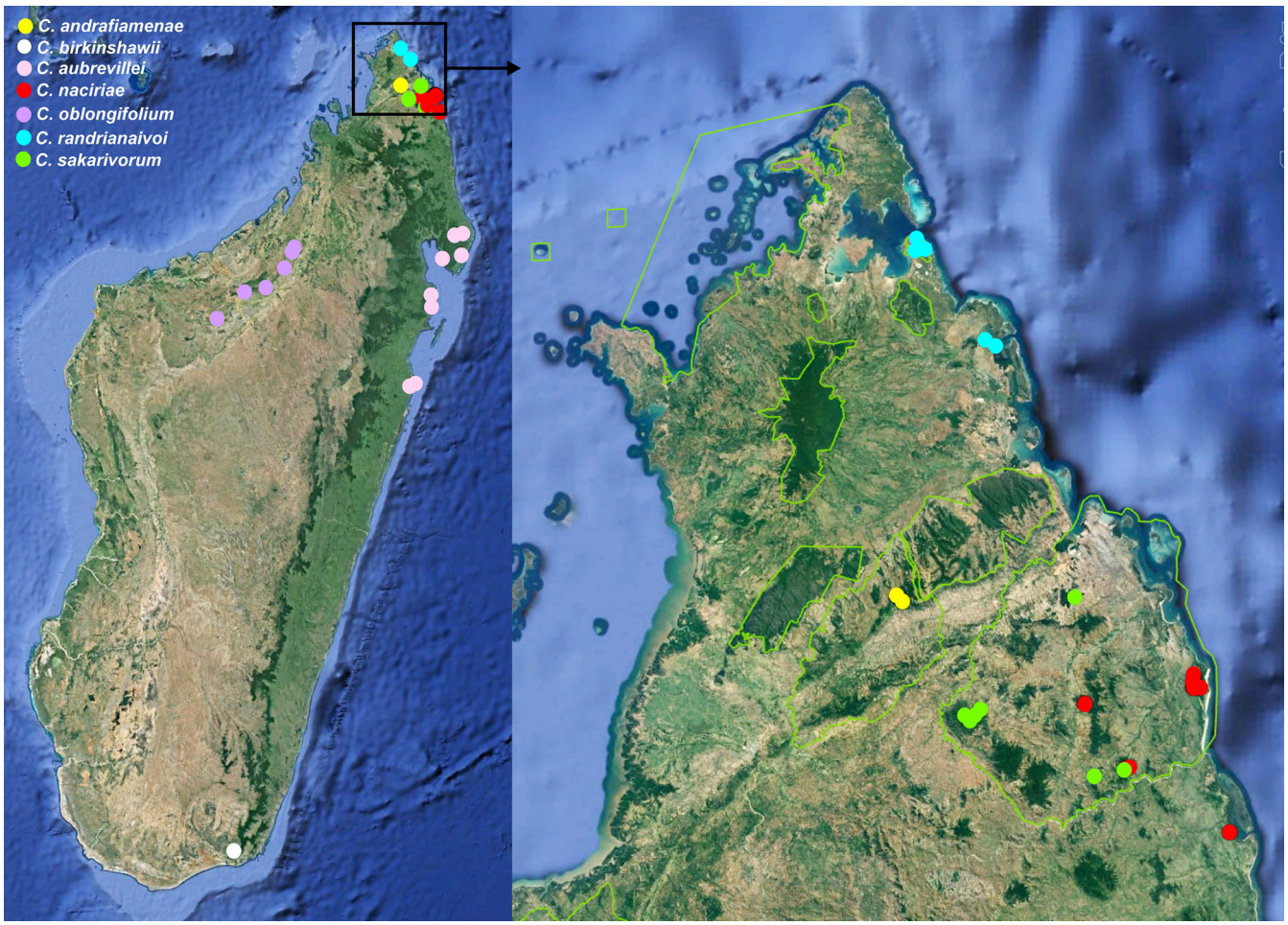

Fig. 7. Map of Madagascar (with the extreme north enlarged on the right), showing the distribution of the new species described.

illegal selective logging. Even inside the protected area the population is likely to experience continuing decline. It is therefore preliminarily assessed as Critically Endangered (CR, B1ab(i,ii,iii,v)+2ab(i,ii,iii,v), IUCN, 2012).

Notes. – *Capurodendron andrafiamenae* superficially resembles *C. greveanum*, which is frequently found in northern Madagascar. Genetically, it is placed at the base of a clade of dry forest species that includes *C. costatum*, *C. randrianaivoi*, *C. sahafariense* and *C. suarezense*, plus an additional undescribed species not represented in this study, all from northern Madagascar except *C. costatum*.

Paratypes. – MADAGASCAR. Prov. Antsiranana: Reg. DIANA, Andrafiamena, forêts aux alentours d'Anjahankely. 12°54′58″S, 049°20′08″E, 540 m, 27 Dec 2010, fl., *Burivalova 138* (G, S, TEF).

Capurodendron aubrevillei L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Antsiranana, Reg. SAVA: District Antalaha, Commune Rurale Ambohitralanana, Fokontany Antanandavakely, 15°19′57″S, 50° 18′11″E, 265 m, 20 Nov 2013, *Gautier & al. 6024* (G barcode G00406707!; isotypes: S No. S15-27736!; TAN!). Figs. 5C–F, 8

Diagnosis. – *Capurodendron aubrevillei* differs from other *Capurodendron* species with marked Aubréville growth pattern and brachyblasts by its oblanceolate, almost glabrous and flat leaves (vs. pubescent and more or less bullate or with markedly raised secondaries on the lower surface in *C. antongiliense*, *C. birkinshawii*, *C. schatzii*, and *C. nodosum*).

Description. – *Tree*, medium to large, documented to 25 m tall and 50 cm DBH but probably larger; bark rather thin, longitudinally fissured, greyish; slash rose and cream, with white latex. Branches displaying marked Aubréville growth pattern, with almost complete cessation of primary axis growth, generating stout brachyblasts with leaves clustered at their apex, new shoots elongating laterally from their base and repeating the structure. Elongations leafless between brachyblasts, 40–85 mm diam., 7–28 cm long, glabrous, woody, with a rather smooth, thin bark, sometimes with small transversal cracks, dark greyish brown; longitudinal lenticels 0.6–5 × 0.5–1.5 mm, circular to long ellipsoidal, with thick, raised margins. Second-year branches with thin, longitudinal and/or transversal cracks. Brachyblasts older than two years clavate, 0.5–6.5 cm long, 0.5–1.5 cm diam., woody, with barely distinguishable marks of seasonal growth; leaf scars visible when young, less apparent later, sometimes with three marks of the vascular bundles. Stipules persisting with leaves, triangular, light green, the apex frequently brownish and desiccated in vivo, 4–6.5 mm long, to 2.5 mm wide at the base, keeled, thick, slightly woody when dry, with caducous dark brown to white trichomes on the outer side, especially on the keel. *Leaves* probably caducous; petiole green, 16–35 × 1–3 mm, glabrous at maturity, covered by white to golden trichomes during development, broader at base, margins of blade decurrent on the petiole and forming a groove on the upper surface in continuation with the midrib; blade membranaceous to chartaceous, oblanceolate, margin entire, 10.0–19.0 × 3.0–5.5 cm, with the broadest width around 3/4 of the leaf length, tapering gradually to a cuneate base, apex rounded, sometimes with a short obtuse to acute tip, lamina with scattered trichomes on both surfaces, glabrescent; primary vein prominent below, sometimes raised above, very pale on fresh material; 6–8 pairs of eucamptodromous secondaries, forming an angle of 70°–80°, arching up and forking at 2/3 to 3/4 of their length; intersecondaries few, sometimes perpendicular to midrib, dissolving in tertiary venation after a few centimeters; tertiary venation reticulate forming irregular polygons, faintly raised on both surfaces; adpressed inconspicuous trichomes regularly spaced on the midrib and proximal part of the secondaries. *Flowers* and *fruits* unknown.

Etymology. – This species is dedicated to André Aubréville, professor at the Muséum National d'Histoire Naturelle in Paris, a famous and sagacious taxonomist of Sapotaceae, and author of the corresponding volume of the *Flore de Madagascar et des Comores* (Aubréville, 1974). The Aubréville growth pattern, dominant in the Sapotaceae family and particularly evident in this species, was also named in his honor (Hallé & al., 1978).

Distribution, ecology and phenology. – *Capurodendron aubrevillei* is found in lowland moist evergreen forests, from the Masoala Peninsula southwards to Foulpointe, from ca. 80 to 400 m elevation (Fig. 7). This very distinctive species has been collected from November to February so far, but never in fertile condition.

Conservation status. – With an estimated EOO of 5324 km^2 and an AOO of 36 km^2 (qualifying for VU and EN under criterion B, respectively); *Capurodendron aubrevillei* is documented from seven locations with respect to the most serious plausible threat, which is deforestation through slash and burn agriculture. Continuing decline due to habitat destruction is projected in the two locations outside the protected area network, but also due to selective logging in all locations. Despite its low AOO, which we consider to be a collection bias, the species is preliminarily assessed as Vulnerable (VU, B2ab(I,ii,iii,iv,v), IUCN, 2012).

Notes. – *Capurodendron aubrevillei* is a low-altitude moist evergreen forest species, apparently absent from littoral forests on sand. It has medium to large leaves clustered on thick, club-like brachyblasts at the top of the short vertical elongations, like several deciduous congeners that occur in dry forest or the spiny thicket. In this aspect, *C. aubrevillei* is reminiscent of some *Terminalia* species of northern deciduous forests (e.g., *T. calcicola*), which could explain why it has been mistaken for the enigmatic *C. pseudoterminalia*, which so far is known only from the type but has a very distinct morphology. *Capurodendron aubrevillei* has never been collected in fertile condition, and we have long hesitated to describe it formally based on vegetative characters alone. However, after several unsuccessful attempts to collect fertile material, we decided that this very distinctive and phylogenetically well-circumscribed species deserved recognition, especially for purposes of conservation.

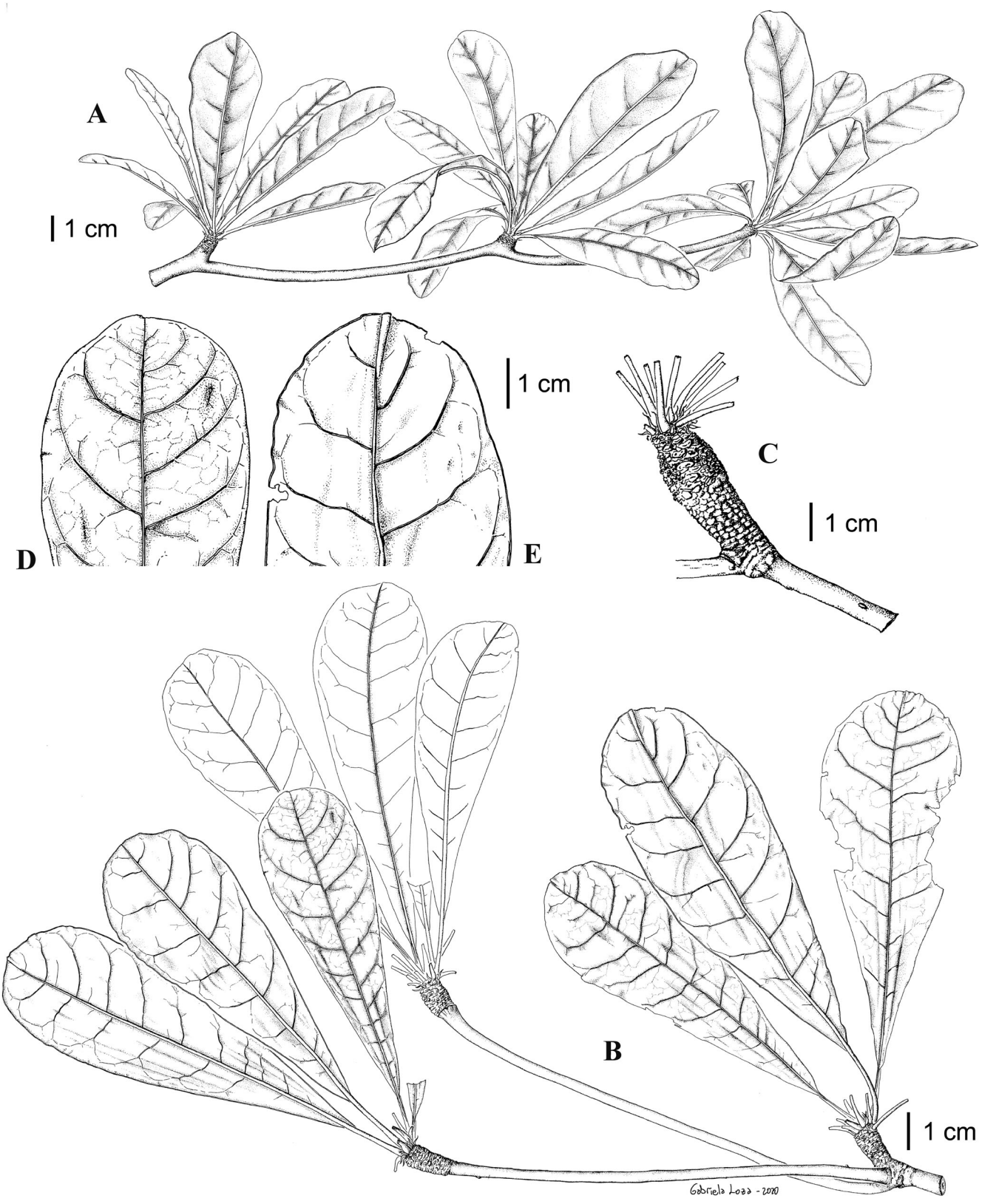

Fig. 8. *Capurodendron aubrevillei*. **A** & **B**, Branch showing the characteristic Aubréville branching pattern; **C**, Brachyblast detail; **D**, Leaf apex (upper surface); **E**, Leaf apex (lower surface). — Drawing: Gabriela Loza.

Paratypes. – MADAGASCAR. Prov. Antsiranana, Reg. SAVA: Disctrict Antalaha, Commune Rurale Ambohitralanana, Fokontany Antanandavakely. Ambalavy, Ambara., alt. 119 m, 15 Dec 2010, *Bernard 1740* (G, MO, P, TAN); Forêt d'Antampinagoaka, Andanapaha, Canton d'Ampanovana, District d'Antalaha, 7 Nov 1951, *Service Forestier 116-R-140* (P); Prov. Toamasina, Reg. Analanjirofo: Tampolo, alt. 115 m, 5 Dec 2010, *Gautier 5544* (G, S, TAN); District de Mananara Nord, Commune de Tanambe, Fokontany de Sahasoa, village de Sahasoa, forêt de Vontaka sud, Parc National de Mananara Nord., alt. 388 m, 1 Feb 2018, *Randrianaivo 3009* (G, TEF); Ibid., alt. 325 m, 1 Feb 2018, *Randrianaivo 3012* (G, TEF); Ibid., alt. 334 m, 1 Feb 2018, *Randrianaivo 3020* (G, TEF); Ibid., Fokontany de Tanambe, village de Tanambe, piste Tanambe-Parc Mananara Nord., alt. 244 m, 4 Feb 2018, *Randrianaivo 3049* (G, TEF); Ibid., forêt d'Ambolohely, alt. 228 m, 6 Feb 2018, *Randrianaivo 3069* (G, TEF); Pointe à Larrée, alt. 281 m, 23 Jan 2018, *Randriarisoa 125* (G, TEF); Reg. Atsinanana: District de Toamasina II, Commune de Mahavelona-Foulpointe, Fokontany de Morarano, Forêt d'Analalava protected area, alt. 78 m, 13 Feb 2018, *Randrianaivo 3122* (G, TEF); Forêt de Mangalimaso, à l'ouest de Foulpointe, 23 Nov 1962, *Service Forestier 22107* (G, P, TEF).

Capurodendron birkinshawii L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Toliara: Reg. Anosy, Andohahela RNI, Parcel 2, Fokontany Mokabe-Tsimelahy, ca. 2 km SE of Tsimelahy, thicket and riverine forest, 24°56′01″S, 46°38′05″E, 282 m, 09–12 May 1997, old fl., *Birkinshaw & al. 438* (P barcode P04621621!; isotypes: G barcode G00419016!, MO No. 5815674 [image!], TAN!).

Fig. 9

Diagnosis. – *Capurodendron birkinshawii* resembles *C. nodosum* by the arrangement of its leaves at the apex of short brachyblasts, but differs by its glabrous ovary, the villous stamen filaments, larger stipules, its broadly rounded to subcordate leaf base (vs. obtuse), its bullate leaf lamina, and the higher number of secondary veins (12–14 vs. 8–12).

Description. – *Small tree*, 4 m tall, 16 cm DBH, with latex; marked Aubréville branching pattern, with leaves appearing only at the apex of stout brachyblasts, new shoots elongating laterally from the base of the brachyblast and ending in a new one. Ultimate twigs between brachyblasts leafless, 5.4–7.0 mm in diam., 5–12 cm long, glabrous, woody, with a rugose thin bark, dark to pale grey, and longitudinal lenticels 0.8–6.2 mm with raised margins. Branches two or more years old with a thicker bark, rugose with transversal cracks. Brachyblasts two-or-more-years-old 2 cm long or more, 6.2–7.8 mm diam., with barely distinguishable marks of seasonal growth every 0.6–1.0 cm; leaf scars with pale grey margin and darker center. Stipules narrowly triangular, 6.2–7.7 mm long, up to 2.8 mm wide at the base, keeled, villous with golden trichomes on the external side, glabrous inside, soon caducous. *Leaves* most likely caducous; petiole 10–15 × 1.5 mm, with a dense golden pubescence, canaliculated on the upper surface; blade chartaceous to coriaceous, 5.0–9.5 × 3.5–4.0 cm, from elliptic to obovate with the broadest width around 2/3 of the leaf length, markedly bullate between the secondary veins especially near the margin, base broadly rounded to subcordate, apex rounded, upper surface slightly pilose with whitish trichomes; margin entire, slightly thickened by a marginal vein; lower surface pale yellow due to the indumentum, which consists of larger trichomes more densely arranged than on the upper surface; primary vein prominent below, depressed above, villous on the upper surface, with trichomes that are golden proximally and whitish distally, densely covered by golden trichomes on the underside; 12–14 pairs of eucamptodromous secondaries, inserted at an angle of 60°–80° with midrib, straight, not arching up or only for a few millimeters distally, fused with the marginal vein, frequently forked distally on the posterior side, forming 1–4 arched lateral nerves reaching or not the margin; intersecondaries sometimes present, thin, usually ending less than half the distance to the margin, sometimes appearing at the posterior base of the secondary veins and directed slightly downwards, forming an angle of ~100° with respect to the midrib; tertiary venation reticulate, faintly marked on the upper surface, more visible in the bullate areas, indistinguishable on the lower surface partially due to the indumentum. *Flowers* (description from post-anthesis flowers with dried corollas) clustered below the leaves; flowering pedicels 7–9 × 0.7–1.2 mm, densely golden-villous. *Sepals* 5, quincuncial, apex obtuse; the two outer ones 6.5–7.5 × 6.0 mm, convex, glabrous inside and densely golden-villous outside, up to 2 mm thick at base, the three inner ones 6.5 × 4.0 mm, glabrous inside and densely golden-villous outside. *Corolla* gamopetalous with 5 lobes, tube mostly glabrous except just below the insertion of the lobes, 4.8 mm long, lobes glabrous, narrowly lanceolate, 3.8 × 0.9 mm. *Stamens* 5, filaments 2.6 mm long, villous, attached at the top of the corolla tube; anther pairs medifixed, extrorse, 3.0 × 0.6 mm at the broadest, connective prolonged in a short 0.3 mm long blunt tip. *Staminodes* 5, alternate with respect to petals and stamens, 3.9 × 1.8 mm, densely villous with up to ca. 2 mm long trichomes, carnose, connivent and concealing the ovary. *Ovary* glabrous, conical, slightly 5-lobed at base, 2.1 mm in diameter at base, 2.8 mm high, with 5 ovules, style 10 mm long, 0.6 mm diameter, glabrous. *Fruit* unknown.

Etymology. – This species honors Chris Birkinshaw, of the Missouri Botanical Garden's Madagascar Program, who collected the type specimen, in recognition of his dedication to the conservation of the Malagasy flora and the training of national botanists.

Distribution, ecology and phenology. – *Capurodendron birkinshawii* is only known from the type collection, collected in the Anosy region of southwestern Madagascar, in or near Andohahela National Park (Fig. 7). Although coordinates were taken with a GPS, they were attributed to all of the collections sampled by Chris Birkinshaw and his team on that day. It is thus unlikely that they represent the exact location of the tree sampled, but rather that of the team's camp site or the central

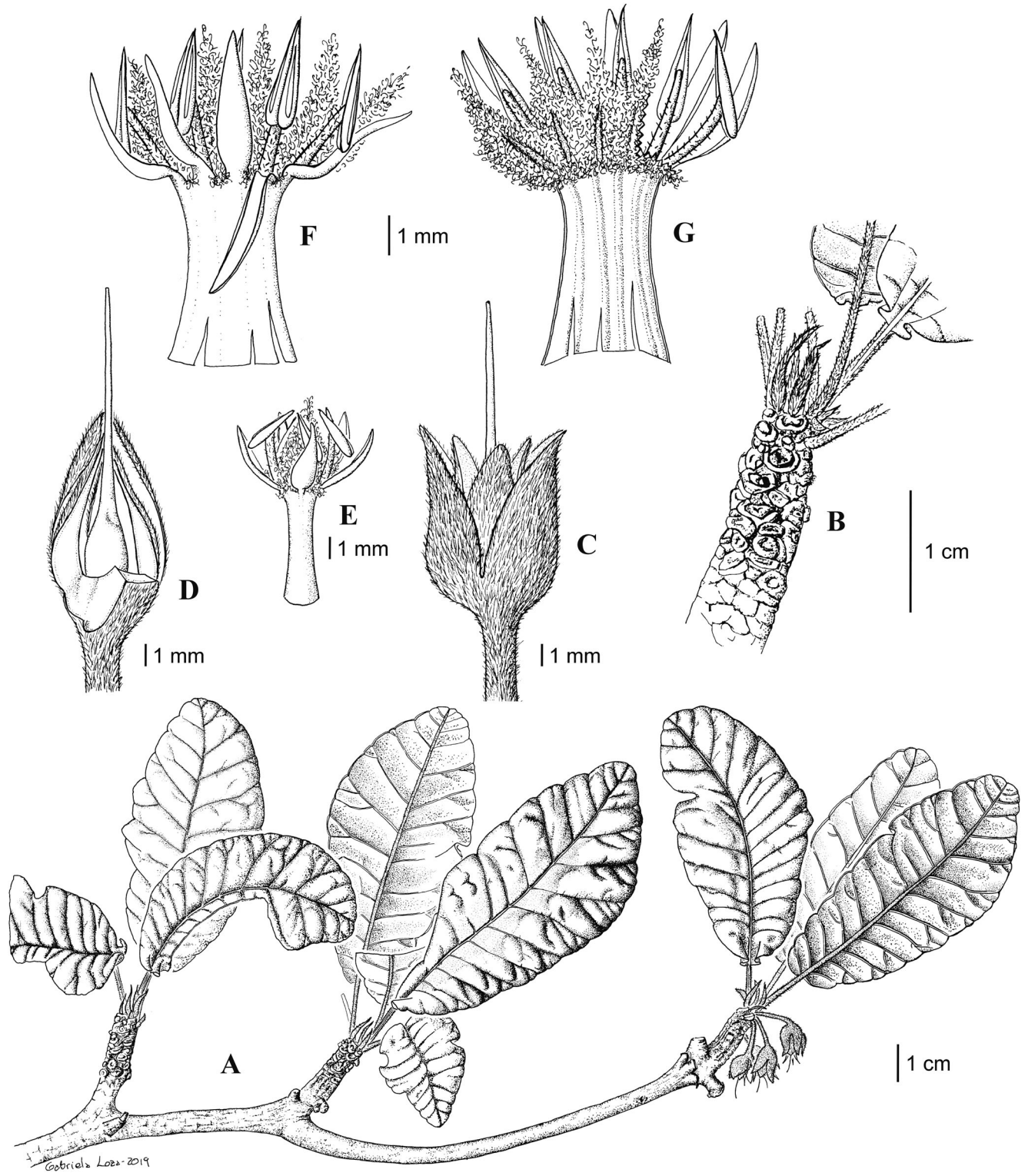

Fig. 9. *Capurodendron birkinshawii*. **A**, Flowering branch showing the characteristic Aubréville branching pattern; **B**, Brachyblast detail; **C**, Calyx; **D**, Flower with two calyx lobes and corolla removed showing ovary; **E**, Outer side of a detached corolla spread and opened with a lobe folded down showing a stamen; **F**, Inner side of a detached corolla spread and opened. — Drawing: Gabriela Loza.

locality for all the collections made that day (C. Birkinshaw, pers. comm.). These coordinates are ca. 500 m east of the limit of Parcel 2, near its southeastern corner. Phytogeographically, this site is located in the extreme southeast of the Southern Domain (sensu Humbert, 1955), amidst a sharp climatic gradient between a subarid climate and a perhumid climate, the latter being prevalent only 5–10 km to the east, in the rainforests of Parcel 1 of Andohahela protected area, at the extreme south of the Eastern Phytogeographic Domain. The one existing collection came from a small tree 4 m high and 16 cm DBH, presumably deciduous, growing in an environment with thicket and riverine forest. It was collected in May and bears old flowers, so flowering probably occurred in late April.

Conservation status. – With an AOO of 4 km^2, an EOO estimated to be less than 100 km^2 (both qualifying for CR under criterion B); only one known location, possibly outside the Andohahela Parcel 2 protected area; being in a region where uncontrolled fires are a serious hazard to natural vegetation; and bearing the observation "rare" on the type label for the single collection, *Capurodendron birkinshawii* is preliminarily assessed as Critically Endangered (CR, B1ab(i,ii,iii,v)+2ab(i,ii,iii,v), IUCN, 2012). As discussed above, a recent search in suitable environments around the type locality failed to locate individuals belonging to the species, suggesting it may be extinct. However, we refrain to attribute a CR (PE) because it is our belief that the species may be found again with deeper investigation.

Notes. – Based on vegetative characters, *Capurodendron birkinshawii* most closely resembles *C. nodosum*, a species endemic to the littoral and low-altitude dry forests on sands and laterite in the extreme northern Madagascar, in other words, some 1350 km to the north. The differences between the two species are presented in the diagnosis. *Capurodendron antongiliense*, a species likewise only known from its type specimen, which was collected in lowland moist evergreen forest approximately 1000 km to the north, also has bullate leaves with villous veins on the underside, but it has larger stipules, the base of the blade is inserted on the petiole to form a clear acute angle, and the pedicels are longer.

Capurodendron naciriae L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Antsiranana: Reg. SAVA, Lac Sahaka, forêt dense sèche caducifoliée, sur sables, 13°04′45″S, 49°54′12″E, 30 m, 27 Nov 2013, fl. fr., *Gautier & al. 6036* (G barcode G00406698!; isotypes: K barcode K001368950!, MO No. 6956137!, P barcode P01155611!, S Nos. S15-27728! & S15-27729!, TAN [no barcode attributed]!).

Figs. 10A–C, 11

Diagnosis. – *Capurodendron naciriae* resembles *C. ludiifolium* in its vegetative characters, especially the size and venation pattern of its leaves. It differs however by its smaller fruits (15–18 × 9–11 vs. 28–38 × 15–21 mm) that are ovoid (vs. elliptic), its larger calyx lobes, at least at fruiting stage, and its distinctly petiolate leaves (vs. subsessile).

Description. – *Small tree*, up to 12 m tall, 25 cm DBH, with white latex. *Ultimate twigs* 1–2 mm in diam., with leaves mainly on the apical portion. Apex of recent shoots densely pubescent with ferruginous trichomes, soon glabrescent, light grey in color, then darker. Twig bark longitudinally wrinkled, rugose. Stipules inconspicuous or lacking. *Leaves* probably caducous; petiole short, 2–5 mm long, up to 1.2 mm wide, pubescent in young leaves, then glabrous. Leaf blade coriaceous, spathulate to obovate, broadest at 4/5 of the leaf length, and from that point almost straight to the acute base, 30–60 × 10–25 mm, apex rounded; glabrous when mature, sometimes with a few trichomes near the base on the lower surface; base decurrent into the petiole; margin entire, faintly thickened; primary vein slightly prominent on the upper surface, much more distinctly below, glabrous on the upper surface, glabrous or slightly pilose on the lower surface, especially near the petiole; secondary venation almost indistinct from the tertiary veins, forming an angle of ca. 30° with the midrib, straight but forked distally a few millimeters from the margin and intermingled with the reticulate tertiary venation; tertiary venation forming elongated polygons. Venation clearly raised above and below on herbarium specimens but not on fresh material. *Flowers* in pairs above the lowest leaves or above the scar of fallen previous season's leaves, with three to four 0.5 mm long scale-like bracts at base of the pedicel, bearing a caducous ferruginous pubescence; flowering pedicels straight, 4.5–7.5 × 0.5–0.9 mm, loosely adpressed-pubescent with brownish trichomes. *Sepals* 5, quincuncial, almost circular, apex rounded to obtuse; the two outer ones 3.0–3.5 mm in diam., convex, brown-villous outside, glabrous inside, the three inner ones 2.8–3.0 mm in diam., densely brown-villous outside except for a glabrous scarious margin, glabrous inside and ciliolate on the margin. *Corolla* gamopetalous with 5 lobes, greenish cream when fresh; tube 2.3 mm long, glabrous, except below staminodes on the outer side; lobes narrowly lanceolate, glabrous, 4.0–4.2 × 1.6–1.8 mm, spreading at anthesis, the distal part enfolding the anther. *Stamens* 5, filaments conical, 3.0 mm long, 0.8 mm broad at base, villous on the outer side, attached at the top of the corolla tube; anther pairs medifixed, extrorse, 2.7 × 1.2 mm at the broadest when fresh (1.6 × 0.8 mm when dry), connective prolonged in a short 0.3 mm mucro. *Staminodes* 5, alternate with respect to petals and stamens, 3–3.9 × 1.9–2.1 mm, densely villous with golden trichomes outside, as well as inside except in the median part, carnose, connivent and concealing the ovary, triangular, and prolonged by a linear apex 1.5–1.8 mm long, curved up and adnate to the style. *Ovary* 5-celled, 0.8–1 mm high × 1.2–1.7 mm broad, densely hirsute with brownish trichomes, with 5 ovules, style 7.7–9.3 mm long, 0.3 mm diameter, glabrous, greenish. *Fruit* with a pedicel the same length as in flower but thicker, up to 2.5 mm in diameter, glabrous; sepals persistent, thicker and slightly bigger than in flower; body of the fruit greenish with a reddish tinge, ovoid, 15–18 mm long, 9–11 mm in diameter, with a persistent style; seeds with chestnut brown testa, 13 × 6 × 5.5 mm, obovoid with an acute base, slightly compressed laterally, faintly

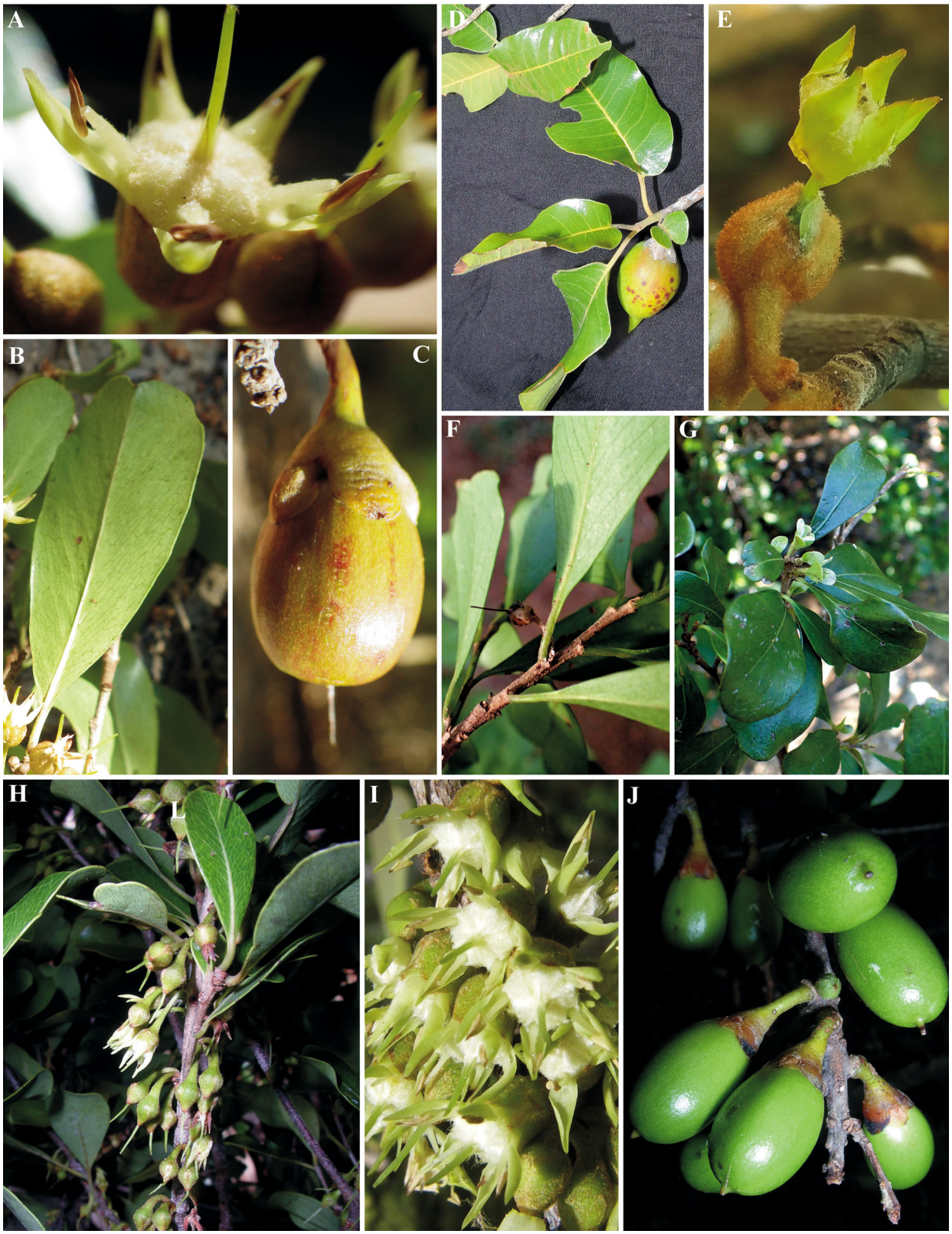

Fig. 10. *Capurodendron naciriae*: **A**, Flower; **B**, Leaf; **C**, Fruit (*Gautier 6036*). *C. oblongifolium*: **D**, Branch with fruits (*Randrianaivo 3349*); **E**, Corolla being expulsed by the calyx contraction (Frank Rakotonasolo, not collected). *C. randrianaivoi*: **F**, Underside of a leaf with remains of a flower (*Randriarisoa 25*); **G**, Twig with mature and growing leaves (*Randriarisoa 50*). *C. sakarivorum* L.Gaut. & Boluda: **H**, Flowering branch (*Nusbaumer 1510*); **I**, Flower clusters (*Ranirison 1095*), **J**, Immature fruits (*Nusbaumer 1902*). — Photos: A–C by Laurent Gautier; D by Richard Randrianaivo; E by Frank Rakotonasolo; F & G by Aina Randriarisoa; H–J by Louis Nusbaumer.

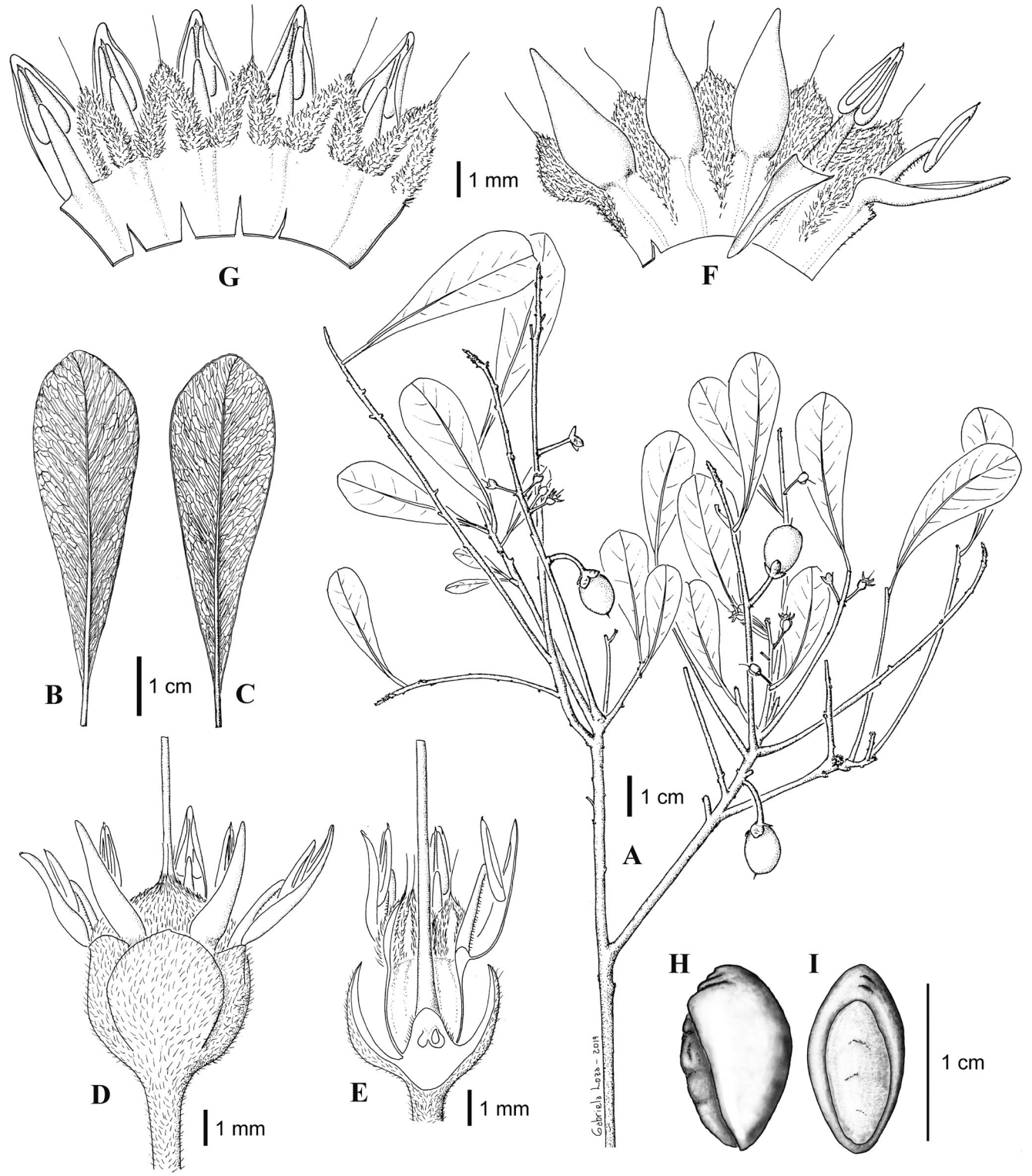

Fig. 11. *Capurodendron naciriae*. **A**, Branch with flowers and fruits; **B**, Leaf (upper surface); **C**, Leaf (lower surface); **D**, Flower; **E**, Flower in longitudinal section; **F**, Outer side of a detached corolla spread and opened with a lobe folded down showing a stamen; **G**, Inner side of a detached corolla spread and opened; **H**, Lateral view of a seed; **I**, ventral view of a seed. — Drawing: Gabriela Loza.

keeled, with a basiventral scar 10 × 4.5 mm covering ca. 1/4 of the seed surface.

Etymology. – This species is dedicated to our colleague and friend Yamama Naciri of the Conservatoire et Jardin botaniques de la Ville de Genève, who was part of the collecting team and is deeply involved in our present efforts to resolve Malagasy Sapotaceae taxonomy and systematics by providing invaluable knowledge in population genetics and molecular phylogeny.

Distribution, ecology and phenology. – *Capurodendron naciriae* is only known from northern Madagascar from: the littoral dry forest on sand at Analabe, near Lac Sahaka; the dry deciduous forest of Bobankora and Bekaraoka, 20 km inland; and forest remnants a few kilometers northwest of Vohémar (Fig. 7). Flowers were observed from October to January, and fruit in November.

Conservation status. – With an EOO of 488 km^2 and an AOO of 24 km^2 (both values qualifying for EN under criterion B), *Capurodendron naciriae* is only known from four locations with respect to most plausible threat, which is habitat destruction due to uncontrolled forest fires, and one location is outside the protected area network. Continuing decline is projected due to habitat destruction for the location outside of protected areas and to selective logging for all locations. *Capurodendron naciriae* is preliminarily assessed as Endangered (EN, B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v), IUCN, 2012).

Notes. – Specimens of *Capurodendron naciriae* belong to a group of collections from northern dry forests that have been variously attributed to *C. ludiifolium* or *C. ankaranense*. The latter species is restricted to inland sites on limestone substrate, whereas *C. ludiifolium* is clearly restricted to eastern lowland humid forests (sublittoral or inland). *Capurodendron naciriae* has leaves that are the most similar to those of *C. ludiifolium*, with secondary and tertiary veins that are almost indistinct and parallel to each other, forming an acute angle with midrib, slightly raised on upper leaf surface when dry, as in several species of *Ludia* (Salicaceae). However, although both species can be found on coastal sand, they are clearly different genetically and geographically (>300 km separate them). Flowers of *C. ludiifolium* being still unknown, the most reliable characters to separate them are fruit and fruiting sepal size and shape. Vegetatively, *C. naciriae* has short but evident petioles, whereas the leaves of *C. ludiifolium* are nearly sessile. The other Northern specimens misidentified as *C. ludiifolium* have secondary venation that is usually distinct from the tertiary venation, and these are described here under *C. randrianaivoi* and *C. sakarivorum*.

Paratypes. – MADAGASCAR, Prov. Antsiranana, Reg. SAVA, 40 km N of Vohémar, near Lac Sahaka, Analabe littoral forest on sand, alt. 50 m, 3 Dec 2004, *Manjakahery 49* (MO, P, TAN, TEF); Ibid., alt. 20 m, 3 Nov 2002, *McPherson 18853* (G, MO, P, TEF); Ibid., May 2004, *Rabehevitra 940* (G, MO, P, TEF); Ibid., alt. 5 m, 5 Nov 2002, *Rabenantoandro 1128* (G, MO, P, TEF); Ibid., alt. 18 m, 10 Oct 2000, *Randrianarivelo 149* (G, MO, P, TAN); Daraina, Forêt du Mont Ambararata Nord, sur crête, alt. 14 m, 5 Oct 2013, *Andriamiarinoro 395* (G, MO, P, TAN); Daraina, Antsahalalina, part of Bobankora Range, 12 km E (100°) of Daraina, 19 Jan 1991, *Meyers 239* (G, MO, P); Vestiges de forêt entre Belinta et Ambatrabe, au N.W. de Vohémar (au sud de Maintialaka), Dec 1966, *Service Forestier 27345* (G, P, TEF).

Capurodendron oblongifolium (Lecomte) L.Gaut. & Boluda, **comb. & stat. nov.** ≡ *Sideroxylon perrieri* var. *oblongifolium* Lecomte in Bull. Mus. Natl. Hist. Nat. 25: 272. 1919 – **Lectotype (designated here):** MADAGASCAR. Prov. Mahajanga: Reg. Boeny, environs du Mt. Tsitondroina, Oct 1903, old fl., *Perrier de la Bâthie 1105* (P barcode P04535203!; isolectotypes: P barcodes P04535201!, P04535202!, P04535206!).

Figs. 10D,E, 12

Description. – *Treelet*, 2–6 m tall, up to 10 cm DBH, bark grey and rough, slash with white latex. Terminal branches 2–4 mm in diam., tomentose with rusty to brown trichomes; 2-year twigs becoming glabrous and dark grey to dark brown, longitudinally wrinkled and sometimes with transversal cracks, sometimes with elongated lenticels. Brachyblasts absent. Stipules early caducous, narrowly triangular, 2.5–4 mm length, keeled, tomentose outside, glabrous inside. *Leaves* caducous; petiole 6–26 mm long, up to 1.5 mm wide, tomentose, semiterete with upper side flat to slightly grooved. Leaf blade coriaceous, from oblong to slightly ovate, broadest in the middle 3.5–8.0 × 2.0–4.5 cm; early glabrous on upper surface except for the main veins, tomentose on lower surface; base truncate to slightly cordate, frequently asymmetrical, apex rounded to obtuse, margin entire, often drying undulate; primary vein prominent on both surfaces, especially below, tomentose on both surfaces with rusty brownish trichomes; 7–12 pairs of weakly brochidodromous secondaries forming an angle of 45°–60° with midrib, straight at first then arching near the margin and often reaching it, raised on lower surface only; intersecondaries sometimes present, starting from the external angle of a secondary vein and dissolving halfway to the margin; tertiary venation faint, reticulate and making regular polygons, partially hidden by pubescence on lower surface. *Flowers* in clusters of 1–3, among the leaves on current year's shoots; flowering pedicels 6–10 × 0.8–1.6 mm, tomentose. *Sepals* 5, quincuncial, almost circular, apex rounded, glabrous inside and tomentose outside; the two outer ones 6.4 × 6.4 mm, the three inner ones 4.8 × 4.4 mm. *Corolla* gamopetalous with 5 lobes, whitish to pale yellow, glabrous; tube 2.2–2.6 mm long; lobes ovate to rounded, 3.2 × 3.2 mm, erect and overlapping at anthesis. *Stamens* 5, filaments villous, 0.8 × 0.2 mm, attached at the top of the corolla tube; anther pairs medifixed, extrorse, 2.1 × 0.6 mm at the broadest; connective sparsely pubescent between anthers on outer side, prolonged into a 0.6 mm mucro. *Staminodes* 5, alternate with respect to petals and stamens, broadly ovate, 1.8 × 1.3 mm, coriaceous, densely villous outside throughout with trichomes 0.6 mm, glabrous on inner side except on the margins, connivent and concealing

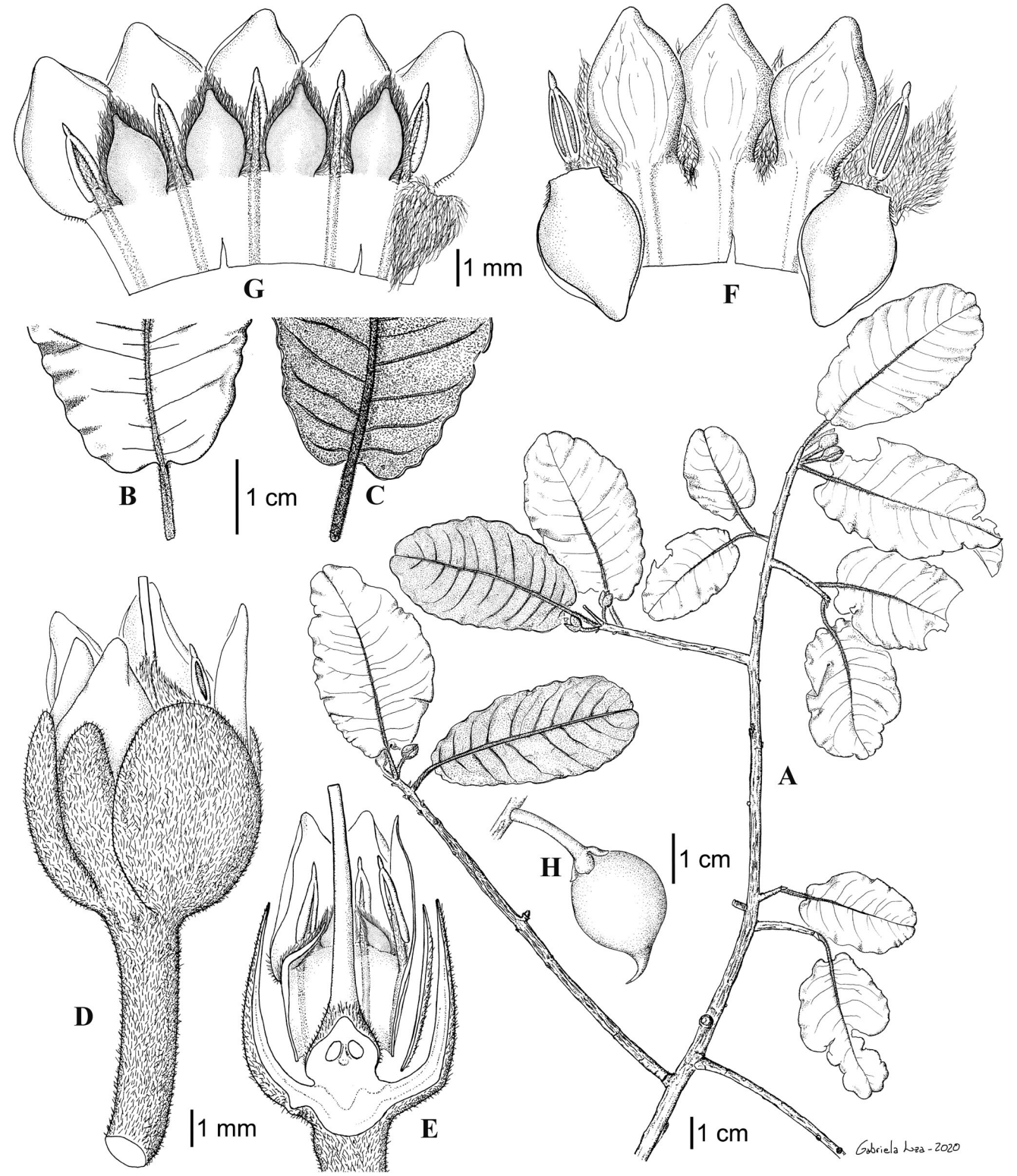

Fig. 12. *Capurodendron oblongifolium*. **A**, Branch with flower buds; **B**, Leaf (upper surface); **C**, Leaf (lower surface); **D**, Flower; **E**, Flower in longitudinal section; **F**, Outer side of a detached corolla spread and opened with two lobes folded down showing the stamens; **G**, Inner side of a detached corolla spread and opened, with a staminode folded down; **H**, Fruit. — Drawing: Gabriela Loza.

the ovary. *Ovary* 5-lobed, 1.5 mm high × 1.5 mm broad, densely hirsute with rusty brown trichomes, with 5 uniovulate locules; style 4.0 × 0.5 mm, 0.8 mm diameter near ovary, glabrous, stigma inconspicuous. *Fruit* on an enlarged 8–15 × 2.5–3 mm pedicel, with a persistent enlarged (ca. 2×) calyx, obpyriform to globose, with the apex attenuated in a beak merging in the persistent style, 30–40 × 20 mm, glabrescent. Seeds (immature, probably flattened by desiccation) 1(–2?) per fruit; ovate, 18 × 13, seed scar basiventral, 11 × 10 mm.

Distribution, ecology and phenology. – *Capurodendron oblongifolium* is known from a limited number of collections from the Boeny and Sofia regions in former Mahajanga Province, western Madagascar, where it occurs in dry deciduous forests on sandstone and limestone (Fig. 7). It flowers from October to December and fruits from December to March.

Conservation status. – The EOO of *Capurodendron oblongifolium* is estimated to be 2024 km^2 and the AOO 24 km^2 (both values qualifying for EN under criterion B); the species is documented from five locations with respect to the most plausible threat, which is habitat destruction due to uncontrolled forest fires, one location being outside the protected area network. With low values in AOO and EOO, and with one location outside the protected area network in a region regularly impacted by forest fires, continuing decline is projected and the species is preliminarily assessed as Endangered (EN, B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v), IUCN, 2012).

Notes. – *Capurodendron oblongifolium* and *C. perrieri* have many morphological features in common, including habit, leaf size, petiole and pedicel lengths, and pubescence of vegetative parts, and the two species are found in similar habitats. Based on the type specimen alone, the former was originally described as a variety of the latter, but this variety was not recognized as distinct by Aubréville (1974). Further collections and genetic analysis have clearly demonstrated that they are two different species. In the phylogeny, *C. oblongifolium* is not sister to *C. perrieri*, but to the third species of the clade, *C. pervillei*, which is clearly morphologically distinct (Boluda & al., 2021). *Capurodendron oblongifolium* is not sympatric with *C. perrieri*, but instead with *C. pervillei*, and its entire range is included within that of *C. pervillei*. *Capurodendron oblongifolium* differs from *C. perrieri* by the merosity of its corolla and ovary (pentamerous vs. hexamerous to heptamerous), its rounded (vs. lanceolate) corolla lobes, the shape of its staminodes (broadly ovate vs. lanceolate), its glabrous fruits (vs. pubescent), and the shape of its leaf blade base (truncate to subcordate vs. acute in *C. perrieri*).

Other specimens. – MADAGASCAR. Prov. Mahajanga, Reg. Sofia: Bongolava, c. 6 km NW of Boriziny (Port Bergé), alt. 185 m, 18 Mar 2010, *Rakotonasolo 1601* (G, MO, TAN); Tsiningia, Marosely, 18 km au Sud de Boriziny, forêt dense sèche de Bongolava, sur un substrat calcaire, alt. 217 m, Nov 2004, *Ramananjanahary 51* (G, MO, P, TEF); Boriziny, Mampikony, Bongolava, Betaramahamay, forêt sèche sur sable d'Ambohimanga, alt. 232 m, 6 Dec 2004, *Razakamalala 1809* (G, MO, P, TEF); Reg. Boeny: Ambato Boeny, Bevazaha, piste dans la réserve naturelle n° 7, 6 Dec 2011, *Andrianaivoravelona 524* (MO, TAN); District de Marovoay, Commune de Marosakoa, Fokontany d'Ampijoroa, Circuit Baobaba, Ankarafantsika AP, forêt dense sèche caducifoliée, alt. 165 m, 25 Feb 2019, *Randrianaivo 3349* (MO, P, TAN).

Capurodendron randrianaivoi L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Antsiranana: Reg. DIANA, Andrafiabe, Ambolobozokely. Forêt d'Anjialava, à 17 km à l'Est d'Andrafiabe, 12°26′19″S, 049°31′14″E, 10 m, 14 Feb 2006, fl., *Richard Randrianaivo & al. 1359* (G barcode G00390293!; isotypes: CNARP, MO No. 6214816!, P barcode P04568837!, TAN!).
Figs. 10F,G, 13

Diagnosis. – *Capurodendron randrianaivoi* is vegetatively similar to *C. sakarivorum*, but differs by its leaf blade length/petiole length ratio of 7–14 (vs. 2–5), its secondary and tertiary veins that have the same green color as the lamina in living specimens (vs. pale green), its usually lower number of secondaries (5–11 vs. 9–13), its staminodes that are glabrous in the central part of their outer side (vs. pubescent), and its beaked fruit with ridges (vs. non-beaked and without ridges).

Description. – *Small tree*, 5–9 m tall, 25 cm DBH, with white latex. Ultimate twigs 1–2 mm in diam., with leaves more or less regularly spaced along most recent elongation; densely pubescent, with 0.3–0.5 mm pale and shiny trichomes. Twig bark usually pale grey, sometimes darker or brownish, longitudinally wrinkled, with inconspicuous lenticels. Twigs older than 3 years with transversal cracks. Brachyblasts absent. Stipules early caducous, linear to narrowly triangular, pubescent, ca. 1 mm long. *Leaves* caducous, petiole short, 2–7 mm long, up to 1.5 mm wide, more or less flattened, with the lamina decurrent on the distal portion, pubescent in developing leaves, soon glabrescent. Leaf blade coriaceous, from obovate to oblanceolate, broadest 2/3–3/4 of leaf length, 2.8–5.0 × 1.0–2.7 cm, soon glabrous, sometimes with a few scattered trichomes on lower surface, base acute, apex rounded or frequently emarginate, margin entire, faintly thickened, slightly involuted; primary vein slightly prominent on both surfaces, glabrous or sometimes with scattered trichomes on lower surface, especially near the petiole; 5–11 pairs of eucamptodromous secondaries forming an angle of 20°–45° with midrib, straight to arching up, forked the last millimeters before the margin and intermingled with the reticulate tertiary venation; intersecondaries sometimes present, merging with the tertiary venation after a few millimeters; tertiary venation reticulate, sparse, forming frequently incomplete polygons, which are variable in shape and size, commonly longitudinal, faintly raised on upper surface, more visible on lower one. *Flowers* solitary or in pairs, on current year's shoots; flowering pedicels 3–4 × 0.8–1.0 mm, densely pubescent. *Sepals* 5, quincuncial, broadly ovate, convex, apex obtuse, glabrous inside and densely pubescent outside; the two outer ones 3.4 × 3.4 mm, up to 0.8 mm thick; the three inner ones 2.5–2.9 mm × 1.9–2.2 mm. *Corolla* gamopetalous with 5

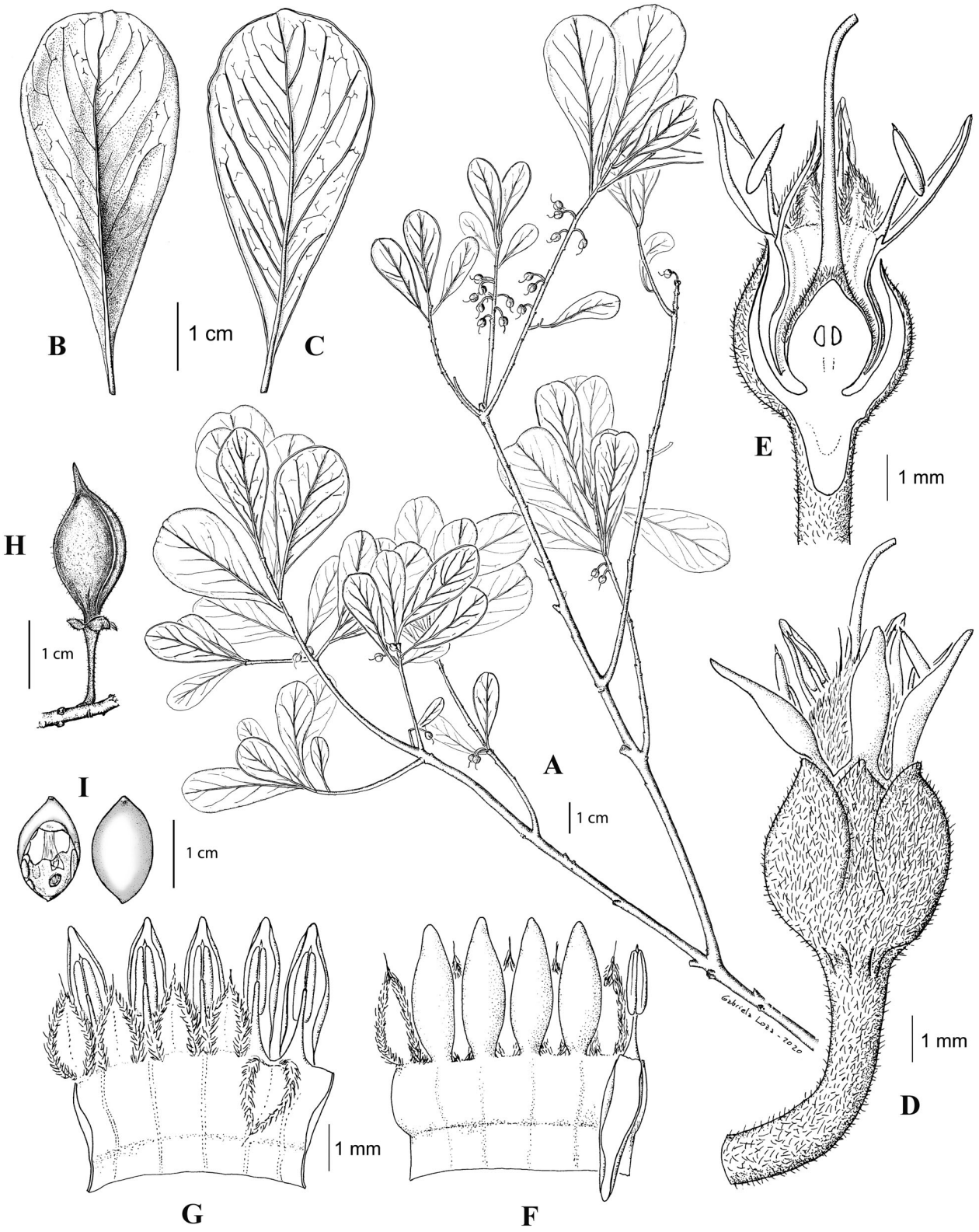

Fig. 13. *Capurodendron randrianaivoi*. **A**, Branch with old flowers; **B**, Leaf (upper surface); **C**, Leaf (lower surface); **D**, Flower; **E**, Flower in longitudinal section; **F**, Outer side of a detached corolla spread and opened with a lobe folded down showing the stamen; **G**, Inner side of a detached corolla spread and opened, with a staminode folded down; **H**, Fruit; **I**, Ventral and dorsal view of a seed. — Drawing: Gabriela Loza.

lobes, glabrous; tube 2.3–3.1 mm long; lobes lanceolate, 3.3 × 1.5 mm, spreading at anthesis. *Stamens* 5, filaments conical, glabrous, 1.6–2.0 mm long and 1.1 mm at base, attached at the top of the corolla tube; anther pairs medifixed, extrorse, 1.6 × 0.8 mm at the broadest, connective villous between the anthers on the outer side, prolonged in a 0.6 mm mucro. *Staminodes* 5, alternate with respect to petals and stamens, 2.5–2.9 × 1.4 mm, glabrous on both sides but densely villous on the margins, probably connivent and concealing the ovary. *Ovary* 5-lobed, 1.6 mm high × 1.9 mm broad, densely hirsute with beige trichomes in the upper half, with 5 uniovulate locules, style 5.4 mm long, 0.4 mm diameter, broader at base, glabrous, stigma inconspicuous. *Fruit* (probably not fully mature), on an elongated 11 mm pedicel, with a persistent and slightly enlarged calyx, ovate, slightly 5-ridged 23 × 11 mm, with a 5 mm beak. Seed solitary, ovate, slightly compressed laterally, 15 × 9 × 7 mm, testa shiny, scar basiventral, broadly ellipsoid, 12 × 7.5 mm, from bottom up to 3/4 of the height.

Etymology. – It is a pleasure to dedicate this species to our colleague and friend Richard Randrianaivo, of the Missouri Botanical Garden's Madagascar Program, who was the first to collect the species in flower, in recognition of his extensive knowledge of Sapotaceae, and in appreciation of the many fine moments we shared while collecting Sapotaceae in the field.

Distribution, ecology and phenology. – *Capurodendron randrianaivoi* is only known from the extreme north of Madagascar, in dry deciduous forest, including in littoral sites (Fig. 7). It flowers from December to February, and the only specimen in fruit was collected in December.

Conservation status. – *Capurodendron randrianaivoi* has an EOO of 26 km^2 (which falls within the values for a CR category under criterion B) and an AOO of 20 km^2 (qualifying for an EN category under criterion B). It is known from six collections representing two subpopulations corresponding to two locations with respect to the most serious threat, which is habitat destruction due to uncontrolled forest fires. Of the two locations, one is outside of the network of protected areas. Continuing decline can be predicted, and as its distribution can be considered severely fragmented, the species is preliminarily assessed as Critically Endangered (CR, B1ab(i,ii,iii,iv,v), IUCN, 2012).

Notes. – *Capurodendron randrianaivoi* has leaves similar to *C. sakarivorum* and *C. ankaranense*, but these species are genetically distant. Some leaf and especially flower characters mentioned in the diagnosis distinguish *C. randrianaivoi* from *C. sakarivorum*, whereas *C. ankaranense* can be differentiated by its much longer petioles (10–12 mm), and by its preference for limestone.

Paratypes. – MADAGASCAR. Prov. Antsiranana: Reg. DIANA, Commune: Ramena, Orangea, Baie des dunes, alt. 2 m, 18 May 2004, *Andrianjafy 428* (G, MO, P, TAN); Ibid., Mamelon vert, alt. 36 m, 17 Dec 2008, *Christian 27* (MO, P, TAN); Ibid., alt. 34 m, 17 Dec 2008, *Christian 32* (MO, P, TAN); Ibid., alt. 100 m, 24 Mar 2017, *Randriarisoa 50* (G, TEF); Baie de Rigny, Ampasimena, alt. 26 m, 21 Mar 2017, *Randriarisoa 25* (G, TEF).

Capurodendron sakarivorum L.Gaut & Boluda, **sp. nov.** – Holotype: MADAGASCAR. Prov. Antsiranana: Reg. SAVA, sous-préfecture de Vohémar, commune rurale de Daraina, forêt d'Ambohitsitondroina. Forêt dense sèche caducifoliée, 13°07.99′S, 49°28.72′, 255 m, 18 Jan 2006, fl., *Ranirison & Nusbaumer 1095* (G barcode G00090523!; isotypes: P barcode P04568827!, MO No. 5997389!, TEF!, Fanamby field station herbarium, Daraina [no barcode or accession number attributed]!).
Figs. 10H–J, 14

Diagnosis. – *Capurodendron sakarivorum* is vegetatively similar to *C. ankaranense* Aubrév., especially in leaf blade shape, dimension and venation, but differs by its stipules, which are lacking or scale-like, inconspicuous and pubescent (vs. linear, 2 mm long, and glabrescent), its shorter petiole (ratio leaf blade length/petiole length of 4.2–8 vs. 2–5), its villous sepals and pedicels (vs. glabrous or with rare scattered trichomes), and its staminodes with the outer side densely villous (vs. glabrous toward the middle).

Description. – *Small tree* up to 8 m tall, 12 cm DBH, with white latex, deciduous. *Ultimate twigs* 1–2.5 mm in diam., with leaves mainly on the 1- to 2-year-old branches. Apex of recent shoots pubescent, with golden-greyish trichomes, glabrescent, beige in color, then brownish. Twig bark longitudinally striated, with circular to ovate white-pruinose lenticels, and transversal cracks on 3-year twigs. Stipules inconspicuous and scale-like or lacking. *Leaves* caducous; petiole 4–9 mm long, 0.8 mm wide, glabrous or with scattered small trichomes. Leaf blade coriaceous, obovate, broadest at 2/3 of the leaf length, 20–50 × 10–22 mm, with an acute base and a rounded to emarginate apex; entirely glabrous when mature, sometimes with a few scattered trichomes on developing leaves; base shortly decurrent into the petiole; margin entire; primary vein prominent on both surfaces, 9–13 pairs of secondary veins distinct from the tertiary venation, forming an angle of 40°–50° with midrib, straight but forked distally in the last millimeters and intermingled with the tertiary venation; tertiary venation reticulate, forming polygons. Venation clearly raised above and below on herbarium specimens with young leaves, less so on older leaves, even and yellow on a green background on fresh material. *Flowers* among the lowest leaves or above the scar of previous year's leaves, fasciculate, up to 10 per node, with several 0.9 mm long scale-like pubescent bracts at the base of the pedicel; flowering pedicels curved downwards, 2.3–5.0 × 0.7 mm, densely pubescent with golden trichomes. *Sepals* 5, quincuncial, almost circular, apex rounded to obtuse; 2.3–3.1 mm in diam., convex, glabrous inside, golden-villous outside, densely so on the three inner ones. *Corolla* gamopetalous with 5 lobes, greenish cream when fresh; tube 2.3 mm long, entirely glabrous; lobes narrowly lanceolate, glabrous, 3.8 × 1.4 mm, spreading at anthesis, the distal half enfolding the anthers in the early stages of anthesis. *Stamens* 5, filaments conical,

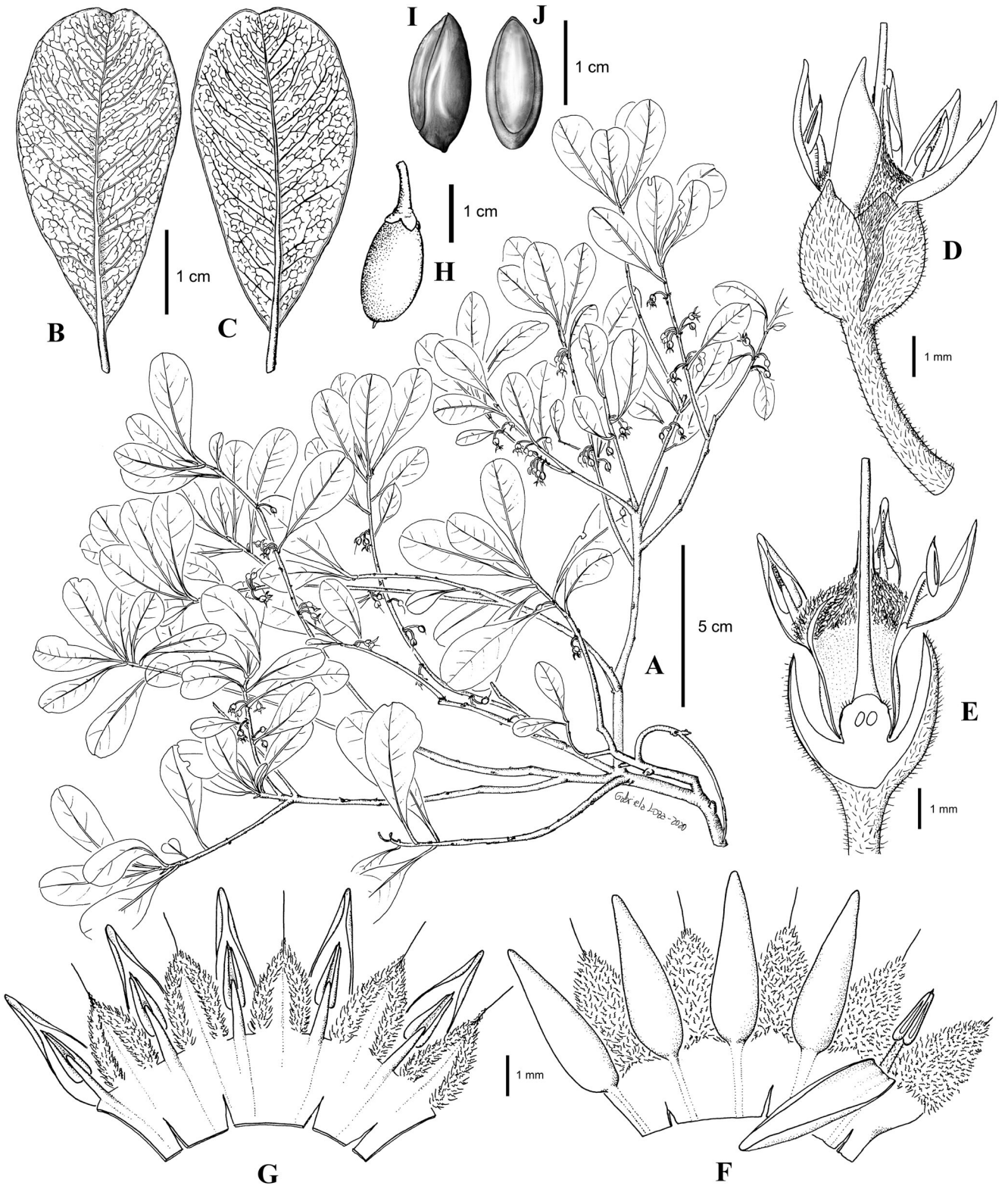

Fig. 14. *Capurodendron sakarivorum*. **A**, Branch with flowers; **B**, Leaf (upper surface); **C**, Leaf (lower surface); **D**, Flower; **E**, Flower in longitudinal section; **F**, Outer side of a detached corolla spread and opened with a lobe folded down showing a stamen; **G**, Inner side of a detached corolla spread and opened; **H**, Lateral view of a seed; **I**, ventral view of a seed. — Drawing: Gabriela Loza

1.5 mm long, 0.3 mm broad at base, villous on the outer side, attached at the top of the corolla tube; anther pairs cream, medifixed, extrorse, 1.6 × 0.5 mm at the broadest, connective prolonged in a short 0.3 mm mucro. *Staminodes* 5, alternate with respect to petals and stamens, 2.6 × 1.2 mm, densely villous with whitish trichomes outside, the central portion glabrous inside (but almost covered with the trichomes of the lateral portions), slightly carnose, connivent and concealing the ovary, triangular, and prolonged by a linear appendix 1.0 mm long curved up and adnate to the style. *Ovary* 5-lobed, 1.2 mm high × 1.5 mm broad, the lobes with long trichomes in their upper half, 5-celled, with 5 ovules, style 5.0–5.9 mm long, 0.3 mm diameter, glabrous, greenish. *Fruit* (almost mature, bright green), with a pedicel longer and thicker than in flower (10 × 1.5 mm, and up to 2.0 mm on the distal part), glabrous; sepals persistent, thicker and slightly bigger than in flower; the body of the fruit ovoid, 20 mm long, 10 mm in diameter, with a persistent style; seeds with a chestnut brown testa, 17 × 7 × 7 mm, obovoid, slightly compressed laterally, with a basiventral scar 10 × 6 mm covering ca. 1/4 of the seed surface.

Etymology. – This species is named after the Malagasy word "sakarivo", which means "blood brother" to honor Patrick Ranirison and Louis Nusbaumer, two former Ph.D. students at Antananarivo and Geneva Universities, respectively, who have both collected this new species. They worked hand in hand for three consecutive seasons in the forest fragments around the municipality of Daraina. They contributed greatly to our knowledge of the flora and vegetation of this area, and to the official recognition of the entire region as the Loky Manambato protected area. At the end of their field work together, they decided to sacralize their friendship through the traditional ceremony of becoming blood brothers.

Distribution, ecology and phenology. – *Capurodendron sakarivorum* is only known from northern Madagascar, in the deciduous forests of the Loky-Manambato protected area (previously Daraina), on laterite or sands (Fig. 7). Flowering recorded from January to February, fruiting starting in January.

Conservation status. – *Capurodendron sakarivorum* has an estimated EOO of 547 km^2 and an AOO of 20 km^2. These figures fall within the values for an EN category under criterion B. The species is documented from three locations with respect to the most plausible threat which is selective logging, including in a protected area. Insufficient protection is likely to lead to the continuing decline in the number of mature individuals; accordingly the species is preliminarily assessed as Endangered (EN, B1ab(v)+2ab(v), IUCN, 2012).

Notes. – *Capurodendron sakarivorum* was initially confused with *C. ankaranense*, a relatively distant species genetically, based on the similar size, shape and venation of the leaves, and because they both occur in dry deciduous forests in the north of the island. However, *C. ankaranense* grows on limestone, whereas *C. sakarivorum* has only been found to date on laterite or on sand. Close examination of the available collections reveals furthermore that the species are quite distinct in several aspects, as enumerated in the diagnosis.

Paratypes. – MADAGASCAR, Prov. Antsiranana, Reg. SAVA, Daraina, Antsahalalina, part of Bobankora Range, 12 km E (100°) of Daraina, 21 Jan 1991, *Meyers 246* (MO, P, TAN); Forêt d'Antsaharaingy, alt. 60 m, 28 Feb 2005, *Nusbaumer 1510* (G, MO, P, TEF); Forêt d'Ambohitsitondroina, alt. 70 m, 31 Oct 2005, *Guittou 184* (G, MO, P, TAN); Ibid., alt. 226 m, 8 Jan 2006, *Nusbaumer 1874* (G, TEF); Ibid., alt. 250 m, 12 Jan 2006, *Nusbaumer 1902* (G, P, TEF); Ibid., alt. 250 m, 5 Jan 2006, *Ranirison 1051* (G, P, TEF); Ibid., alt. 315 m, 16 Jan 2006, *Ranirison*, *1089* (G, MO, P, TEF).

■ AUTHOR CONTRIBUTIONS

All authors designed the research. CGB, YN and LG collected the samples. CGB conducted the laboratory work. CGB and CC analyzed the data with the supervision of YN. All authors interpreted the results. CGB wrote the manuscript with the supervision and participation of CC, YN and LG. — CGB, https://orcid.org/0000-0001-7922-8718; CC, https://orcid.org/0000-0003-0517-4731; YN, https://orcid.org/0000-0001-6784-8565; LG, https://orcid.org/0000-0003-4157-3713

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Appendix 1. Information on the specimens used. Original identification in bold face, followed by country of origin, collection year, collector and number, nature of sample (if sampled on a herbarium specimen: herbarium code, if sampled in the field then "Silica gel" linked to an herbarium voucher in herb. G), and BioSample number.

Bemangidia aff. ***lowryi*** L.Gaut., Madagascar, 2011, *Gautier 5790*, Silica gel, SAMN17141888. ***Bemangidia*** aff. ***lowryi***, Madagascar, 2007, *Razakamalala 3976* (G), SAMN17141889. ***Capurodendron androyense*** Aubrév., Madagascar, 2017, *Gautier 6343*, Silica gel, SAMN17141906. ***Capurodendron androyense***, Madagascar, 2017, *Gautier 6376*, Silica gel, SAMN17141892. ***Capurodendron androyense***, Madagascar, 2017, *Randrianaivo 2954*, Silica gel, SAMN17141913. ***Capurodendron androyense***, Madagascar, 2004, *Rogers 474* (G), SAMN17141850. ***Capurodendron ankaranense*** Aubrév., Madagascar, 1951, *Humbert 25489* (Type) (G), SAMN17141846. ***Capurodendron ankaranense***, Madagascar, 2016, *Gautier 6241*, Silica gel, SAMN17141911. ***Capurodendron ankaranense***, Madagascar, 2017, *Randriarisoa 40*, Silica gel, SAMN17141776. ***Capurodendron ankaranense***, Madagascar, 1954, *RN 6118* (P), SAMN17141886. ***Capurodendron ankaranense***, Madagascar, 1958, *SF 18545* (G), SAMN17141939. ***Capurodendron apollonioides*** Aubrév., Madagascar, 1953, *SF 8672* (P), SAMN17141941. ***Capurodendron apollonioides***, Madagascar, 1964, *SF 21804* (P), SAMN17141884. ***Capurodendron bakeri*** (Scott Elliot) Aubrév., Madagascar, 2017, *Gautier 6390*, Silica gel, SAMN17141779. ***Capurodendron costatum*** Aubrév., Madagascar, 1952, *Leandri 2038* (G), SAMN17141844. ***Capurodendron costatum***, Madagascar, 2012, *Gautier 5864*, Silica gel, SAMN17141868. ***Capurodendron delphinense*** Aubrév., Madagascar, 2011, *Gautier 5801*, Silica gel, SAMN17141867. ***Capurodendron delphinense***, Madagascar, 2007, *Ramison 471* (G), SAMN17141781. ***Capurodendron delphinense***, Madagascar, 2006, *Randriatafika 722* (G), SAMN17141782. ***Capurodendron gracilifolium*** Aubrév., Madagascar, 2011, *Gautier 5736*, Silica gel, SAMN17141915. ***Capurodendron gracilifolium***, Madagascar, 2017, *Randrianaivo 2972*, Silica gel, SAMN17141943. ***Capurodendron gracilifolium***, Madagascar, 1998, *Messmer 607* (G), SAMN17141920. ***Capurodendron greveanum*** Aubrév., Madagascar, 1997, *Jongkind 3623* (G), SAMN17142036. ***Capurodendron greveanum***, Madagascar, 2017, *Randriarisoa 28*, Silica gel, SAMN17141784. ***Capurodendron greveanum***, Madagascar, 2000, *Ranaivojaona 267* (G), SAMN17141786. ***Capurodendron greveanum***, Madagascar, 2017, *Randrianaivo 2974*, Silica gel, SAMN17141785. ***Capurodendron ludiifolium*** Aubrév., Madagascar, 2018, *Randrianaivo 3014*, Silica gel, SAMN17141975. ***Capurodendron ludiifolium***, Madagascar, 2018, *Randrianaivo 3063*, Silica gel, SAMN17141972. ***Capurodendron ludiifolium***, Madagascar, 2018, *Randrianaivo 3126*, Silica gel, SAMN17141973. ***Capurodendron ludiifolium***, Madagascar, 2018, *Randrianaivo 3162*, Silica gel, SAMN17141973. ***Capurodendron ludiifolium***, Madagascar, *SF s.n.* (P, P04609609), SAMN17141945. ***Capurodendron madagascariense*** (Lecomte) Aubrév., Madagascar, 1952, *SF 5407* (G), SAMN17141863. ***Capurodendron madagascariense***, Madagascar, 1956, *SF 16962* (P), SAMN17141946. ***Capurodendron madagascariense***, Madagascar, 1957, *SF 18033* (G), SAMN17141859. ***Capurodendron mandrarense*** Aubrév., Madagascar, 2004, *Andriamihajarivo 1532* (G), SAMN17141927. ***Capurodendron*** aff. ***mandrarense***, Madagascar, 2017, *Gautier 6329*, Silica gel, SAMN17141789. ***Capurodendron mandrarense***, Madagascar, 2017, *Gautier 6351*, Silica gel, SAMN17141797. ***Capurodendron mandrarense***, Madagascar, 2017, *Gautier 6356*, Silica gel, SAMN17141798. ***Capurodendron mandrarense***, Madagascar, 2002, *Phillipson 5603* (G), SAMN17141848. ***Capurodendron mandrarense***, Madagascar, 2005, *Randrianaivo 1187* (G), SAMN17141881. ***Capurodendron mandrarense***, Madagascar, 2017, *Randrianaivo 2956*, Silica gel, SAMN17141802. ***Capurodendron mandrarense***, Madagascar, 2017, *Randrianaivo 2980*, Silica gel, SAMN17141812. ***Capurodendron microphyllum*** (Scott Elliot) Aubrév., Madagascar, 2017, *Gautier 6382*, Silica gel, SAMN17141814. ***Capurodendron microphyllum***, Madagascar, 2017, *Gautier 6393*, Silica gel, SAMN17141815. ***Capurodendron microphyllum***, Madagascar, 1963, *SF 22411* (G), SAMN17141947. ***Capurodendron nanophyllum*** L.Gaut. & Naciri, Madagascar, 1968, *SF 28521* (Type) (G), SAMN17141852. ***Capurodendron nodosum*** Aubrév., Madagascar, 2017, *Randriarisoa 6*, Silica gel, SAMN17141817. ***Capurodendron nodosum***, Madagascar, 2017, *Randriarisoa 26*, Silica gel, SAMN17141938. ***Capurodendron perrieri*** (Lecomte) Aubrév., Madagascar, 1992, *Noyes 1044* (G), SAMN17141820. ***Capurodendron perrieri***, Madagascar, 2010, *Razakamalala 5177* (G), SAMN17141821. ***Capurodendron perrieri***, Madagascar, 2003, *Randrianaivo 969* (G), SAMN17141882. ***Capurodendron perrieri***, Madagascar, 2017, *Randrianaivo 2968*, Silica gel, SAMN17141810. ***Capurodendron perrieri***, Madagascar, 2017, *Randrianaivo 2976*, Silica gel, SAMN17141819. ***Capurodendron perrieri*** var. ***oblongifolium*** Lecomte, Madagascar, 2015, *Rakotonasolo 1601* (G), SAMN17141818. ***Capurodendron perrieri*** var. ***oblongifolium***, Madagascar, 2004, *Ramananjanahary 51* (G), SAMN17141822. ***Capurodendron perrieri*** var. ***oblongifolium***, Madagascar, 2004, *Razakamalala 1809* (G), SAMN17141823. ***Capurodendron pervillei*** (Engl.) Aubrév., Madagascar, 2005, *Labat 3557* (G), SAMN17141847. ***Capurodendron pervillei***, Madagascar, 2004, *Ramananjanahary 244* (G), SAMN17141928. ***Capurodendron pervillei***, Madagascar, 2004, *Razakamalala 1677* (G), SAMN17141929. ***Capurodendron pervillei***, Madagascar, 2013, *Randrianaivo 2397* (G), SAMN17141824. ***Capurodendron rubrocostatum*** (Jum. & H.Perrier) Aubrév., Madagascar, 2005, *Andriamihajarivo 782* (P), SAMN17141956. ***Capurodendron rubrocostatum***, Madagascar, 2012, *Gautier 5936*, Silica gel, SAMN17141869. ***Capurodendron rubrocostatum***, Madagascar, 2012, *Luino 21* (G), SAMN17141845. ***Capurodendron sahafariense*** L.Gaut. & Naciri, Madagascar, 1954, *Rakotonandrasana 1207* (G), SAMN17141830. ***Capurodendron sahafariense***, Madagascar, 1993, *Ratovoson 1217* (Type) (G), SAMN17141831. ***Capurodendron sahafariense***, Madagascar, 1963, *SF 23087* (G), SAMN17141855. ***Capurodendron sakalavum*** Aubrév., Madagascar, 2004, *Gautier 4670* (G), SAMN17141826. ***Capurodendron sakalavum***, Madagascar, 2012, *Gautier 5825* (G), SAMN17141866. ***Capurodendron sakalavum***, Madagascar, 2015, *Gautier 6179* (G), SAMN17141912. ***Capurodendron*** aff.

Appendix 1. Continued.

schatzii L.Gaut. & Naciri, Madagascar, 2018, *Randrianaivo 3064*, Silica gel, SAMN17141971. ***Capurodendron suarezense*** Aubrév., Madagascar, 1997, *Andrianantoanina 1043* (MO), SAMN17141836. ***Capurodendron suarezense***, *Randrianasolo 632*, Madagascar, 2007 (MO), SAMN17141835. ***Capurodendron suarezense***, Madagascar, 1998, *Razafimandimbison 274* (MO), SAMN17141834. ***Capurodendron suarezense***, Madagascar, 2017, *Randriarisoa 36*, Silica gel, SAMN17141919. ***Capurodendron suarezense***, Madagascar, 2017, *Randriarisoa 46*, Silica gel, SAMN17141918. ***Capurodendron*** aff. ***tampinense*** (Lecomte) Aubrév., Madagascar, 2011, *Gautier 5780*, Silica gel, SAMN17141875. ***Capurodendron tampinense***, Madagascar, 2000, *Ludovic 719* (MO), SAMN17142037. ***Capurodendron tampinense***, Madagascar, 2018, *Randriarisoa 146*, Silica gel, SAMN17141983. ***Capurodendron tampinense***, Madagascar, 2018, *Randrianaivo 3089*, Silica gel, SAMN17141982. ***Capurodendron*** cf. ***tampinense***, Madagascar, 2018, *Randrianaivo 3095*, Silica gel, SAMN17142002. ***Capurodendron tampinense***, Madagascar, 1967, *SF 28059* (TEF), SAMN17141962. ***Capurodendron tampinense*** var. ***analamazaotrense*** Aubrév., Madagascar, 2018, *Randriarisoa 156*, Silica gel, SAMN17141983. ***Capurodendron tampinense*** var. ***analamazaotrense***, Madagascar, 2018, *Randriarisoa 161*, Silica gel, SAMN17141967. ***Capurodendron* sp. 1**, Madagascar, 2010, *Gautier 5520* (G), SAMN17142035. ***Capurodendron* sp. 4**, Madagascar, 2013, *Gautier 6036* (G), SAMN17141871. ***Capurodendron* sp. 4**, Madagascar, 2004, *Rabehevitra 940* (G), SAMN17141932. ***Capurodendron* sp. 4**, Madagascar, 1966, *SF 27345* (G), SAMN17141854. ***Capurodendron* sp. 5**, Madagascar, 2006, *Ranirison 1089* (G), SAMN17141948. ***Capurodendron* sp. 5**, Madagascar, 2006, *Ranirison 1095* (G), SAMN17141949. ***Capurodendron* sp. 5**, Madagascar, 2005, *Guittou 184* (G), SAMN17141921. ***Capurodendron* sp. 6**, Madagascar, 2018, *Randrianaivo 3175*, Silica gel, SAMN17141969. ***Capurodendron* sp. 9**, Madagascar, 1996, *Antilahimena 343* (G), SAMN17141833. ***Capurodendron* sp. 11**, Madagascar, 2010, *Gautier 5544*, Silica gel, SAMN17141873. ***Capurodendron* sp. 11**, Madagascar, 2013, *Gautier 6024*, Silica gel, SAMN17141876. ***Capurodendron* sp. 11**, Madagascar, 2018, *Randriarisoa 125*, Silica gel, SAMN17141984. ***Capurodendron* sp. 11**, Madagascar, 2018, *Randrianaivo 3012*, Silica gel, SAMN17141985. ***Capurodendron* sp. 11**, Madagascar, 2018, *Randrianaivo 3020*, Silica gel, SAMN17141988. ***Capurodendron* sp. 11**, Madagascar, 2018, *Randrianaivo 3049*, Silica gel, SAMN17141986. ***Capurodendron* sp. 11**, Madagascar, 2018, *Randrianaivo 3122*, Silica gel, SAMN17141987. ***Capurodendron* sp. 12**, Madagascar, 1997, *Birkinshaw 438* (G), SAMN17141829. ***Capurodendron* sp. 15**, Madagascar, 2005, *Razakamalala 2609* (G), SAMN17141828. ***Capurodendron* sp. 16**, Madagascar, 2005, *Ranirison 1029* (G), SAMN17141827. ***Capurodendron* sp. 19**, Madagascar, 1999, *Ratovoson 43* (P), SAMN17141959. ***Capurodendron* sp. 20**, Madagascar, 2016, *Gautier 6276*, Silica gel, SAMN17141910. ***Capurodendron* sp. 22**, Madagascar, 2010, *Gautier 5395*, Silica gel, SAMN17141872. ***Capurodendron* sp. 23**, Madagascar, 2004, *Andrianjafy 428* (G), SAMN17141930. ***Capurodendron* sp. 23**, Madagascar, 2017, *Randriarisoa 25*, Silica gel, SAMN17141840. ***Capurodendron* sp. 23**, Madagascar, 2017, *Randriarisoa 50*, Silica gel, SAMN17141841. ***Capurodendron* sp. 23**, Madagascar, 2006, *Randrianaivo 1359* (G), SAMN17141950. ***Capurodendron* sp. 24**, Madagascar, 2012, *Ramandimbimanana 260* (G), SAMN17141839. ***Donella fenerivensis*** Aubrév., Madagascar, 2018, *Randrianaivo 3081*, Silica gel, SAMN17141989. ***Donella fenerivensis***, Madagascar, 2018, *Randrianaivo 3091*, Silica gel, SAMN17141990. ***Faucherea*** aff. ***parvifolia*** Lecomte, Madagascar, 2018, *Randriarisoa 140*, Silica gel, SAMN17141991. ***Faucherea*** aff. ***parvifolia***, Madagascar, 2018, *Randrianaivo 3097*, Silica gel, SAMN17142003. ***Faucherea* sp.**, Madagascar, 2018, *Randrianaivo 3068*, Silica gel, SAMN17141996. ***Inhambanella guereensis*** (Aubrév. & Pellegr.) T.D.Penn., Ivory Coast, 1968, *Aké Assi 10149* (G), SAMN17142023. ***Inhambanella henriquezii*** (Engl. & Warb.) Dubard, Zimbabwe, 1962, *Goldsmith 176/62* (G), SAMN17142024. ***Inhambanella henriquezii***, Zimbabwe, 1962, *Goldsmith 178/62* (G), SAMN17142025. ***Isonandra compta*** Dubard, Sri Lanka, 1979, *Kostermans 27571* (G), SAMN17141901. ***Lecomtedoxa klaineana*** (Pierre ex Engl.) Dubard, Cameroun, 2008, *Parmentier-Mambo 4803* (BRLU), SAMN17142027. ***Lecomtedoxa klaineana***, Cameroun, 2005, *Van der Burgt 727* (G), SAMN17142017. ***Mimusops capuronii*** Aubrév., Madagascar, 2013, *Gautier 6027*, Silica gel, SAMN17141870. ***Mimusops* sp.**, Madagascar, 2018, *Randrianaivo 3071*, Silica gel, SAMN17142032. ***Mimusops* sp.**, Madagascar, 2018, *Randrianaivo 3178*, Silica gel, SAMN17141976. ***Neolemonniera batesii*** (Engl.) Heine, Equatorial Guinea, 1997, *Lisowski M-580* (BRLU), SAMN17142030. ***Neolemonniera batesii***, Cameroun, 2000, *Tchouto 3001* (G), SAMN17142029. ***Sideroxylon gerrardianum*** (Hook.f.) Lecomte, Madagascar, 2018, *Randriarisoa 149*, Silica gel, SAMN17141896. ***Sideroxylon gerrardianum***, Madagascar, 2018, *Randrianaivo 3087*, Silica gel, SAMN17141895. ***Tsebona macrantha*** Capuron, Madagascar, 2010, *Gautier 5509*, Silica gel, SAMN17141890. ***Tsebona macrantha***, Madagascar, 2018, *Randrianaivo 3131*, Silica gel, SAMN17141970. ***Tsebona macrantha***, Madagascar, 2018, *Randrianaivo 3149*, Silica gel, SAMN17141902.

Appendix 2. Information on the specimens used for clades age estimation, with species name, country, collection year, collector code, and origin of the sample.

Baillonella toxisperma Pierre, Gabon, 1999, *Breteler* 14777, Randriarisoa & al., in prep. (G). ***Bemangidia*** aff. ***lowryi*** L.Gaut., Madagascar, 2011, *Gautier 5790*, this paper (G). ***Bemangidia*** aff. ***lowryi***, Madagascar, 2007, *Razakamalala 3976*, this paper (G). ***Capurodendron ludiifolium*** Aubrév., Madagascar, 2018, *Randrianaivo 3014*, this paper (G). ***Capurodendron ankaranense*** Aubrév., Madagascar, 2017, *Randriarisoa 40*, this paper (G). ***Capurodendron ankaranense*** Aubrév., Madagascar, 1958, *SF 18545*, this paper (G). ***Capurodendron madagascariense*** (Lecomte) Aubrév., Madagascar, 1952, *SF 5407*, this paper (G). ***Capurodendron madagascariense***, Madagascar, 1957, *SF 18033*, this paper (G). ***Capurodendron mandrarense*** Aubrév., Madagascar, 2004, *Andriamihajarivo 1532*, this paper (G). ***Capurodendron mandrarense***, Madagascar, 2017, *Gautier 6356*, this paper (G). ***Capurodendron microphyllum*** (Scott Elliot) Aubrév., Madagascar, 2017, *Gautier 6393*, this paper (G). ***Capurodendron nanophyllum*** L.Gaut. & Naciri, Madagascar, 1968, *SF 28521*, this paper (G). ***Capurodendron perrieri*** (Lecomte) Aubrév., Madagascar, 2017, *Randrianaivo 2976*, this paper (G). ***Capurodendron rubrocostatum*** (Jum. & H.Perrier) Aubrév., Madagascar, 2005, *Andriamihajarivo 782*, this paper (G). ***Capurodendron sahafariense*** L.Gaut. & Naciri, Madagascar, 1963, *SF 23087*, this paper (G). ***Capurodendron sakalavum*** Aubrév., Madagascar, 2004, *Gautier 4670*, this paper (G). ***Capurodendron suarezense*** Aubrév., Madagascar, 1997, *Andrianantoa 1043*, this paper (G). ***Capurodendron tampinense*** (Lecomte) Aubrév., Madagascar, 2018, *Randrianaivo 3089*, this paper (G). ***Capurodendron tampinense*** var. ***analamazaotrense*** Aubrév., Madagascar, 2018, *Randriarisoa 156*, this paper (G). ***Capurodendron* sp. 11** (= *C. aubrevillei* L.Gaut & Boluda sp. nov.), Madagascar, 2013, *Gautier 6024*, this paper (G). ***Capurodendron* sp. 11** (= *C. aubrevillei* sp. nov.), Madagascar, 2018, *Randrianaivo 3049*, this paper (G). ***Diploknema butyracea*** (Roxb.) H.J.Lam., India, 1974, *Dobremez 2591*, Christe & al., 2021 (G). ***Donella fenerivensis*** Aubrév., Madagascar, 2018, *Randrianaivo 3081*, this paper (G). ***Donella fenerivensis***, Madagascar, 2018, *Randrianaivo 3091*, this paper (G). ***Faucherea ambrensis*** Capuron ex Aubrév., Madagascar, 2006, *Gautier 5007*, Randriarisoa & al. in prep. (G). ***Faucherea laciniata*** Lecomte, Madagascar, 2018, *Randriarisoa 173*, Randriarisoa & al. in prep. (G). ***Gluema ivorensis*** Aubrév. & Pellegr., Liberia, 2014, *Jongkind 12344*, Christe & al., 2021 (G). ***Gluema korupensis*** Burgt., Cameroun, 2005, *Burgt 732*, Christe & al., 2021 (G). ***Inhambanella guereensis*** (Aubrév. & Pellegr.) T.D.Penn., Ivory Coast, 1968, *Aké Assi 10149*, this paper (G). ***Inhambanella henriquezii*** (Engl. & Warb.) Dubard, Zimbabwe, 1962, *Goldsmith 176/62*, this paper (G). ***Isonandra compta*** Dubard., Sri Lanka, 1979, *Kostermans 27571*, this paper (G). ***Labourdonnaisia madagascariensis*** Pierre ex Baill., Madagascar, 1952, *SF 4429*, Randriarisoa & al. in prep. (G). ***Labourdonnaisia revoluta*** Bojer., Mauritius, 2010, *Daffreville LR43*, Randriarisoa & al. in prep. (G). ***Labramia bojeri*** A.DC., Madagascar, 2011, *Gautier 5774*, Randriarisoa & al. in prep. (G). ***Labramia costata*** (M.M.Hartog ex Baill.) Aubrév., Madagascar, 2011, *Gautier 5752*, Randriarisoa & al. in prep. (G). ***Labramia platanoides*** Capuron ex Aubrév., Madagascar, 2007, *Gautier 5211*, Randriarisoa & al. in prep. (G), ***Lecomtedoxa klaineana*** (Pierre ex Engl.) Dubard, Gabon, 1985, *Louis 1839*, Christe & al., 2021 (G). ***Lecomtedoxa plumosa*** Burgt., Cameroun, 2005, *Burgt 771*, Christe & al., 2021 (G). ***Lecomtedoxa saint-aubinii*** Aubrév. & Pellegr., Gabon, 2009, *Dauby 1944*, Christe & al., 2021 (G). ***Manilkara cuneifolia*** (Baker) Dubard, Africa, 1994, *DeWilde 11385*, Christe & al., 2021 (G). ***Manilkara fasciculata*** (Warb.) H.J.Lam & Maas Geest., Indonesia, 2008, *Armstrong 353*, Randriarisoa & al. in prep. (G). ***Manilkara hexandra*** (Roxb.) Dubard., Sri Lanka, 1974, *Kostermans 25308*, Randriarisoa & al. in prep. (G). ***Manilkara longifolia*** (A.DC.) Dubard., Brasil, 1998, *Santana 675*, Randriarisoa & al. in prep. (G). ***Manilkara udoido*** Kaneh., Indonesia, 1996, *Slappy LR26622*, Randriarisoa & al. in prep. (G). ***Mimusops* sp.**, Madagascar, 2018, *Randrianaivo 3178*, this paper (G). ***Neolemonniera batesii*** (Engl.) Heine, Cameroun, 2000, *Tchouto 3001*, this paper (G). ***Sideroxylon gerrardianum*** (Hook.f.) Lecomte, Madagascar, 2018, *Randriarisoa 149* (G). ***Sideroxylon gerrardianum***, Madagascar, 2018, *Randrianaivo 3087*, this paper (G). ***Tieghemella heckelii*** (A.Chev.) Roberty, Ivory Coast, 1980, *Zwetstloot 33*, Randriarisoa & al. in prep. (G), ***Tsebona macrantha*** Capuron, Madagascar, 2010, *Gautier 5509*, this paper (G). ***Vitellaria paradoxa*** C.F.Gaertn., Ghana, 1999, *Schmidt 3309*, Randriarisoa & al. in prep. (G).