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Systematics and biogeography of subtribe Schreberinae (Oleaceae), with recircumscription and revision of its Malagasy members

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ABSTRACT Clarifying generic circumscriptions within Oleaceae improves its complicated infrafamilial classification. Focusing on the small and disjunctly-distributed subtribe Schreberinae, we use phylogenomic data from plastid and nuclear DNA from an extensive sampling to assess its phylogenetic patterns and biogeographic history. Results show paraphyly among its members, with *Comoranthus* nested within *Schrebera*, leading us to synonymize these genera. *Schrebera s.l.* occurs in four major regions of the world, but its center of origin remains uncertain with three possible ancestral ranges identified. However, the diversification of this genus is estimated to have started in the Early Oligocene (ca. 34 Mya), and its current distribution pattern is best explained by dispersal between landmasses rather than continental vicariance. Madagascar is the center of diversity of *Schrebera s.l.*, where ten endemic species, of which five are new, were recovered from analyses of morphological, molecular, and ecoclimatic data. Therefore, a taxonomic treatment of the species from Madagascar and the Comoro Islands is presented. As currently circumscribed, *Schrebera s.l.*, and thus the monotypic subtribe, includes 16 species (one in South America, two in Southeast Asia, three in Africa, of which one is shared with Madagascar, and 11 in Madagascar and the Comoro Islands).

ADDITIONAL KEYWORDS: *Comoranthus* – conservation status – disjunct distribution – divergence time – heterostyly – morphometry – museomics – Oleaceae – *Schrebera* – taxonomy.

INTRODUCTION

The Oleaceae, a subcosmopolitan family of 28 genera and ca. 700 species, have been the focus of several molecular studies at the family, genus, and species levels in the last two decades, which have greatly improved its infrafamilial classification, and the phylogenetic placement and circumscription of several of its members (Wallander & Albert, 2000; Li, Alexander & Zhang, 2002; Lee *et al.*, 2007; Besnard *et al.*, 2009, Yuan *et al.* 2010; Guo *et al.*, 2011; Hong-Wa & Besnard, 2013; Zedane *et al.*, 2016; Jeyarani *et al.*, 2018; Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Li *et al.*, 2020, 2022; Dong *et al.*, 2022a, b; Dupin *et al.*, 2022). Five tribes are

now recognized (i.e., Fontanesieae, Forsythieae, Jasmineae, Myxopyreae, and Oleae), the largest being Oleae, which in turn comprises four subtribes (Fraxininae, Ligustrinae, Oleinae, and Schreberinae) and 19 genera (Wallander & Albert, 2000; Nesom, 2012; de Juana Clavero, 2020; Li *et al.*, 2020; Dupin *et al.*, 2022). Although there is ambiguity regarding the position of three of the five tribes, namely Fontanesieae, Forsythieae, and Myxopyreae (Wallander & Albert, 2000; Lee *et al.*, 2007; Dupin *et al.*, 2020; Dong *et al.*, 2022a), all studies found Jasmineae and Oleae to be sister clades. The tribe Oleae is characterized by complicated relationships among its members, especially in the subtribe Oleinae where generic relationships are mostly unresolved and where paraphyly and polyphyly are common occurrences. Generic reorganizations have thus recently taken place, with some members of *Chionanthus* L. placed within *Noronhia* Stadtm. ex Thouars (Hong-Wa & Besnard, 2013; Hong-Wa, 2016); some *Olea* L. resurrected as the genus *Tetrapilus* Lour. (de Juana Clavero, 2020); and lastly some *Osmanthus* Lour. moved into three genera, namely *Cartrema* Raf. (Nesom, 2012), *Chengiiodendron* C.B. Shang, X.R. Wang, Yi F. Duan & Yong F. Li (Li *et al.*, 2020), and *Notelaea* Vent. along with all species of *Nestegis* Raf. (Dupin *et al.*, 2022).

Here, we focus on the subtribe Schreberinae, which is a distinct group easily recognized among other Oleaceae members by its hairy corolla and its woody capsular fruits with winged seeds. It is a clade supported by anatomical (Baas *et al.*, 1988; Rowher, 1996), phytochemical (Harborne & Green, 1980), morphological (Johnson, 1957; Green, 2004), and molecular evidences (Wallander & Albert, 2000; Lee *et al.*, 2007; Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Dong *et al.*, 2022a), the latter also firmly supporting its inclusion within tribe Oleae. Although the monophyly of Schreberinae is well-supported, its position within Oleae has not been stable. Indeed, in the *rps16* and *trnL-F* tree presented by Wallander & Albert (2000), Schreberinae was sister to Fraxininae and Oleinae, whereas Lee *et al.* (2007) showed it as sister only to Oleinae in their *ndhF* and *rbcL* tree. In more recent studies that used plastid and nuclear phylogenomic data (Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Dong *et al.*, 2022a), Schreberinae has assumed its new position as sister to all other three subtribes within Oleae.

Within Schreberinae, two small genera are known. These are *Comoranthus* Knobl. and *Schrebera* Roxb., but their boundaries are unclear and their taxonomy is deemed outdated in light of additional collections (Johnson, 1957; Bosser & Rabevohitra, 1985; Schatz, 2001). The genus *Comoranthus* comprises three species known only from Madagascar and the Comoro Islands, whereas *Schrebera*, with its eight currently accepted species involving 34 heterotypic synonyms [sensu Turrill, 1952; Kupicha, 1983; Green, 2006; see also Roxburg, 1799; Welwitsch, 1871; Gilg, 1901; Chevalier, 1912; Kostermans, 1953; Bosser & Rabevohitra, 1985], is more widespread although with a strict tropical distribution within the continents of Africa, Asia, and South America, and also on the island of Madagascar. The affinity between *Comoranthus* and *Schrebera* has been noted since 1949 (Perrier de la Bâthie, 1949, 1951, 1952; Schatz, 2001), based on their shared tubular flowers, hairy corolla, woody capsular fruits, and winged seeds, and was also supported by chemotaxonomy (Harborne & Green, 1980), and wood and fruit anatomy (Baas *et al.*, 1988; Rowher, 1996). However, distinguishing features such as leaf complexity, corolla pubescence, stamen insertion, and style length (Bosser & Rabevohitra, 1985) are also evident, albeit sometimes overlapping. In particular, *Comoranthus* can be characterized by having simple leaves, smaller (usually ≤ 10 mm), white flowers that are pubescent on both sides, and stamens that are inserted at the base of the corolla tube. Meanwhile, the Malagasy *Schrebera* can be recognized by its compound leaves except for the Afro-Malagasy species, *S. trichoclada* Welw., its larger (usually ≥ 11 mm), white to red flowers that are pubescent only at the corolla throat, and its stamens that are inserted on the upper half of the corolla tube.

It is worth noting that at the time *Comoranthus* was described (Knoblauch, 1934), *Schrebera* had not been documented from Madagascar yet, although specimens had already been collected in 1922. When describing *Comoranthus*, Knoblauch (1934) noted an affinity with *Chionanthus*, *Haenianthus* Griseb., and *Linociera* Sw. ex Schreb., so it is unclear whether he saw any Malagasy specimen of *Schrebera* at all. Collections accumulated from Madagascar since the time of description expanded the concept of these two genera, raising questions about their boundaries and taxonomic diversity. It is also interesting to note that *Schrebera* is often described as heterostylous in Africa and Madagascar [e.g., *S. alata* (Hochst.) Welw., *S. arborea* A.Chev., and *S. capuronii* Bosser & R.Rabev. (Verdoorn, 1956; Kupicha, 1983; Bosser & Rabevohitra, 1985)]. But this floral dimorphism has never been reported among its Asian and South American species (Roxburg, 1799; Zahlbruckner, 1892; Kostermans, 1953). In contrast, *Comoranthus* is exclusively homostylous (Perrier de la Bâthie, 1951; Bosser & Rabevohitra, 1985), and the switch from one morph to another within Schreberinae may correlate with a transition from outcrossing to selfing as *Comoranthus* and Malagasy *Schrebera* are reported to be autogamous and allogamous, respectively (Perrier de la Bâthie, 1951; Bosser & Rabevohitra, 1985).

While the monophyly of subtribe Schreberinae as a whole has been substantiated (Wallander & Albert, 2000; Lee *et al.*, 2007; Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Dong *et al.*, 2022a), the relationship between its members, namely *Comoranthus* and *Schrebera*, has remained elusive. Early phylogenetic studies supported a sister-group relationship between *Comoranthus* and *Schrebera* (Wallander & Albert, 2000; Hong-Wa & Besnard, 2013, 2014; Zedane *et al.*, 2016), but additional data revealed instead a case of paraphyly between them (Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Dong *et al.*, 2022a). Despite the inclusion of more *Schrebera* taxa, these latter studies, however, still lacked the South American species and had just one Malagasy member, raising questions about the origin of this group, colonization patterns of landmasses, and the identity and cohesiveness of the Malagasy assemblage (i.e., *Comoranthus* and Malagasy *Schrebera*). Therefore, with yet additional material, both molecular and morphological, we here (1) clarify the generic limit between *Comoranthus* and Malagasy *Schrebera*, (2) revise the taxonomy of the Malagasy taxa, and (3) assess the biogeographic patterns of Schreberinae.

MATERIALS AND METHODS

TAXONOMIC ASSESSMENT OF MALAGASY SCHREBERINAE

Material housed at DOV, K, MO, P, TAN, and TEF and digital images from K, MO, and P [acronyms as per Thiers (2021)] were examined and included a century's worth of collections of just 45 specimens of Malagasy *Schrebera* and 101 specimens of *Comoranthus*. While three species of *Schrebera* are currently known from Madagascar (*S. capuronii*, *S. orientalis* Bosser & R.Rabev., and *S. trichoclada*), the diversity of leaf, flower, and fruit morphologies suggested five additional entities. In particular, there is quite a variation in the number of leaflets, the presence/absence of petiolule, the lamina shape, size, and texture, the venation pattern, the size, shape, margin, and pubescence of the perianth, and the size and shape of the fruits. Except for *S. trichoclada*, which is widespread in Africa, none of the morphogroups matched any other species found outside of Madagascar. In contrast, although one species of *Comoranthus*, namely *C. minor* H.Perrier, can be easily recognized, boundaries between the other two species (*C. madagascariensis* H.Perrier and *C. obconicus* Knobl.) are rather obscure due to overlapping morphological variation, and they are at times informally considered as a single, but widespread and variable species. Because of the informal recognition of only two species

within *Comoranthus* (i.e., *C. minor* and *C. obconicus*), all specimens previously identified as *C. madagascariensis*, which is endemic to Madagascar, have been assigned de facto to *C. obconicus*, which is endemic to the Comoro Islands. But it remains unclear whether two or three species exist within *Comoranthus* given the patterns of morphological variation, so each of its three described species is here considered as a distinct morphogroup, with their respective specimens identified as such in all analyses carried out here. This distinction is based mostly on characteristics of the leaf (shape, size, texture, pubescence, and venation) and fruit (shape, size, and surface). Overall, 11 morphogroups are recognized within the generic complex *Comoranthus-Schrebera* in the Malagasy Region (i.e., Madagascar and the Comoro Islands), and proposed names are assigned to these groups for ease of presentation (i.e., 'australis', 'capuronii', 'humbertii', 'littoralis', 'madagascariensis', 'minor', 'montana', 'obconicus', 'orientalis', 'trichoclada', and 'trifoliata'), which will be used consistently hereafter.

Principal component analyses (PCA), conducted on SPSS v.28 (IBM, USA), were used to assess patterns of variation in leaf, flower, and fruit morphologies within this generic complex. Measurements of mature structures were taken from 18 and 43 specimens of Malagasy *Schrebera* and *Comoranthus*, respectively (Supplementary Information, Table S1). Although morphogroups were defined based on a combination of qualitative (e.g., color, pubescence, and texture) and quantitative (e.g., number and size as in "small" vs. "large") traits, only continuous quantitative characters were used for analyses. These were new twig diameter, petiole length and diameter, lamina length and width, vein number as well as distance between them and distance from margin, and acumen length for vegetative characters. Measured flower features were inflorescence length, peduncle length, pedicel length, calyx length and width, and both the entire corolla and the corolla tube lengths. Fruit measurements included peduncle length, pedicel length and diameter, and calyx length to account for accrescence of these structures, as well as fruit length and diameter. For the lamina and fruit, the length to width or diameter ratio was also used to capture their shape, which is quite variable among species.

Given the distinction between *Comoranthus* and Malagasy *Schrebera*, separate analyses were carried out to assess species boundaries within each of them while a combined analysis looked at their patterns of morphological variation. As most specimens were incomplete, either having only flowers or fruits, separate analyses were also conducted for each organ, which thus allowed maintaining a workable samples-to-variables ratio. The morphogroups were hypotheses of species and were reconciled with molecular data when DNA could be successfully extracted. Here, the basis for species recognition is one or more of four criteria (i.e., distinguishability, monophyly, reproductive isolation, and niche preference), whereas it is solely monophyly for generic status (Schrire & Lewis, 1996; de Queiroz 1998, 2007). Reproductive isolation and niche preference were assessed mostly from natural history observations rather than through computational methods. Specifically, flowering phenologies, compiled from herbarium specimens, were compared to infer reproductive isolation. Similarly, niche preference was inferred from specimen label data when such information was available and by mapping morphogroups' distribution onto the five simplified bioclimatic zones (Schatz, 2000; after Cornet, 1974), the simplified geology (Du Puy & Moat, 1996; after Besairie, 1964), and the vegetation of Madagascar (Moat & Smith, 2007), respectively. Recognized species are discussed in the taxonomic treatment.

PHYLOGENETIC ANALYSES

We reconstructed a phylogenetic tree of subtribe Schreberinae that included 23 accessions representing all but one of its currently accepted species and two putatively new species, with at least two samples from each continent where the subtribe occurs. As outgroups, we chose

subtribe Fraxininae (six *Fraxinus* L. species; Table 1; Supplementary Information, Table S2) due to the fossil availability in this subtribe (see below), which will be relevant in subsequent analyses. Several sequences from plastid markers (either full plastid genomes or individual markers) and/or the nuclear ribosomal DNA (nrDNA) were already available in GenBank. We newly assembled the plastid genome and nrDNA for six accessions, and the nrDNA of accessions that only had their plastid genome available publicly (Supplementary Information, Table S2). Sequences for this study were generated using a genome skimming approach (Zedane *et al.*, 2016). In short, we extracted total genomic DNA from leaf samples from herbaria vouchers and constructed sequencing libraries using 10 to 200 ng of double stranded DNA with TruSeq Nano HT Sample kit (Illumina), following the default instructions. Each sample was paired-end sequenced (150 bp) on an Illumina HiSeq3000 lane and shotgun sequenced through the facilities of the Genopole platform of Toulouse, France. We then generated a consensus sequence of the plastid genome and the nrDNA cluster and mapped short reads onto them to check assembly quality in GENEIOUS v.9.0.5 (<https://www.geneious.com>). We annotated the plastid genomes using GeSeq (Tillich *et al.*, 2017) by choosing genomes of congeneric species available in GenBank as reference. This sampling of 23 accessions included ten taxa from Africa and the Malagasy Region (including nine accessions from Africa, and ten accessions from Madagascar and the Comoro Islands), one taxon from South America [i.e., two specimens of *S. americana* (Zahlbr.) Gilg], and one taxon from Asia [i.e., two specimens of *S. swietenoides* Roxb.].

We used a concatenated matrix of 14 regions that included 13 plastid regions (genes *matK*, *ndhF*, *rbcL*, *rpoC1*, *rpoC2*, *rps16*, *trnK*, *ycf1*, *ycf2*, and intergenic spacers *trnL-trnF*, *trnQ-rps16*, *trnS-trnG*, *trnT-trnL*) and the nrDNA cluster. This set of molecular markers was selected to maximize the number of regions shared between accessions (Supplementary Information, Table S2), and to include highly informative plastid genes (Walker *et al.*, 2019). Before using the nrDNA dataset for the subsequent phylogenetic analyses, we transformed the data from regular nucleotide-coding to a purine-pyrimidine only coding. Previous studies have shown unreliable results when using the nrDNA cluster to estimate phylogenetic relationships in the tribe Oleaceae, and this was attributed to the highly variable GC content in nrDNA (Hong-Wa & Besnard, 2013; Ha *et al.*, 2018; Olofsson *et al.*, 2019). With a purine-pyrimidine only coding (usually referred to as RY-coding), one can effectively reduce the influence of biased GC-content (Phillips, Delsuc & Penny, 2004).

We used the program IQ-Tree v.2.0.6 (Minh *et al.*, 2020) to estimate a species tree and assess the genealogical concordance between partitions. We selected the best partition scheme and the best-fit model per partition through ten rounds of selection using ModelFinder (Kalyaanamoorthy *et al.*, 2017). Then, using the best partition scheme (the one with the lowest BIC score), we estimated a species tree using a concatenation approach with an edge-linked proportional partition model (Chernomor, Von Haeseler & Minh, 2016) and assessed branch support with 1000 ultrafast bootstrap replicates (Hoang *et al.*, 2018). Finally, to assess the concordance between the partitions, we calculated the gene concordance factor (gCF) and the site concordance factor (sCF) for each branch of the species tree (Minh, Hahn & Lanfear, 2020); where the gCF represents the fraction of gene trees that is concordant with a given branch, and the sCF shows the proportion of alignment sites supporting a given branch.

We further complemented our species tree inference with time calibration. We dated our best ML tree from the IQ-Tree results using a penalized likelihood approach in treePL (Smith & O'Meara, 2012). We generated confidence intervals for the node ages in the dated ML tree by making 500 bootstrap trees (i.e., trees with the same topology as the best ML tree but with varying branch lengths; Sauquet, 2013) and dating them as well (Magallón *et al.*, 2015; Lagomarsino *et al.*, 2016). To run analyses in treePL, we determined the best value for the

smoothing parameter by cross-validation, where we tested 27 smoothing values, separated by one order of magnitude (from $1e-20$ to $1e+6$), using the best ML tree as input. For calibration, we used the *Fraxinus* fossil described by Call & Dilcher (1992) to set the minimum and maximum ages of the stem age of the *Fraxinus* lineage. Samaras of *Fraxinus wilcoxiana* Berry, an extinct lineage, are from Middle Eocene sediments in two different locations in the USA (Call & Dilcher, 1992). So, we set the minimum and maximum ages of the root node as the boundaries of the Middle Eocene stage, 37.8 and 47.8 million years ago (Mya), respectively. We finally summarized the age statistics of internal nodes from the 500 bootstrap trees with TreeAnnotator v.1.7.5 (Drummond & Rambaut, 2007), using the best ML tree, dated, as the input target tree, but allowing the node heights to be adjusted as median heights. This final, summary tree was used for the biogeographic analyses.

BIOGEOGRAPHIC ANALYSES

For the biogeographic analyses, we pruned the ML tree to leave only Schreberinae species in it. There were two main reasons not to include outgroups in these analyses. First, the natural choice of outgroups for Schreberinae would be either the other subtribes in Oleaceae, given that Schreberinae is equally related to all subtribes, or the tribe Jasmineae, which is the current sister clade of Oleaceae. For Oleaceae, we would have to extensively sample 17 other genera (including ca. 430 species). A large sampling effort would also be required in the case of Jasmineae, given the large number of species in this clade (ca. 230 species). In both cases, such sampling would also need to be well-balanced to avoid introducing biases in the species distributions later estimated (e.g. Turner, Smith & Callery, 2009). Second, outgroups from Oleaceae or Jasmineae would include clades with widespread distributions, whose ancestral areas are themselves difficult to assess. Such complexity of the outgroups of Schreberinae requires a family-wide analyses which is, in turn, beyond the scope of this work. For those reasons, we simplified our approach to look into Schreberinae species only, even if that means a potential lack of resolution.

We used the R package “BioGeoBEARS” v.1.1.2 (Matzke, 2018a, b; Matzke, Sidje & Schmidt, 2019) to estimate ancestral ranges within Schreberinae. ‘BioGeoBEARS’ implements maximum likelihood (ML) methods that replicate the key assumptions of three most commonly used methods in historical biogeography, namely DEC (dispersal–extinction–cladogenesis; Ree & Smith, 2008), DIVA (dispersal–vicariance analysis; Ronquist, 1997), and BayArea (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis *et al.*, 2013), the latter two methods are referred to as DIVALIKE and BAYAREALIKE within ‘BioGeoBEARS’ (Matzke, 2013). Collectively, these models allow for processes of within-area speciation, vicariance, range expansion, and range contraction. We also tested models with and without founder-event speciation (range switching occurs at nodes), which is incorporated with the j parameter (Matzke, 2014). In total, we implemented six methods, DEC, DIVALIKE and BAYAREALIKE, and their variations with the addition of the j parameter. For all of those, we also included the parameter w , a matrix exponent that we set to be freely estimated in order to optimize the dispersal matrices. Given the issues with direct statistical comparison between biogeographic models (Ree & Sanmartín, 2018), we implemented all methods in parallel, and used Akaike weights (Burnham & Anderson, 2002) to rank the fit of each model to the data. We estimated all models using as input the summary tree from the tree search in IQ-Tree and dating in treePL. For these biogeographic analyses, we classified native species distributions into four areas: (A) South America, (B) South and Southeast Asia, (C) Continental Africa, and (D) Madagascar and the Comoro Islands (Supplementary Information, Table S2); and we set the parameter *maxareas* to two.

RESULTS

TAXONOMIC ASSESSMENT OF MALAGASY SCHREBERINAE

Morphometric analyses showed that both *Comoranthus* and Malagasy *Schrebera* formed coherent clusters in the quantitative morphological space, but overlapped slightly in all three categories, i.e., vegetative, flower, and fruit analyses (Fig. 1A-C). The first component explained over 40% of the variations, with lamina width, corolla length, and fruit diameter weighting the most on this component in all three categories, respectively. Within *Comoranthus*, there was no real gap in vegetative morphology, but with 'minor' being more coherent than either 'madagascariensis' or 'obconicus' was (Fig. 1D). By contrast, flower and fruit morphologies showed more distinctiveness among the three morphogroups (Fig. 1E-F). In particular, 'madagascariensis' showed intermediate morphologies between 'minor' and 'obconicus', slightly overlapping with the former in flower characteristics. The characters with the most weight on the first component, which accounted for over 40% of the variations, were lamina width for vegetative analysis, and calyx width and fruit diameter in flower and fruit analyses, respectively. Within Malagasy *Schrebera*, the patterns were blurred by the paucity and incompleteness of specimens that resulted in the exclusion of some morphogroups from some analyses; and a few morphogroups included only one or two specimens. However, 'trichoclada' appeared the most distinct in all analyses while 'humbertii' and 'trifoliata' were somewhat coherent in vegetative and fruit morphologies (Fig. 1G-I). Morphogroup 'trifoliata' was also distinct in flower space (Fig. 1H). In fact, both 'trifoliata' and 'trichoclada' were very distinct from all other Malagasy Schreberinae in terms of flower (Fig. 1B, lower right corner). The first component explained over 40% of the variations within Malagasy *Schrebera*, with lamina length, inflorescence length, and pedicel diameter accounting heavily for the variation in leaf, flower, and fruit on this axis.

The phenological and ecological assessments, although qualitative in nature, showed that taxa within *Comoranthus* largely overlap in their ecological preference and flowering time. For instance, both 'madagascariensis' and 'minor' occupy the drier areas of Madagascar (Fig. 1J), grow on similar substrates (e.g., lavas, limestones, and sands), and flower and fruit throughout the year. On the Comoro Islands, 'obconicus' also shares these preferences, although with a narrower range, growing predominantly on lavas and being reproductive between February and December. By contrast, there is more ecological variability within the Malagasy *Schrebera*, with members occupying at least three of the five bioclimatic zones (Fig. 1J), and each often being restricted to a particular bioclimate, substrate, or elevation (e.g., dry area and basaltic and calcareous substrate for 'capuronii' vs. humid area and sandy substrate for 'orientalis', low elevation for 'littoralis' vs. high elevation for 'montana'). In general, there are also smaller overlaps in their phenology, with flowering occurring in shorter periods and at different times of the year (e.g., October to February for 'capuronii' and April for 'orientalis'), although this could also be biased by the paucity of collections in Malagasy *Schrebera*.

PHYLOGENETIC INFERENCES AND DIVERGENCE TIMES

Phylogenetic results are heavily skewed by the signal coming from the plastid dataset. The final character matrix had 29 accessions with five partitions and 38,050 sites (with ca. 10% of missing data), where 739 sites were parsimony-informative (ca. 2%). Out of the total number of sites, 30,045 sites are from plastid markers and only the remaining 8,005 correspond to the nrDNA region. The information from nrDNA was further reduced by the necessary step of RY-

coding this dataset. As a consequence, we found no parsimony-informative sites in the RY-coded nrDNA alignment. Hence, for nrDNA, all information came from sites where gaps were found (difference between total number of sites and invariant sites; Table 2). The original 14 partitions were rearranged in a new, 5-partition scheme (Table 2) following the selection of models of substitutions with ModelFinder.

The best ML tree showed that members of Schreberinae form a clade, with *Schrebera americana*, the South American species, as sister to the remaining species. Next, the Asian *S. swietenioides* is then sister to a subclade of African and Malagasy species (Fig. 2). Within that subclade, two distinct sister-groups of both African and Malagasy species emerged. One group includes several accessions of *S. trichoclada* from Africa and Madagascar and one accession of *S. arborea* from Africa. The Malagasy *S. trichoclada* is sister to the remainder of the accessions in this group in which the Western-Central African taxa cluster together (i.e., *S. arborea* [accession *Letouzey 5136* from Cameroon] + *S. trichoclada* [accession *Hart 1544* from DR Congo]) and Eastern African *S. trichoclada* (i.e., Mozambique and Tanzania) cluster together. The second group is a larger assemblage composed of the African *S. alata* that is sister to the Malagasy *Schrebera* and *Comoranthus*. For the Malagasy *Schrebera*, 'australis' was recovered as sister to a group formed by 'humbertii' and the sister-taxa 'capuronii' + 'orientalis'. Relationships within *Comoranthus* are not fully resolved because of the dual position of 'madagascariensis', with one accession being sister to 'obconicus' and another accession nested within accessions of 'minor', although the latter placement is only weakly supported (Fig. 2). Most nodes presented moderate ($\geq 75\%$) to high ($\geq 95\%$) bootstrap support, with four exceptions – all four of those in clades with one or more accessions that had a limited number of markers (Fig. 2; Supplementary Information, Table S2). High bootstrap support was coupled with moderate to high concordance at "gene" level, which is expected given the dominance of data regions from the plastid genome. Finally, values for site concordance factors were fairly even-distributed between 0 and 100, which is likely a result of a dataset that is rich in one type of data (plastid) with few parsimony-informative sites (only ca. 2%).

Our divergence time estimation places the beginning of the diversification of Schreberinae in the Early Oligocene (at ca. 34 Mya), at which time the divergence between the South American species and the remaining taxa occurred (Fig. 3). The Asian and the Afro-Malagasy lineages split at ca. 31 Mya, which was then followed by diversification within Africa and Madagascar. Finally, the divergence between the two major subclades within the Afro-Malagasy clade took place from the Mid-Oligocene to Early-Miocene (between ca. 28 and 22 Mya; Fig. 3; Table 3). It is worth noting that there is a relative deep divergence, dated to the Late Miocene, between the Malagasy *S. trichoclada* and the African members of the species plus *S. arborea*. This warrants a population level exploration of the disjunct *S. trichoclada*, whose current circumscription may encompass unrecognized entities.

BIOGEOGRAPHY

The results of the biogeographic analyses show a lot of uncertainty around the early diversification of Schreberinae (Fig. 3). The best-fit biogeographic model was the DIVALIKE model (Table 4), and it shows that the center of origin of Schreberinae is uncertain, with three possible ancestral ranges. The next node, the ancestor of *Schrebera swietenioides* and its sister clade, also lacks confidence with two possible ranges (Asia+Africa or Asia+Madagascar) with ca. 50% probability each. There is also a lack of confidence about the ancestral range for the African+Malagasy lineage, as it could be, equally, Africa or Madagascar. Nevertheless, we are able to say that the clade formed by *S. trichoclada* and *S. arborea* had an ancestral range of parts of both Africa and Madagascar, with *S. trichoclada* retaining both areas as its range, while

S. arborea has its range within Africa only. An Africa+Madagascar ancestral range was also estimated for the ancestor of *S. alata* and its sister clade, with *S. alata* later retaining only Africa as its range while the other species diversified within the Madagascar area. Those two nodes that present a high probability of an Africa+Madagascar ancestral range (in green in Fig. 3) indicate that two main dispersal events happened between Africa and Madagascar, but we cannot infer their directionality.

DISCUSSION

TAXONOMIC IMPLICATIONS OF MORPHOLOGICAL, MOLECULAR, AND ECOLOGICAL ASSESSMENTS OF MALAGASY SCHREBERINAE

This study is the first to include an extensive sampling of Schreberinae and shows that the genus *Schrebera* is paraphyletic with regard to *Comoranthus*. However, morphometric analyses showed little overlap in their vegetative and reproductive characteristics (Fig. 1A-C), which supports Bosser & Rabevohitra's (1985) continued recognition of distinct genera. Meanwhile, phylogenetic inferences recovered a strongly supported sister-group relationship between *Comoranthus* and the Malagasy *Schrebera* (Fig. 2). Nevertheless, to avoid naming paraphyletic groups, *Comoranthus* is here subsumed under *Schrebera*, which has priority (Turland *et al.*, 2018). Nomenclatural changes are presented in the taxonomic treatment below.

Species boundaries within *Comoranthus* and Malagasy *Schrebera* were assessed using one or more of four criteria (i.e., distinguishability, monophyly, reproductive isolation, and niche preference). A contrasting pattern emerged from morphometric and phylogenetic analyses. While both *Comoranthus* and Malagasy *Schrebera* taxa showed morphological distinction, except in vegetative morphology (Fig. 1D-I), only the phylogenetic relationships within Malagasy *Schrebera* were fully resolved (Fig. 2). Although most morphogroups included only one molecular sample to fully assess the monophyly criterion, satisfying any of the four criteria is considered evidence of the existence of a lineage (de Queiroz, 2007). For instance, 'capuronii' and 'orientalis' share the same floral morphology and are sister to each other, but are presumably reproductively isolated due to non-overlapping phenology (see Taxonomic treatment) and differ in niche preference (i.e., dry forests on basaltic and calcareous substrates for 'capuronii' vs. humid forests on sandy substrates for 'orientalis'; Fig. 1). By contrast, distinguishability can be established for *Comoranthus* taxa, but the other three criteria remain equivocal as 'madagascariensis', 'minor', and 'obconicus' display unresolved relationships and overlapping phenologies and niches (Fig. 1). However, our datasets suffer from imperfect sampling and lack both morphological and molecular samples from a large part of the range of 'madagascariensis', including mostly northern and southern specimens in the morphometry and only northern specimens in phylogenetic inferences.

Preliminary morphometric analyses showed that at least four groups may be distinguished within the 'madagascariensis' morphogroup based on specimens from its northern and southern distribution. Two of these groups were represented in the molecular phylogeny; one from northern Madagascar (represented by accession *Ratovoson et al. 1116*; Table 1; Supplementary Information, Tables S1-S2) is phylogenetically closely related to 'obconicus' (Fig. 2) from Ilots Choazil in the Comoro Islands (represented by accession *Mas 98*; Table 1; Supplementary Information, Tables S1-S2). They are most similar in leaf size (Fig. 1D), but the leaf shapes differ as the leaves of the northern 'madagascariensis' subgroup are broadly elliptic to almost orbicular and the 'obconicus' leaves are elliptic; their fruits are also different (Fig. 1F). This clade is phylogenetically distant from another northern 'madagascariensis' group with leaves narrowly oblanceolate to narrowly elliptic (represented by accession *Service*

Forestier 20913; Fig. 2; Table 1; Supplementary Information, Table S2). None of these accessions exhibits the vegetative morphology of the typical 'madagascariensis' (e.g., leaves lanceolate to oblong) and 'obconicus' (e.g., leaves elliptic-ovate), which were not included in the phylogeny, although their fruit morphology is more typical of each taxon. These groups may represent putative new species distinct from both 'madagascariensis' and 'obconicus', or possibly hybrids between them. Thus, an extensive morphological sampling and a population genetics approach may provide better insights into the boundaries of these species. In light of these preliminary results, we deem it preferable to keep the species status of all *Comoranthus* taxa unaltered until more data are gathered. In sum, the 11 morphogroups are here recognized as 11 species and are treated accordingly in the taxonomic section below.

PHYLOGENETIC RELATIONSHIPS AND DIVERGENCE TIMES

In the larger context, Schreberinae is the smallest subtribe of Oleae, composed only hereon of a single genus, *Schrebera* s.l., with 16 species distributed in the tropical Old World and the Neotropics. Results show that phylogenetic patterns strongly correlate with geography, with distinct clades found in South America, Asia, and Africa and the Malagasy Region (Fig. 2). Although the genus' origin is uncertain, its center of diversity is Madagascar, which harbors ten endemic species. One species is restricted to South America and is currently known only from a few (possibly just six) specimens collected at above 1,500 m elevation in Peru. Two and three species occur in Asia and Africa, respectively, with one of the African species, *S. trichoclada*, shared with Madagascar. The three African species belong to two subclades that contain *S. alata* on one hand, and *S. arborea* and *S. trichoclada* on the other hand, with *S. arborea* nested within *S. trichoclada* (Fig. 2). While *S. arborea*'s placement could be the result of specimen misidentification, meaning that the sister-taxa are either *S. arborea* or *S. trichoclada*, it is also possible that the results reflect a deeper taxonomic issue. The two species overlap in their ranges (POWO, 2022) and morphologies. And with only one accession of *S. arborea* included in this study and no thorough taxonomic assessment of African species, it would be premature to amend its nomenclature. Besides, both *S. arborea* and *S. trichoclada* include several heterotypic synonyms (three and nine, respectively), as does *S. alata* (17 synonyms). Additionally, numerous subclades with divergence dates from the Late Miocene to the Pliocene were recovered in both *S. trichoclada* and *S. alata* groups (Fig. 3). Therefore, both a phylogenetic study that accounts for these synonyms and a comprehensive taxonomic revision should be undertaken to better elucidate phylogenetic and taxonomic patterns of African *Schrebera*. Ultimately, the recovered phylogenetic placement of *S. arborea* could also reflect its "true" position, revealing perhaps a lineage that shares an ancestor with Central African *S. trichoclada*.

Moreover, phylogenetic results provided some insights into the evolution of floral dimorphism within Schreberinae. Heterostyly is hypothesized to be the ancestral state of tribe Oleae (Besnard *et al.*, 2020) and its retention within some members of subtribe Schreberinae may support this inference (Olofsson *et al.*, 2019). Indeed, *Comoranthus* is reported to be exclusively homostylous and autogamous (Perrier de la Bâthie, 1951; Bosser & Rabevohitra, 1985), whereas *Schrebera* is described as heterostylous and allogamous, but this has only been reported for some of its African and Malagasy members (Verdoorn, 1956; Kupicha, 1983; Bosser & Rabevohitra, 1985). And heterostyly has not been reported among Asian and South American *Schrebera* species (Roxburg, 1799; Zahlbruckner, 1892; Kostermans, 1953), so it can only be assumed that such condition was not apparent in these taxa. In light of the phylogenetic tree presented here, it would seem that heterostyly is an acquired trait and evolved several times within Schreberinae. However, as the probability to switch from homostylous selfing to heterostylous self-incompatibility or the inverse should not be the same (Igic, Lande,

& Kohn, 2008), it is premature to conclude on the evolutionary origin of heterostyly within subtribe Schreberinae based on current knowledge. More studies should be devoted to this question, especially by investigating genes involved in this trait among Oleaceae.

Results of divergence times for Schreberinae place the beginning of this clade's diversification at ca. 34 Mya. The crown age estimate for Schreberinae that we present here is similar to the one presented by Olofsson *et al.* (2019), the only other study that sampled several *Schrebera* species in a phylogenetic context. In our study and in theirs, the split between *S. swietenoides* and Afro-Malagasy Schreberinae is estimated as having taken place around 29 Mya. Other ages within Schreberinae vary and that is likely due to the differences in sampling, as we have more species represented. It is relevant to point out, though, that the ages in both of these studies are older than what is shown in another study that also had *Schrebera* species in it. Indeed, Smith & Brown (2018) show in their megaphylogenetic tree that the split between African and Malagasy taxa [i.e., *S. alata* and *S. minor* (H.Perrier) Hong-Wa & Besnard] happened around 7.4 Mya (vs. 22-28 Mya in ours and Olofsson *et al.*'s). We attribute this major difference in node ages to differences in sampling and calibration points. In our study, we used one calibration point within *Fraxinus* from a fossil date, Olofsson *et al.* (2019) used a mix of fossil calibrations and secondary calibration points all within Oleaceae, and Smith & Brown (2018) did not have specific calibrations points within Oleaceae. Such contrast between results highlights that inferred node ages are highly dependent upon the existence and number of fossil records within a particular group, the placement of such fossils, and the sampling used. Additionally, the marked differences in molecular evolution within lineages of Oleaceae (Dupin *et al.*, 2020; Dong *et al.*, 2022a) represent another challenge when dating this group.

BIOGEOGRAPHY

Schreberinae's current disjunct distribution on three continents is the result of dispersal events between areas rather than vicariance. For continental vicariance events to be the main explanation behind the clade's distribution, Schreberinae would have to have originated before the breakup of Gondwana. Such breakup started during the Jurassic (ca. 180 Mya) and, by the mid-Cretaceous (ca. 94 Mya), there was already significant separation between the main landmasses (McLoughlin, 2001). Whereas, here we report an origin of Schreberinae at ca. 34 Mya that clearly post-dates that breakup. The alternative explanation, and the most likely one, is that dispersal events were the main process behind the distribution of lineages. Such dispersal could have taken place through ancient land connections between areas at different times. For instance, Australia and Antarctica did not fully separate until ca. 35-30 Mya, thus possibly still providing land connection between South America and Asia (McLoughlin, 2001; van den Ende, White & van Welzen, 2017). At the same time, a connection between Africa and Eurasia formed with the initial collision of the Afro-Arabian plate with Eurasia, which occurred in the Late Eocene at ca. 35 Mya (Jolivet & Faccenna, 2000; Allen & Armstrong, 2008), thus likely allowing for land migration between these two continents. While already separated at ca. 80 Mya, India and Madagascar could still have maintained a connection through the fragmented microcontinent Mauritia that could have served as stepping stones in the Western Indian Ocean (Warren *et al.*, 2010). Transoceanic long-distance dispersal events from Southeast Asia to Madagascar, afforded by fast-moving south equatorial currents from the Oligocene to the Miocene (von der Heydt & Dijkstra, 2006; Ali & Huber, 2010), have also been reported (Federman *et al.*, 2015) and could potentially explain a colonization route of Schreberinae from Asia to Madagascar.

Within the Africa-Madagascar region, it is clear that dispersals between the two areas helped shape the distribution of Schreberinae. Even though the results presented here are not

conclusive regarding the directionality of events between Africa and Madagascar, Schreberinae fits a pattern seen in other clades. In particular, migration patterns of in-and-out of Madagascar from an African source, as well as back-colonization of Africa, have been reported in several groups across kingdoms (e.g., Raxworthy, Forstner & Nussbaum, 2002; Le Péchon *et al.*, 2010; Krüger, Razafimandimbison & Bremer, 2012; Strijk *et al.*, 2012; Hong-Wa & Besnard, 2013; Samonds *et al.*, 2013; Bukontaite *et al.*, 2015; Kainulainen *et al.*, 2017; Razafimandimbison *et al.*, 2017). These migration patterns are consistent with ancient and more recent water circulations, which flowed eastward toward Madagascar in the Paleogene and westward from Madagascar in the Miocene (Ali & Huber, 2010; Samonds *et al.*, 2012).

In Madagascar, where species diversity is highest, there is a marked disjunction in species distribution between the northern (i.e., $\leq 18^\circ\text{S}$) and southern (i.e., $\geq 23^\circ\text{S}$) regions of the eastern half of the island, especially within the Malagasy *Schrebera s.s.* subclade (Fig. 1J). There is a gap in the Central Highlands and the Central East, with *Schrebera madagascariensis* (H.Perrier) Hong-Wa & Besnard and *S. trichoclada* seemingly serving as a link between the north and the south through the western part of the island. Such geographic disjunction for plants with winged seeds that are presumably wind-dispersed is rather surprising. But these plants mostly occur in forested habitats where wind dispersal may be limited (Gorrilliot *et al.*, 2021; Salmona *et al.*, 2023), while there is also more habitat openness for wind dispersal on the west than on the east. Phylogenetically, though, the split appears to be between the dry and the humid parts of the island (Figs 1J, 2). Indeed, species formerly placed within *Comoranthus* occur predominantly in drier areas (except a few specimens of *S. madagascariensis* found in the subhumid northeast), and they have larger geographic ranges. Whereas, species of Malagasy *Schrebera s.s.* are predominantly found in humid areas (except *S. capuronii* and *S. trichoclada*, which occur in the drier north and west), and they have narrower geographic ranges, with two narrow endemics (i.e., *S. orientalis* and *S. trifoliata* Frasier, G.E. Schatz & Hong-Wa). Thus, it is difficult to pinpoint the center of origin of *Schrebera s.l.* species in Madagascar. However, within the Malagasy *Schrebera s.s.* subclade, diversification may have started in the southeastern part of the island given that the southeastern species (i.e., *S. australis* Frasier, G.E. Schatz & Hong-Wa; Fig. 2) is sister to the remaining ones, although the placement of the other southeastern species (i.e., *S. trifoliata* Frasier, G.E. Schatz & Hong-Wa) is currently unknown. A southeastern origin of a clade is a pattern that was recovered in another Malagasy plant group (tribe Danaideae, Rubiaceae; Razafimandimbison *et al.*, 2022). But there are also both strikingly large geographic disjunction (ca. 642 km apart) and deep divergence (dated at ca. 11 Mya) between northern and southern species of this subclade (Figs 1J, 3), suggesting perhaps the possibility of unknown entities. The divergence between *Comoranthus* and the Malagasy *Schrebera s.s.* also runs deep (ca. 22 Mya; Fig. 3), further suggesting that, upon arriving on Madagascar, the ancestral lineage diverged along different evolutionary trajectories marked by their current morphological distinction (Fig. 1A-C) and probably driven by ecogeographic factors given their respective adaptation to dry and humid climates.

Still, the gap in species distribution between northern and southern regions and narrow endemism recovered in Malagasy *Schrebera s.l.* overall have also been found within its confamilial relative, *Noronhia*, the largest genus of Oleaceae in Madagascar (Hong-Wa, 2016). As with *Noronhia*, centers of diversity of Malagasy *Schrebera* are in topographically complex areas, involving a matrix of lowlands and highlands (e.g., Montagne des Français in the north, and Anosy Mountain chain in the south). Such a biogeographic pattern highlights the role of spatial heterogeneity as a driving force in species diversification among Malagasy Oleaceae (Hong-Wa & Besnard, 2014; Hong-Wa, 2016). Such pattern is also consistent with the finding of several studies that point at both the northern and the southeastern massifs of Madagascar as evolutionary cradles of species diversity for animals and plants (Raxworthy & Nussbam, 1995; Janssen *et al.*, 2008; Wollenberg *et al.*, 2008; Stone, 2012).

TAXONOMIC TREATMENT

Based on morphological, molecular, and ecoclimatic assessments, *Comoranthus* is here subsumed under *Schrebera*, and the 11 morphogroups within the generic complex *Comoranthus*-Malagasy *Schrebera* are recognized as distinct species. The following presents the required generic combination and the taxonomic revision of the genus *Schrebera s.l.* in Madagascar and the Comoro Islands. The treatment includes detailed information on each species' description, distribution, ecology, phenology, and conservation status, along with maps and illustrations of new species. Descriptions were derived from observation of physical and/or digital specimens and from literature review. Geographic coordinates, when assigned post facto, are put in brackets. Coordinates of all known specimens were used to map the species' distributions (ArcGIS Pro 2.7, ESRI) as well as to estimate the extent of occurrence (EOO) and the area of occupancy (AOO) using the GeoCAT tool (Bachman *et al.*, 2011) and a 2 x 2 km grid. The conservation status for each species was then evaluated according to the guidelines for the IUCN Red List Categories and Criteria (IUCN, 2022).

Schrebera Roxb., Pl. Coromandel 2: 1. 1799.

Type: *Schrebera swietenoides* Roxb.

= *Comoranthus* Knobl., Notizbl. Bot. Gart. Berlin-Dahlem 11: 1032. 1934.

Type: *Comoranthus obconicus* Knobl.

Key to the species of *Schrebera s.l.* in Madagascar and the Comoro Islands

- | | |
|--|--------------------------------------|
| 1. Leaves simple | 2 |
| 1'. Leaves compound | 5 |
| 2. New twigs flattened, leaves coriaceous | 3 |
| 2'. New twigs terete, leaves papyraceous to subcoriaceous | 4 |
| 3. Secondary veins conspicuous below, inflorescence multiflorous, fruit \geq 1 cm wide | 5. <i>S. madagascariensis</i> |
| 3'. Secondary veins rather obscure below, inflorescence pauciflorous, fruit < 1 cm wide | 6. <i>S. minor</i> |
| 4. Leaves papyraceous, base rounded to obtuse, fruit \geq 4 cm long | 10. <i>S. trichoclada</i> |
| 4'. Leaves chartaceous to subcoriaceous, base decurrent, fruit < 4 cm long | 8. <i>S. obconicus</i> |
| 5. Leaves trifoliolate | 11. <i>S. trifoliata</i> |
| 5'. Leaves pinnate | 6 |
| 6. Leaflets sessile | 1. <i>S. australis</i> |
| 6'. Leaflets petiolulate | 7 |
| 7. Leaflets ovate, secondary veins raised below | 8 |
| 7'. Leaflets elliptic to obovate, secondary veins raised on both sides | 9 |
| 8. Lenticels present on new twigs, petiolules \geq 8 mm long | 9. <i>S. orientalis</i> |
| 8'. Lenticels absent on new twigs, petiolules < 8 mm long | 7. <i>S. montana</i> |
| 9. Base attenuate, lamina generally discolorous | 4. <i>S. littoralis</i> |
| 9'. Base cuneate to decurrent, lamina generally concolorous | 10 |
| 10. Lamina papyraceous to subcoriaceous, margin undulate | 2. <i>S. capuronii</i> |
| 10'. Lamina coriaceous, margin revolute | 3. <i>S. humbertii</i> |

1. *Schrebera australis* Frasier, G.E. Schatz & Hong-Wa, **sp. nov.** (Fig. 4)

Diagnosis: *Schrebera australis* can be recognized by its flattened to quadrangular petioles, its sessile leaflets that are discolourous, often glossy, and with a midvein that is raised on the upper surface near the base. It closely resembles *S. capuronii* but can be distinguished by having 3-5 sessile leaflets (vs. 5-9 petiolulate leaflets), a calyx with no lobes or with 4-9 small projections (vs. a calyx with 4 rounded lobes), and a corolla with a crenulate (vs. undulate) margin.

Type: MADAGASCAR, Sud (limite orientale), PK 448 de la route Amboasary-Fort Dauphin (aux environs est de Bevilany), [25°00'S 46°36'E], 13 Jan. 1963, fl., *Service Forestier 22400*, (holo-, P [P06774785!]; iso-, MO [MO-3188405!], TEF!).

Paratypes: MADAGASCAR, **Province Fianarantsoa, Region Atsimo-Atsinanana**, Vangaindrano, Ranomena, forêt de Vohimany, à environ 1600 m à l'ouest du village Mahavelo, [23°25'S 47°16'E], 50 m, 20 Oct. 1952, st., *Service Forestier 55-R-206*, (TEF!); **Province Toliara, Region Anosy**, Fort-Dauphin, Manantenina, Ampasimena, sur le Mont Tsimokotra, Vohimavo, 24°20'S 47°08'E, 542-547 m, 30 Nov. 2001, fl., *Hong-Wa 22*, (MO [MO-3188400!], P [P00887961!], TAN!, TEF!); Sud (extrême limite orientale), pentes moyennes et supérieures du massif de Vohitsiandriana (au sud-ouest de Fort-Dauphin), [25°10'S 46°39'E], 300-500 m, 11 Jan. 1964, st., *Service Forestier 22387bis*, (P [P06774790!], TEF!).

Trees up to 10 m tall, dbh up to 20 cm. New twigs light gray, flattened to terete, glabrous, lenticels sparse. Leaves persistent, imparipinnate, with 3-5 leaflets; petioles 1.7-3.0 cm, yellowish to reddish-brown, flattened to quadrangular, canaliculate above, glabrous; rachis brown to olive, canaliculate, glabrous; leaflets elliptic, 3.9-8.8 x 1.7-3.6 cm, subcoriaceous, discolourous, upper surface glossy, glabrous, glandular-punctate on both sides, less so below but with small white dots, base decurrent, margin slightly revolute, apex acute to rounded, venation brochidodromous, midvein slightly impressed above and below, secondary veins 7-9, conspicuous, raised on both sides; sessile. Inflorescences cymose, axillary or pseudoterminal (axillary to terminal leaves), 7.4-12.0 cm, with 5-25 flowers; peduncles 2.5-6.3 cm, glabrous; pedicels 0.2-0.4 cm, glabrous; calyx 2-3 mm, lobes absent or up to 4-9 indistinct projections, white circular glands on interior, tuberculate, glabrous, margin glabrous; corolla white with purplish-brown throat, salverform to campanulate, outside glabrous, tuberculate, inside glabrous with ring of thick dark hairs at throat, tube 4-6 mm, with 5-6 lobes, 3-4 mm, margin crenulate; filament 3 mm, glabrous, anther 3 mm; ovary rounded, 1 x 1 mm, style 5-6 mm, glabrous, stigma 1-1.5 mm, globose to bilobed, exserted, glabrous. Fruits unknown.

Etymology: *Schrebera australis* is named in reference to its southern distribution.

Distribution, habitat, and phenology: This species occurs in humid and transition forests at low- to mid-elevation, on basement rocks, in southeastern Madagascar (Fig. 1J). It bears flowers between November and January.

Conservation status: *Schrebera australis* is currently known from four specimens representing four subpopulations. Its EOO and AOO are 3,089 km² and 16 km², respectively. Various threats are reported for the sites of collection and include shifting cultivation, illegal timber exploitation for local and regional demands, and artisanal mining, all of which will result in continuing decline in the species' EOO, AOO, habitat quality, number of subpopulations, and number of mature individuals. Moreover, four locations are identified with regard to shifting cultivation as the most serious plausible threat, and none occurs within protected areas. Therefore, *S. australis* is preliminarily assessed as "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Vernacular names: Tsiacomposan'ala (*Hong-Wa* 22), tsitongamposa (*Service Forestier* 55-R-206), tsianimposa (*Service Forestier* 55-R-206).

2. *Schrebera capuronii* Bosser & R.Rabev.

Bulletin du Muséum National d'Histoire Naturelle, séries 4, Section B, Adansonia. Botanique Phytochimie 7(1): 62 (1985). Type: MADAGASCAR, Ouest (Nord): massif calcaire de l'Ankarana, près d'Ambondromifehy, [12°54'S 49°12'E], 17 Feb. 1962, fl., *Service Forestier* 22030, (holo-, P [P00062743!]; iso-, K [K000233235!], MO [MO-345960!], P [P00062744!, P00062745!, P00062746!], TEF [TEF000361!]).

Additional material: MADAGASCAR, **Province Antsiranana, Region DIANA**, Antsiranana II, Andranofanjava, forêt de Beanamalao, bord de la rivière, [12°41'S 49°15'E], 17 Oct. 1985, *Service Forestier* 31138 (TEF!); collines et plateaux calcaires d'Analamera, vallée de l'Analabe, sous-affluent du Rodo (province de Diégo-Suarez), [12°48'S 49°27'E], 50 m, Jan. 1938, fr., *Humbert* 19229 (P [P06774792!, P06774793!], TEF!); Ouest (Nord): plateau calcaire de l'Ankarana, près d'Ambondromifehy, [12°54'S 49°12'E], 4-6 Oct. 1954, fr., *Service Forestier* 11258 (P [P0062747!, P00062748!, P00062749!], TEF!); **Region SAVA**, Vohémar, Daraina, forêt d'Ampondrabe, 12°57'29"S 49°41'52"E, 578 m, 21 Feb. 2005, fr., *Ranirison & Nusbaumer* PR940 (K [K000197191!], P [P06774794!]); Ouest (Nord): versant est du massif de l'Ankerana (partie sud du massif de Mafokovo), au nord de Vohémar, [13°18'S 49°51'E], 50-450 m, 17 Dec. 1966, fr., *Service Forestier* 27371 (P [P06774795!], TEF!).

Trees up to 20 m tall, dbh up to 12 cm. New twigs gray to brown, terete to flattened, widened at the nodes, glabrous, lenticels sparse. Leaves persistent, imparipinnate, or occasionally paripinnate, with 5-9 leaflets; petioles 1.4-3.7 cm, brown, terete to flattened, canaliculate above, glabrous; rachis brown, canaliculate, glabrous; leaflets elliptic, 2.8-7.6 x 1.6-3.1 cm, papyraceous to subcoriaceous, concolorous to slightly discolorous, upper surface occasionally glossy, glabrous, sparsely glandular-punctate on both sides, almost absent below, base cuneate or decurrent, margin undulate in thinner leaflets or flat and only revolute near base in thicker leaflets, apex rounded to acute, venation brochidodromous, midvein impressed above, raised below, secondary veins 7-10, conspicuous to somewhat obscure, raised on both sides; petiolules 0.3-1.8 cm. Inflorescences cymose, pseudoterminal, 5.2-12.5 cm, with 25-40 flowers; peduncles 2.5-4.6 cm, glabrous; pedicels 0.2-0.3 cm, glabrous; calyx 2-3 mm, with 4 rounded lobes, glabrous, margin entire; corolla white, tubular to salverform, outside glabrous, inside with ring of brown glandular hairs at throat, tube 8 mm, with 5-6 lobes, 3-5 mm, margin undulate; filament 2.5 mm, glabrous, anther 3-4 mm; ovary rounded, 1.2 x 1.2 mm, style 8 mm, glabrous, stigma 1 mm, lobed, exserted. Capsules 3.5-4.4 x 1.3-1.7 cm, brown, clavate to obovate, apex rounded, lenticels absent. Seeds flat, winged, 2.5 x 0.7 cm.

Distribution, habitat, and phenology: *Schrebera capuronii* is restricted to the north of Madagascar (Fig. 1J) and occurs in low- to mid-elevation dry forests, on lavas, limestones, and basement rocks. It has flowers and fruits between October and February.

Conservation status: Six collections were available for analysis, which resulted in an EOO of 1,660 km² and an AOO of 20 km². Five subpopulations representing five locations were identified based on the particular impacts of shifting cultivation and wildfires. Other threats to this species' habitat include increased illegal logging for timber and for charcoal production, poaching of precious woods such as ebony, and artisanal mining of sapphire and gold. Although three of the locations occur within protected areas (i.e., Analamerana, Ankarana, and Loky-Manambato), they are still impacted by these threats at varying degrees. Therefore, continuing decline in habitat quality and number of mature individuals is expected both within

and outside the protected areas along with an overall decline in EOO, AOO and number of subpopulations. As such, *Schrebera capuronii* is assigned a preliminary status of "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Vernacular name: None recorded.

Notes: The texture of the leaflets of the type specimen is thinner and the venation is more prominent in comparison to that of the other collections, except for one basal leaflet that is thicker and glossy. All specimens are from the same general vicinity in Madagascar and it is possible that variations in habitat (shade vs. full sun) could cause the discrepancies.

3. *Schrebera humbertii* Capuron ex Frasier, G.E. Schatz & Hong-Wa, **sp. nov.** (Fig. 5)

Diagnosis: *Schrebera humbertii* can be distinguished by its coriaceous leaves with prominent raised venation on both sides, and strongly revolute margin.

Type: MADAGASCAR, Ouest (Nord) aux confins de l'Est: massif de Bezavona, entre la Fanambana et la Manambery: pentes inférieures de la rive droite de l'Andilana, [13°32'S 49°54'E], 450 m, 13 Dec. 1966, fr., *Service Forestier* 27233 (holo-, P [P06774781!]; iso-, P [P06774782!], TEF!).

Paratypes: MADAGASCAR, **Province Antsiranana, Region SAVA**, Sambava, flanc sud de l'Anjenabe (vallée de l'Androranga), [14°18'30"S 49°49'00"E], 600 m, 3 May 1950, fr., *Service Forestier* 743 (P [P06774771!], P06774772!, P06774773!], TEF!); Vohémar, Daraina, forêt d'Antsahabe, à 25 km à l'ouest de Daraina, 13°12'31"S 49°33'12"E, 644 m, 4 Nov. 2005, st., *Rakotondrifara et al.* 384 (CNARP, MO [MO-1914439!], P [P06774774!], TAN!); Vohémar, Fanambana, forêt d'Analalava, Amboay, 2 heures de marche à pied (ou 6 km) sud-ouest de Fanambana, 13°35'35"S 49°58'38"E, 260 m, 24 Nov. 2000, fr., *Randrianaivo et al.* 602 (MO [MO-3188407!], P [P06774783!], TAN!); vallée inférieure de l'Androranga, affluent de la Bemarivo (Nord-Est) aux environs d'Antongondriha, Mont Anjenabe, [14°17'S 49°46'E], 500 m, 3-7 Nov. 1950, fr., *Humbert* 24034 (P [P06774780!]); **Province Toamasina, Region Atsinanana**, Réserve Naturelle Intégrale de Betampona, entre les PK 2 et 3.5, 17°55'S 49°13'E, 300-400 m, 6 Oct. 1994, fr., *Andrianarisata et al.* 231 (MO [MO-3188406!], P [P06774775!]).

Trees up to 25 m tall, dbh up to 50 cm. New twigs cream, light brown, or gray, terete, glabrous, lenticels present. Leaves persistent, imparipinnate, or occasionally paripinnate, with 5-9 leaflets; petioles 1.2-4.6 cm, brown, terete, canaliculate above, glabrous; rachis brown, canaliculate, glabrous; leaflets elliptic, rarely oblong, 3.0-9.6 x 1.4-4.3 cm, coriaceous, generally concolorous, occasionally the lower surface paler than the upper, glabrous, densely glandular-punctate above, very sparingly below, base cuneate to decurrent, margin strongly revolute, apex acute to rounded, rarely emarginate, venation brochidodromous, midvein flat above, strongly raised below, secondary veins 7-9, very conspicuous, raised on both sides, sometimes flat above; petiolules 0.4-2.7 cm. Inflorescences cymose, axillary and pseudoterminal (axillary to terminal leaves), none intact, glabrous; flowers unknown, calyx 2.5-5 x 4-5 mm in fruit. Capsules 3.1-5.8 x 1.5-2.7 cm, grayish-brown, tinged red when immature, pyriform, apex retuse to mucronate, lenticels absent, sometimes punctate. Seeds flat, winged, 2.3-4 x 0.8-1 cm.

Etymology: *Schrebera humbertii* is named for Jean-Henri "Henri" Humbert (1887-1967), a prominent plant collector in Madagascar. This species epithet was chosen by René Capuron and noted on herbarium sheets at P and TEF, but never published.

Distribution, habitat, and phenology: This species occurs in the northeast of Madagascar (Fig. 1J) in low- to mid-elevation humid and rupicolous forests, on lavas and basement rocks. It bears fruits between October and May.

Conservation status: The assessment included six collections representing four subpopulations and yielded an EOO of 12,790 km² and an AOO of 24 km². Threats to *Schrebera humbertii*'s habitat include shifting cultivation, overexploitation of timber, artisanal mining for gold, illegal logging for precious woods, and wildfires. Four locations, of which two occur within the protected areas of Betampona and Loky-Manambato, were estimated based on the impacts of shifting cultivation and wildfires. Although decline in EOO is not expected in the near future, reduction in habitat quality both within and outside protected areas is ongoing, which will also result in declining number of subpopulations and mature individuals. Thus, *S. humbertii* is preliminarily assessed as "Endangered" [EN B2ab(i,ii,iii,iv,v)].

Vernacular names: Hidiny (*Humbert 24034*), hidina (*Service Forestier 743*), vavalozza (*Service Forestier 32964*).

Notes: The specimen *Service Forestier 27233*, considered here as the type specimen, appeared to be a polyploid individual based on the phytochrome genes (data not used in these analyses). However, although more than two alleles could be identified from this individual with this family of genes, formally testing its ploidy level turned out to be tricky. While the prevalence of polyploidy within *Schrebera* is unknown, polyploidy has been detected in other taxa within Oleaceae, albeit at a low frequency [e.g., *Noronhia* (Gorrilliot *et al.*, 2021) and *Olea* (Besnard *et al.*, 2008)].

4. *Schrebera littoralis* Frasier, G.E. Schatz & Hong-Wa, **sp. nov.** (Fig. 6)

Diagnosis: *Schrebera littoralis* can be recognized by its discoloured, ovate to oblong leaflets with the secondary venation slightly impressed on the upper surface.

Type: MADAGASCAR, **Province Toamasina, Region Analanjirofo**, PK 154 route Tamatave - Soanierana 7 km, [17°00'S 49°32'E], 2 Sep. 1957, fr., *Service Forestier 18186* (holo-, P [P00062755!], iso-, P [P00062754!], TEF!).

Paratypes: MADAGASCAR, **Province Toamasina, Region Atsinanana**, 2 km à l'ouest d'Andranotsara, [17°38'18"S 49°29'04"E], 5 m, 6 Mar. 1987, fr., *Service Forestier 32964* (TEF!).

Trees big (size unknown). New twigs cream to gray, terete, glabrous, lenticels present. Leaves persistent, imparipinnate, with 7 leaflets; petioles 3.2-6.5 cm, brown, terete, canaliculate above, glabrous; rachis dark brown, canaliculate, glabrous; leaflets elliptic to obovate, 6.4-10.5 x 3.0-4.8 cm, coriaceous, slightly discoloured, darker above, glabrous, glandular-punctate above, very sparingly almost absent below, base shortly attenuate, rarely equilateral, margin entire, occasionally gently undulate, revolute near base, apex rounded to shortly cuspidate, venation brochidodromous, midvein impressed above, raised below, secondary veins 7-12, conspicuous, slightly impressed above, strongly to barely raised below; petiolules 0.6-1.4 cm. Inflorescences cymose, pseudoterminal, 12.3-13.6 cm, with ca. 3 flowers (inflorescences broken); peduncles 5.3-6.6 cm, glabrous; pedicels 0.4-2.9 cm in fruit, glabrous; flowers unknown, calyx broken in fruit, with 4 lobes, glabrous. Capsules 4.5-6.6 x 3.0-3.3 cm, brown, pyriform, apex rounded, lenticels absent. Seeds flat, winged, 4.6-4.9 x 1.1-1.6 cm.

Etymology: *Schrebera littoralis* is named for the habitat type in which it is found.

Distribution, habitat, and phenology: This species occurs in littoral forests on sand, in eastern Madagascar (Fig. 1J). It bears fruits between September and March.

Conservation status: *Schrebera littoralis* is known only from two specimens representing two subpopulations, ca. 71 km apart from each other, and is assigned an AOO of 8 km². Two locations are identified based on the current threats imposed by shifting cultivation, none of which is part of a protected area. Current trends will potentially lead to a reduction in location, hence a decline in EOO as well. Therefore, *S. littoralis* is assigned a preliminary status of "Critically Endangered" [CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Vernacular name: Voansanaka (*Service Forestier 18186*).

Notes: Although there are no records of the size of this tree, one herbarium label reads "very big tree". Formerly a paratype of *Schrebera orientalis* (Bossert & Rabehohitra, 1985), the specimen *Service Forestier 18186* is here considered as the type of *S. littoralis*, which can be distinguished from the former by having coriaceous leaves, with rounded to cuspidate tips (vs. chartaceous to subcoriaceous leaves with acute to acuminate tips). In fact, Bossert & Rabehohitra (1985) already pointed out some differences between the specimens *Service Forestier 27716* and *Service Forestier 18186* but decided to keep them both within *S. orientalis*.

5. *Schrebera madagascariensis* (H.Perrier) Hong-Wa & Besnard, **comb. nov.**

≡ *Comoranthus madagascariensis* H.Perrier. Mémoires de l'Institut Scientifique de Madagascar, Série B, Biologie Végétale 2: 305 (1949). Type: MADAGASCAR, bassin de la Malio, affluent du Mangoky (piste Ranohira-Beroroha), près d'Ambalabe, forêt sèche et "bush" sur grès inférieur de l'Isalo, Canton de Menamaty, [21°58'S 45°18'E], 400-450 m, 23-27 Nov. 1946, fl.-fr., *Humbert 19345* (lecto-, P [P00298598!] (here designated), isolecto-, B [B100159947!], BR [BR0000006499761!], P [P00298597!], WAG [WAG0002482!]).

Additional material: MADAGASCAR, **Province Antsiranana, Region DIANA**, Antsiranana II, Mahavanona, Ampitiliantsambo, 15 km à l'est d'Andranomanitra, 12°23'30"S 49°22'45"E, 257 m, 16 Jun. 2004, fr., *Be et al. 5* (CNARP, MO [MO-1058879!], P [P03532901!], TAN!); Antsiranana II, Andrafiabe, Ambolobozokely, Ambatomisokitra, Nosy Laliara, 7 km au nord-est d'Ambolobozokely, 12°25'54"S 49°28'52"E, 9 m, 17 Jun. 2005, fr., *Be et al. 141* (CNARP, MO [MO-3188437!], P [P03532902!], TAN!); Antsiranana II, Mahavanona, Andranomanitra, Ankisatra, à 2 km au nord d'Andranomanitra, Montagne des Français, 12°23'16"S 49°20'06"E, 315 m, 31 Mar. 2004, fl., *Randrianasolo et al. 404* (CNARP, MO [MO-524178!], P [P03533298!], TAN!); Diégo-Suarez, Montagne des Français, [12°18'S 49°18'E - 12°26'S 49°25'E], 1000 m, 4 Aug. 1952, fr., *Service Forestier 5536* (P [P03532880!, P03532881!], TEF!); Diégo-Suarez, Montagne des Français, Betahitra, [12°22'01"S 49°19'31"E], 250 m, 12 Jul. 1955, fr., *Service Forestier 14214* (P [P03532864!, P03532865!], TEF!); Diégo-Suarez, Montagne des Français, sommet d'Anosiravo, [12°22'05"S 49°21'00"E], 1000 m, 13 Feb. 1962, fl., *Service Forestier 20913* (K, P [P03532871!, P03532872!], TEF!); Diégo-Suarez, Montagne des Français, plateau supérieur de l'Anosiravo, [12°18'S 49°18'E - 12°26'S 49°25'E], 28 Jan. 1966, fl., *Service Forestier 24426* (MO [MO-3188420!], P [P03532862!, P03532863!], TEF!); Andrafiabe, Ambolobozokely, Baie de Rigny, Nosy Voanio, 12°26'11"S 49°28'58"E, 10 m, 23 Mar. 2006, fr., *Ratovoson et al. 1116* (CNARP, MO [MO-2108577!], P [P03532891!], TAN!); Montagne des Français, point de vue Anosiravo, 12°19'34"S 49°20'11"E, 19 Apr. 2007, fr., *Bardot-Vaucoulon & Véné 1732* (K, MO [MO-3188416!], P [P00643279!], TAN!); Ramena, Montagne des Français, Andavakoera, 6 km à l'est d'Ampasanandriana, 12°21'10"S 49°21'06"E, 94 m, 12 Aug. 2004, fr., *Razafitsalama et al. 605* (CNARP, MO [MO-1440645!],

P [P03532883!], TAN!); **Region SAVA**, Vohémar, Fanambana, forêt d'Analalava, 13°33'S 49°59'E, 0-50 m, 26 Sep. 1988, fr., *Rakotozafy 2182* (TAN!); Vohémar, Tsarabaria, Manakana, forêt d'Ambondrobe, 13°43'06"S 50°05'52"E, 53 m, 16 Jul. 2003, fr., *Razakamalala 602* (MO [MO-3188414!], P [P03532884!], TEF!); 35 km S of Vohémar, Tsarabaria, Manakana, 13°42'56"S 50°06'01"E, 5 m, 25 Oct. 2002, fr., *McPherson et al. 18796* (MO [MO-3188415!, MO-326534!], P [P03532892!], TEF!); **Province Mahajanga, Region Betsiboka**, Ouest: Kama-Kama, sur le plateau d'Ankara (Boina), [17°13'S 46°16'E], Jul. 1901, fr., *Perrier de la Bâthie 1281* (P [P03532887!, P03532889!]); **Region Boeny**, Réserve no. 8, [16°21'S 45°15'E - 16°33'S 45°26'E], Oct. 1964, fr., *Morat 898* (P [P03532888!], TAN!); **Region Melaky**, Maintirano, [18°04'S 44°02'E], 50 m, May 1977, *Service Forestier 30518* (TEF [TEF000782!]); Maintirano, Ambararatakely, [17°51'S 45°20'E], 15 Jun. 1956, fr., *Service Forestier 16334* (P [P03532869!], TEF!); Maintirano, Amboloando, [18°01'30"S 44°06'30"E], 0-50 m, 7 Sep. 1954, fr., *Service Forestier 10695* (P [P03532874!], TEF!); Maintirano, Ampandra, forêt d'Ampandra, [17°57'S 44°07'E], 0-50 m, 24 Feb. 1956, fr., *Service Forestier 16364* (P [P03532870!], TEF!); Maintirano, Ankirijifoty sis à environ 3 km ouest du village d'Amboloando, forêt d'Amboloando-Maintirano, [18°01'S 44°06'E], 50 m, 14 May 1955, fr., *Service Forestier 14104* (P [P03532873!], TEF!); Maintirano, Belitsaky, Antsakoabe, 18°05'06"S 44°32'52"E, 312 m, 20 Nov. 2012, fr., *Rakotovao et al. 6293* (MO, P, TAN!); Maintirano, Mangabe, 1 km est du campement Mokotra, forêt d'Analalava, [18°51'30"S 44°43'30"E], 50 m, 22 Feb. 1955, fr., *Service Forestier 14783* (P [P03532867!], TEF!); 5 km de Maintirano, sur la route de Tsiroanimandidy, forêt d'Ambararatakely, [17°51'S 45°20'E], 300 m, 10 Oct. 1981, fr., *Service Forestier 32018* (TEF!); Beanka, 18°06'21"S 44°28'19"E, 172 m, 19 Mar. 2013, fr., *Luino 77* (G [G00377915], K, MO [MO-3188444!], P [P00982084!], TEF); Beanka, Ambinda-Nord, 17°56'23"S 44°28'20"E, 199 m, 14 Nov. 2011, fr., *Gautier et al. 5596* (G [G00376003], K, MO, P [P00888351!], TEF, WAG); Beanka, Sarodrano, 18°03'29"S 44°30'53"E, 337 m, 4 Mar. 2012, fr., *Hanitrarivo et al. 250* (BR, G [G00376696], K, MO, P [P00992066!], TEF); Beanka, Andoloposa, 18°00'09"S 44°30'22"E, 399 m, 23 Mar. 2012, fr., *Hanitrarivo et al. 377* (BR, G [G00376768], K, MO, P [P00992075!], TEF); Belitsaka, 17°32'37"S 44°16'53"E, 23 Oct. 2009, fr., *Rakotonasolo et al. 1453* (MO [MO-3188443!], P [P00722524]); près de Besaraha, de Bemiha et de Soahanina, [18°39'S 44°17'E], 0-20 m, 23 Dec. 1952, fl., *Leandri et al. 2223* (P [P03532893!, P03532894!, P03532896!, P03532897!, P03532898!, P03532899!]); Ouest (Menabe): forêt de Tsienimpihy aux environs du village de Besara (Antsalova), [18°35'S 44°15'E], 0-25 m, 23 Dec. 1952, fl., *Service Forestier 6857* (P [P03532877!, P03532878!, P03532879!], TEF [TEF000781!]); **Region Sofia**, Analalava, Ambolobozo, Antanimora, forêt d'Antanimora, [14°58'S 47°54'E], 20 Apr. 1956, fl., *Service Forestier 15788* (P [P03532868!], TEF!); **Province Toliara, Region Anosy**, Fort-Dauphin, Ambatoabo, Ankoba, forêt d'Ankoba, à 8 km au nord d'Ambatoabo, à 3 km est d'Ankoba, 24°47'48"S 46°43'16"E, 664 m, 21 Jul. 2011, fr., *Randrianaivo et al. 1896* (MO [MO-3188418!], P [P00887964!, P00887965!], TAN); Sud (extrême limite orientale): massif du Vohitsiandriana (au sud-ouest de Fort-Dauphin), [25°10'S 46°39'E], 300-500 m, 11 Jan. 1963, fr., *Service Forestier 22392* (P [P03532866!], TEF!); **Region Atsimo-Andrefana**, Sakaraha, Amboronabo, Marotsiraka Betsileo, Tazohin'i Tanimena, forêt d'Analavelona, 22°40'09"S 44°11'22"E, 1164 m, 19 Mar. 2011, st., *Randrianarivony et al. 335* (MO [MO-3188419!], TAN); Sakaraha, Antragnodrebona, NE of the camp, NE of Antanimena forest patch, 22°44'10"S 44°11'25"E, 1137 m, 7 Dec. 2009, fl.-fr., *Randrianasolo 1245* (MO [MO-3188417!], P [P00887962!, P00887963!]); Sakaraha, Mahaboboka, Marotsiraka Betsileo, Ambinanintelo, forêt d'Analasarotsy, 22°48'34"S 44°16'27"E, 400 m, 25 Apr. 2016, fr., *Randrianarivony et al. 832* (MO, P, TAN!); Sakaraha, Mahaboboka, Ambinanintelo, forêt d'Analavelona, forêt d'Andohaniankokoky, 22°41'29"S 44°09'40"E, 931 m, 7 Dec. 2015, fr., *Randrianarivony et al. 830* (DOV!, MO!, P [P01198281!], TAN); Sakaraha, Mahaboboka,

Marotsiraka Betsileo, Analavelona, forêt d'Andranoheza, 22°40'49"S 44°09'23"E, 1084 m, 30 Jan. 2012, fl., *Randrianarivony et al.* 450 (DOV!, MO!, P [P01199601!], TAN); Sakaraha, Mahaboboka, Marotsiraka Betsileo, Analavelona, forêt de Tanimena, 22°39'56"S 44°11'18"E, 1181 m, 6 Feb. 2012, fr., *Randrianarivony et al.* 475 (DOV!, MO!, P [P02290443!], TAN); Sakaraha, Mahaboboka, Marotsiraka Betsileo, forêt d'Analavelona, campement Antanimena, 22°40'11"S 44°11'29"E, 1093 m, 19 Apr. 2012, fr., *Razanatsima et al.* 1039 (MO, P [P00859916!], TAN); Sakaraha, Mikoboka, Fanjakà Mahabo, forêt d'Analavelona, forêt de Vohimary, 22°42'06"S 44°08'19"E, 1009 m, 17 Dec. 2017, fr., *Randrianarivony et al.* 970 (DOV!, MO, P, TAN!); Sakaraha, Mikoboka, Soatàna, forêt d'Analavelona, piste Famoaha, 22°42'16"S 44°09'01"E, 974 m, 6 Dec. 2015, fr., *Rakotoarivelo et al.* 728 (MO, P [P01198265!], TAN); Analavelona, [22°57'00"S 43°28'30"E], 30 May 1952, fr., *Service Forestier* 5253 (P [P03532882!, P03532886!], TAN!, TEF!); Analavelona, [22°07'S 44°06'E - 22°53'S 44°21'E], 500 m, 27 Nov. 1954, fr., *Service Forestier* 12104 (P [P03532875!], TEF!); Mahaboboka, 6 km au nord de Mitia, forêt d'Ihara, [22°53'S 44°32'E], 460-500 m, 25 Apr. 1955, fr., *Service Forestier* 13374 (MO [MO-3188413!], P [P03532876!], TEF!); km 63 Route Tuléar-Sakaraha, [22°56'S 44°33'E], 10 Nov. 1952, fl., *Service Forestier* 5925 (P [P03532885!], TEF!); Ouest (confins du Centre): bassin de la Mananadabo dans le Massif de l'Analavelona, au nord du Fiherenana, 1000-1300 m, [22°37'S 44°07'E], 13-15 Dec. 1962, *Service Forestier* 22193bis (P, TEF!); Sud-Ouest: Mt Ambohibe près de Mahiamalona (Manombo du Sud), [22°58'S 43°58'E], fr., *Perrier de la Bâthie* 4384 (P [P03532988!]); sur le Zomandao, à l'ouest du Betsileo, [21°33'S 45°26'E], Sep. 1919, fr., *Perrier de la Bâthie* 18581 (P [P03532890!]).

Trees up to 20 m tall, dbh up to 70 cm. New twigs yellowish-brown to gray, flattened, widened at the nodes, glabrous to pubescent, lenticels present. Leaves semi-caducous, simple, narrowly lanceolate to almost orbicular, 4.8-14.2 x 1.6-4.8 cm, coriaceous, concolorous to discolorous, darker and glossy above, paler and dull below, glabrous to sparsely pubescent at base and along lower midvein, glandular-punctate on both sides, less so above, base acute to obtuse, sometimes decurrent, margin revolute, sometimes undulate, apex rounded, sometimes acute to slightly acuminate, venation brochidodromous, midvein flat to raised above, sometimes canaliculate, slightly to strongly raised below, secondary veins 6-17, barely to strongly conspicuous on both sides, slightly raised above and below; petioles 0.5-2.2 cm, greenish to light brown, flattened, flat to slightly canaliculate above, swollen at the base, glabrous to pubescent. Inflorescences cymose, axillary and pseudoterminal, up to 5 cm, with up to 35 flowers (usually 3 per branch); peduncles 0.4-1.5 cm, glabrous to pubescent; pedicels 0.2-0.3 cm, glabrous to pubescent; calyx 1.5-3 mm, glabrous to pubescent, rugose, margin denticulate to distinctly 4-lobed, ciliate; corolla grayish-white, tubular to campanulate, outside and inside pubescent, the inside visibly stipitate glandular, tube 2.3-6 mm, with 4 lobes, 2-3 mm, margin entire; filament 0.5 mm, sparsely glandular-pubescent, anther 1.6 mm; ovary conical, 0.5 x 1 mm, style subnull (0.5 mm), glabrous, stigma less than 1 mm, capitate. Capsules 2-4.5 x 1.1-2.4 cm, brown to black, obovate to pyriform, sometimes punctate, rarely covered with a transparent pellicle, apex rounded to apiculate, lenticels absent. Seeds flat, winged, 2-3 x 0.5-1 cm.

Distribution, habitat, and phenology: *Schrebera madagascariensis* occurs in littoral, dry, and sub-humid forests at low- to mid-elevation from northeastern to southern Madagascar within its western part (Fig. 1J). It grows on lavas, limestones, both sandstones and unconsolidated sands, and basement rocks; and it has flowers and fruits throughout the year.

Conservation status: Our assessment was based on 50 specimens representing 25 subpopulations and provided an EOO of 506,514 km² and an AOO of 176 km². Despite the smaller AOO, *Schrebera madagascariensis* is widely distributed and certainly occupies a larger area within its EOO than what was estimated. This species' habitat is subjected to various

threats such as annual wildfires, shifting cultivation, illegal timber logging, and overexploitation of wood for charcoal production. Twenty-four locations were identified based on the threats imposed by annual wildfires and shifting cultivation, with three of these locations occurring in protected areas (i.e., Alandraza Analavelona, Beanka, and Montagne des Français). Thus, *S. madagascariensis* is preliminarily assessed as "Least Concern" [LC].

Vernacular names: Sandramiramy (*Razafitsalama et al.* 605), vavalozza (*Randrianarivony et al.* 335, 475, 830; *Ratovoson et al.* 1116; *Service Forestier* 5253, 6857, 10695, 12104, 13374, 14104, 14214, 14783, 16334, 16364, 30518, 32018, 59253), voantsahanaka (*Service Forestier* 5536).

Notes: *Schrebera madagascariensis* displays a wide range of variation both in vegetative and reproductive morphologies. Leaves vary greatly in shape, size, texture, venation appearance, and pubescence; while flowers and fruits vary mostly in shape, size, and pubescence. In the north, three clusters can be distinguished in principal component space, whereas specimens from the southern part form one group, with some outliers representing extreme morphologies that are visibly from resprouting shoots (unpub. data). Although these clusters may represent distinct taxa, the analyses included only one-third of the collections, largely missing specimens from the west, which resulted in some clusters consisting of only a single specimen or a few with incomplete material (i.e., with either flower or fruit characters only). Therefore, it is preferable to consider a variable *S. madagascariensis* until data from most, or all, specimens can be gathered. It is worth noting that northern specimens were unknown at the time of the species description, being collected only after 1950. Although the specimen *Humbert 19345* is marked as the type, sometimes with Perrier de la Bâthie's handwriting (e.g., on sheets at B, BR, and WAG), the specimen itself was not included in the protologue. But it is chosen as the lectotype here as it is the one apparently selected by the author of the species.

6. *Schrebera minor* (H.Perrier) Hong-Wa & Besnard, **comb. nov.**

≡ *Comoranthus minor*, Mémoires de l'Institut Scientifique de Madagascar, Série B, Biologie Végétale 2: 306. (1949). Type: MADAGASCAR, **Province Toliara, Region Atsimo-Andrefana**, Sud-Ouest, éboulis calcaires du plateau Mahafaly, bords du lac Tsimanampetsotsa, [24°07'S 43°47'E], 38-114 m, Jun. 1910, fl.-fr., *Perrier de la Bâthie 10163* (lecto-, P [P00298599!]) (here designated), isolecto-, unknown).

Additional material: MADAGASCAR, **Province Toliara, Region Androy**, Ambovombe, Antanimora, forêt de Sakave, [24°53'S 45°52'E], 300 m, 8 Sep. 1953, fr., *Service Forestier* 7740 (P [P03532986!, P03532989!], TEF!); Androy, Sud-Ouest: Basse Menarandra: entre Bevontaka et Bevoalavo, [25°12'S 44°31'E], 100-150 m, Mar. 1955, fl.-fr., *Service Forestier* 11874 (P [P03532962!, P03532963!, P03532064!, P03532965!]); Androy, Sud-Ouest: massif de l'Angavo, à l'est d'Antanimora, [24°50'30"S 45°48'00"E], 200-530 m, Feb. 1955, fl., *Service Forestier* 11725 (P [P03532960!, P03532961!], TEF!); Androy, massif de l'Angavo, [24°50'30"S 45°48'00"E], 200-530 m, 23 Jan. 1963, fl., *Service Forestier* 22478 (P [P03532982!], TEF!); Menarandra, Bevoalava-Ankazondranto, [25°17'S 44°30'E], 1-150 m, 12 Mar. 1955, fl.-fr., *Humbert & Capuron*, 29363 (P [P03532957!]); **Region Anosy**, Amboasary Sud, Mahaly, Anadabolava, Bekinagna, forêt d'Anadabolava, 24°14'23"S 46°17'59"E, 265 m, 28 Apr. 2012, fr., *Ravelonarivo et al.* 4402 (DOV!, MO!, P, TAN!); Fort-Dauphin, Ambatoabo, Ankoba, forêt d'Ankoba, 24°47'12"S 46°42'25"E, 300 m, 25 Feb. 2009, fr., *Randrianaivo et al.* 1757 (MO [MO-3188433!], P [P04492690!], TAN!); Fort-Dauphin, Ranopiso, Marokoto, 24°46'S 46°38'E, 300-330 m, 11 Feb. 1995, fr., *Eboroke* 969 (MO [MO-3188408!], P [P03532990!], TAN!); Ihazofotsy, Andohahela RNI, Réserve Intégrale no. 11,

24°50'S 46°32'E, 100 m, 23 Jul. 1996, fr., *Laha 248* (MO [MO-3188427!], TAN!); Andohahela RNI, [24°36'S 46°42'E], 16 Nov. 1994, fr., *Rakotomalaza 337* (MO [MO-3188432!], P [P03532997!]); Anjiozio, Vohimainty, Behara, [24°54'30"S 46°35'00"E], 500-1000 m, 17 Apr. 1952, fl., *Service Forestier 5291* (P [P03532966!, P03532969!], TAN!, TEF!); NE of Ankoba, near E edge of Andohahela National Park, Parcel 1, 24°47'22"S 46°42'04"E, 225 m, 24 Jan. 2008, fr., *Lowry et al. 6997* (MO [MO-1914932!, MO-3098351!], P [P06233780!], TAN!); Emanany, Antanimora, Ambovombe, [24°41'S 46°48'E], 12 Sep. 1953, fr., *Service Forestier 7750* (P [P03532985!, P03532987!], TEF!); Mandrare, forêt de Beara, [24°57'10"S 46°23'00"E], 50 m, 16 Sep. 1950, *Service Forestier 66-R-1* (TEF!); Sud-Ouest: Cap d'Andrahomana (au Sud de Ranopiso–Fort-Dauphin), [25°11'S 46°38'E], Mar. 1955, fr., *Service Forestier 11829* (P [P03532954!, P03532955!, P03532956!]); **Region Atsimo-Andrefana**, Betioky, Beheloka, Ifoetse, Réserves Naturelles de Tsimanampetsotsa, 24°00'27"S 43°44'50"E, 50 m, 14 Mar. 2008, fl., *Ratovoson 1457* (MO [MO-3188435!], P [P00936857!], TAN!); Toliara II, Belalanda, Ranobe, Ankena, 23°00'08"S 43°42'52"E, 200 m, 13 Mar. 2006, fl., *Ranaivojaona et al. 1386* (DOV!, MO [MO-3188434!], P [P06233782!], TAN!); Belalanda, Ranobe, 23°03'21"S 43°42'18"E, 107 m, 18 Mar. 2006, fl., *Andrianjafy et al. 1688* (MO [MO-3188426!], P [P06233781!], TAN!); Belalanda, Ranobe, 22°58'21"S 43°41'41"E, 112 m, 6 Sep. 2006, fr., *Andrianjafy et al. 1838* (MO [MO-3188436!], P [P03532973!], TAN!); Ambohimahavelona, Sept Lacs, 23°31'24"S 44°09'10"E, 4 Sep. 1998, *Rakotomalaza & Messmer 1668* (G [G00188828], MO!); Anketa-Tuléar, [23°07'S 44°17'E], 29 Jan. 1952, fr., *Service Forestier 4565* (P [P03532971!], TEF!); Itambono Corridor between Betioky and Beheloka, 18 km from RN 10, 23°52'S 44°12'E, 250 m, 30 Dec. 1987, fr., *Phillipson 2751* (MO [MO-3188424!], P [P03533297!], TAN!); Maromandia-Tuléar, forêt d'Ambolikira, [23°17'30"S 43°50'00"E], 100 m, 4 Jun 1954, fr., *Service Forestier 10219* (P [P03532984!], TEF!); Pointe Sud du lac Tsimanampetsotsa, [24°12'S 43°47'E], Feb. 1962, fl., *Bosser 15853* (MO [MO-3188431!], P [P03532975!, P03532976!], TAN!); Réserve Naturelle du lac Tsimanampetsotsa, [24°03'S 43°43'E - 24°12'S 43°51'E], Feb. 1962, fr., *Keraudren 1421* (MO [MO-3188430!], P [P03532991!, P03532992!]); Saint Augustin, [23°33'S 43°45'E], Apr. 1968, fr., *Rakotozafy 757bis* (P [P03532998!], TAN!); road to Saint Augustin (Anatsogno), S of Tuléar, [23°28'S 43°46'E], 50 m, 23 Mar. 1985, fr., *Dorr 4135* (MO [MO-3188423!], P [P03532995 !], TAN!); ca. 18 km S of Tuléar near St. Augustin, [23°33'S 43°45'E], 20-150 m, 11 Nov. 1978, fr., *Lorence 1935* (MO [MO-3188421!], TAN!); km 37, Route Tuléar-St. Augustin, [23°31'30"S 43°46'00"E], 9 Sep. 1952, fl., *Service Forestier 5920* (P [P03532967!, P03532970!], TEF!); near Soalara, at mouth of Onilahy River, E of Soalara, 23°35'S 43°44'E, 50 m, 6 Oct. 1990, fr., *Phillipson et al. 3706* (MO [MO-3188425!], P [P03532996!], TAN!); Sud-Ouest: Befoly (PK 35-40 de la route Tuléar-Sakaraha), [22°04'00"S 43°44'30"E], 50-100 m, 27 Jun. 1958, fr., *Service Forestier 18626* (P [P03532959!], TEF!); Sud-Ouest: à l'est de Bevovoka (à l'est de Besamata, au nord-ouest du Lac Tsimanampetsotsa), [23°59'30"S 43°42'00"E], 0-50 m, 2 Jul. 1958, fr., *Service Forestier 18652* (MO [MO-3188429!], P [P03532978!], TEF!); Sud-Ouest (confins de l'Ouest): PK 28 de la route Tuléar-Sakaraha, [23°20'00"S 43°51'30"E], 300 m, Dec. 1961, fl., *Service Forestier & Chauvet 20785* (DOV!, MO [MO-3188428!], P [P03532979!, P03532980!, P03532981!], TEF!); Sud-Ouest: près de St. Augustin, [23°33'S 43°45'E], Aug. 1919, fr., *Perrier de la Bâthie 12789* (P [P03532999!, P03533001!]); Sud-Ouest: Tuléar (PK 18 route de Sakaraha), [23°23'S 43°48'E], 18 Nov. 1961, fr., *Chauvet 209* (P [P03532972!, P03532977!], TEF!); Sud-Ouest: Tuléar, PK 28 Route de Tananarive, [23°19'S 43°52'E], 21 Nov. 1962, fl., *Chauvet 376* (DOV!, MO [MO-3188422!], P [P03532993!, P03532994!], TEF!); **Region Menabe**, route Menarandra-Ampanihy (30 km), [20°52'S 44°40'E], 10 Dec. 1953, fl.-fr., *Service Forestier 8021* (P [P03532983!], TEF!).

Shrubs or trees up to 13 m tall, dbh up to 17 cm. New twigs gray to yellowish-brown, flattened, widened at the nodes, pubescent, lenticels absent to sparse. Leaves semi-caducous, simple,

narrowly elliptic to obovate, 3.2-6.5 x 0.8-2.1 cm, coriaceous, sometimes slightly discoloured, darker and glossy above, paler and dull below, glabrous, glandular-punctate on both sides, base decurrent, margin revolute, apex rounded to obtuse, rarely emarginate, venation brochidodromous, midvein flat to slightly raised above at the base, raised below, secondary veins 5-9, conspicuous and slightly raised above, often rather obscure and barely raised below; petioles 0.3-1.4 cm, yellowish to brown, terete, flat to canaliculate above, often sparsely pubescent. Inflorescences cymose, axillary, rarely pseudoterminal, 1.2-2.7 cm, with 3-8 flowers, usually 5; peduncles 0.2-0.9 cm, pubescent; pedicels 0.1-0.3 cm, pubescent; calyx 1-2.5 mm, pubescent, margin shallowly 4-lobed, ciliate; corolla yellowish to white, tubular to campanulate, outside and inside glandular-pubescent, tube 2.5-6 mm, with 4 lobes, 1-2.5 mm, margin entire; filament 1.5 mm, glandular-pubescent, anthers 1.4 mm; ovary conical, 0.8 x 0.7 mm, style null to subnull (0-1 mm), pubescent, stigma 0.5 mm, capitate. Capsules 1.4-2.1 x 0.6-0.9 cm, brown, clavate to obovate, often covered with a transparent pellicle, apex rounded or apiculate, lenticels absent. Seeds flat, winged, 0.9 x 0.3 cm.

Distribution, habitat, and phenology: *Schrebera minor* is found in bush and dry forests at low- to mid-elevation, on lavas, limestones, both sandstones and unconsolidated sands, and basement rocks, from the west to the southeast of Madagascar (Fig. 1J). It bears flowers and fruits throughout the year.

Conservation status: With 39 specimens representing 29 subpopulations, the analysis yielded an EOO of 94,430 km² and an AOO of 144 km². Although *Schrebera minor* is only found in southern Madagascar, uncollected areas with suitable habitat where the species could occur will likely increase its AOO. Various threats are encountered in this species' known habitat such as wildfires, slash-and-burn agriculture, illegal wood exploitation for timber and charcoal, and mineral exploitation of mica. This leads to an estimate of 19 locations based on the most serious threats imposed by wildfires and slash-and-burn agriculture. Although three locations are within the protected areas of Amoron'i Onilahy, Andohahela, and Tsimanampetsotsa, these areas also suffer from population encroachment. Nonetheless, *S. minor* is not expected to suffer a dramatic decline in the near future and is thus assigned the preliminary status of "Least Concern" [LC].

Vernacular names: Farehitse (*Service Forestier 66-R-1*), halomboha (*Service Forestier 7750*), hatambogna (*Laha 248*), hantambona (*Service Forestier 4565*), hatambona (*Service Forestier 5291*), hazomainty (*Eboroke 969*), mahatamboha (*Service Forestier 7740*), tsinano (*Service Forestier 8021*), vavalozza (*Service Forestier 10219*).

Notes: The protologue includes two syntypes (*Perrier de la Bâthie 10163* and *Perrier de la Bâthie 12789*). However, the specimen *Perrier de la Bâthie 10163* bears the mention "Type" and is, thus, chosen as the lectotype here. No isolectotype is currently recorded.

7. *Schrebera montana* Frasier, G.E. Schatz & Hong-Wa, **sp. nov.** (Fig. 7)

Diagnosis: *Schrebera montana* can be recognized by the absence of conspicuous white lenticels on the young branches, the impressed secondary venation on the upper surface of the leaflets, and the evidently raised secondary venation on the lower surface of the leaflets. It closely resembles *S. orientalis* but differs from it by the absence (vs. presence) of lenticels on the new twigs, and by having 3-5 leaflets (vs. 5-7 leaflets) and shorter petiolules (< 8 mm vs. ≥ 8 mm).

Type: MADAGASCAR, au-dessous du cpt. 1 (Marofanamo), [14°28'30"S 48°46'00"E], 1600 m, 3 Feb. 1951, fr., *Service Forestier 974* (holo-, P [P06774779!], iso-, P [P06774777!, P06774778!], TEF!).

Paratypes: MADAGASCAR, **Province Antsiranana, Region DIANA**, montagnes au nord de Mangindrano (Haute Maevarano) jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga: Centre-Nord), [14°16'S 48°56'E], 1800-2000 m, 19 Jan. - 12 Feb. 1951, fr., *Humbert 25161bis* (P [P06774776!]).

Trees up to 30 m tall, dbh up to > 50 cm. New twigs gray to brown, flattened, glabrous, lenticels absent. Leaves persistent, imparipinnate, with 3-5 leaflets; petioles 2-4 cm, yellowish to brown, terete, canaliculate above, glabrous; rachis brown, canaliculate, glabrous; leaflets ovate, 4.9-9.3 x 2.2-5.1 cm, papyraceous to coriaceous, discolorous, darker above, glabrous, rarely to sparingly glandular-punctate on both sides, base cuneate, sometimes equilateral, margin undulate, revolute near leaf base, apex acute to shortly attenuate, venation brochidodromous, midvein impressed above, raised below, secondary veins 8-10, conspicuous, impressed above, slightly raised below; petiolules 0.4-0.7 cm. Inflorescences cymose, apparently pseudoterminal, detached from specimen and broken; flowers unknown. Capsules 3.1-3.9 x 1.5-1.6 cm, brown, clavate, apex rounded to slightly retuse, lenticels absent. Seeds unknown.

Etymology: This collection was given the herbarium name *Schrebera madagascariensis* by René Capuron (R.Capuron ined., 1956). While we also recognize it as a valid species, we prefer to adopt a different epithet than the suggested one as it is overused. Besides, the name *S. madagascariensis* is already occupied due to synonymy of *Schrebera* and *Comoranthus*. Thus, *S. montana* is named for its occurrence at high elevation.

Distribution, habitat, and phenology: This species occurs in humid forests at high elevation (> 1,600 m) in Massif of Ambohimirahavavy in the northern mountain region of Madagascar (Fig. 1J). It grows on gneiss-derived lateritic substrate, and produces fruits in February.

Conservation status: Known only from two specimens collected over 70 years ago and representing two subpopulations that are ca. 48 km apart, *Schrebera montana* has an estimated AOO of 8 km². Although it occurs at a fairly high elevation (> 1,600 m), a review of Google Earth Pro images (Maxar Technologies imagery date 11/05/2014 and CNES/Airbus imagery date 7/19/2019) shows that it occurs in heavily degraded areas. Moreover, various threats are reported from these areas, including shifting cultivation, clearing of forest understory for cultivation of cash crops, illicit selective logging, wildfires, and mineral exploitation of various precious stones. Two locations are identified with regards to the most serious threat of shifting cultivation, of which one is within the COMATSA Nord protected area. Due to ongoing threats that will likely result in the continuing decline of this species' EOO, AOO, habitat quality, number of locations, and number of mature individuals, it is assigned a preliminary status of "Critically Endangered" [CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Vernacular name: Zanana (*Service Forestier 974*).

8. *Schrebera obconicus* (Knobl.) Hong-Wa & Besnard, **comb. nov.**

≡ *Comoranthus obconicus*, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 11: 1032 (1934). Type: MAYOTTE, Mt Bini [M'Bini, Majimbini], forêt de Mazé, [12°44'35"S 45°09'16"E], 16 May 1884, fl., *Humboldt 1137* (cited as 137) (holo-, P [P00184563!], iso-, K [K000614539!], LG [LG0000090026706!], P [P00184564!, P00184565!]).

Additional material: COMOROS, **Grande Comore (Ngazidja)**, entre Mitsamiouli et Ivoini, [11°22'40"S 43°20'15"E], 3 Dec. 1967, fr., *Bernardi 11695* (G, MO [MO-3188438!], P [P00184562!]). MAYOTTE, **Grande Terre**, Boueni, falaise du Boungoudranavi, [12°54'30"S 45°05'08"E], 17 Nov. 2004, fr., *Barthelat et al. 1386* (MO [MO-3188439!], P [P00631048!]);

Chiconi, Réserve Forestière de Sohoa, [12°49'20"S 45°06'14"E], 5 Apr. 2001, fl., *Barthelat et al.* 344 (G, K, MO [MO-3188442!], P [P00229325!]); Chirongui, Mont Chongui, [12°52'50"S 45°09'46"E], 18 Feb. 2004, fl., *Barthelat et al.* 1305 (K, MO [MO-3188441!], P [P00437970!]); Ilots Choazil, [12°40'37"S 45°03'28"E], 29 Apr. 1999, fr., *Mas* 98 (MO [MO-3188440!], P [P00176499!]); Ilots Choazil, Malandzamiayatsini, 12°40'37"S 45°03'28"E, 50-60 m, 29 Apr. 1999, fr., *Pignal* 1367 (P [P00181635!]); Mamoudzou, Mbouzi, 12°48'49"S 45°14'03"E, 126 m, 24 Apr. 2017, st., *Traclet & Boulet*, 446 (MAO, MO [MO-3120558!], P [P02435929!]); Outsoungui [place not found in Mayotte (Choungui? 12°57'S 45°08'E?)], 750 m [elevation higher than highest point in Mayotte, perhaps collected in Comoros], 25 Mar. 1957, *Service Forestier* 16769 (TEF!).

Trees up to 15 m tall, dbh unknown. New twigs light gray to brown, terete to flattened towards the nodes, glabrous, lenticels present. Leaves caducous, simple, oblong to elliptic, 5.2-9.5 x 2.5-3.9 cm, chartaceous to subcoriaceous, concolorous, glossy above, dull below, glabrous, glandular-punctate, sparsely above, densely below, base decurrent, margin revolute, apex acute to slightly acuminate, sometimes abnormally rounded or emarginate, venation brochidodromous, midvein flat above, raised below, secondary veins 8-10, conspicuous, raised slightly on both sides; petioles 0.7-1.2 cm, yellowish to reddish-brown, terete to flattened, canalicate above, glabrous. Inflorescences cymose, axillary and pseudoterminal, up to 7 cm, with 30-60 flowers (3-5 per branch); peduncles 0.9-1 cm, glabrous; pedicels 0.2-0.3 cm, glabrous; calyx 2-3 mm, glabrous, rugose, margin entire, often with one slit, to denticulate, with 4 small teeth, to less frequently distinctly 4-lobed, ciliate; corolla white, tubular to salverform, outside and inside pubescent, the inside visibly stipitate glandular, tube 5-6 mm, with 4 lobes, 2-4 mm, margin entire; filament 1.5-1.8 mm, sparsely glandular-pubescent, anther 2.8-3 mm; ovary conical, 0.8 x 1 mm, style null, glabrous, stigma less than 1 mm, capitate, emarginate. Capsules 3.1-3.4 x 1.6-2.1 cm, light to dark brown, obovate, rarely covered with a transparent pellicle, apex rounded to slightly apiculate, lenticels absent. Seeds flat, winged, 2-2.5 x 0.5-1 cm.

Distribution, habitat, and phenology: *Schrebera obconicus* occurs in mixed forests at low- to mid-elevation, on lavas, in Grande Comore and Mayotte (Fig. 1J). It flowers and fruits between February and December.

Conservation status: Within the Comoro Islands, *Schrebera obconicus* is known from one collection from Grande Comore and eight others from Mayotte, of which two are from the isle of Ilots Choazil and one from the isle of Ilot Mbouzi. Excluding the marine environment renders an EOO of 88 km² for Mayotte only where most collections were made whereas the cumulative AOO within the archipelago is 32 km² (i.e., 4 km² each for Grande Comore, Ilots Choazil, and Ilot Mbouzi, and 20 km² for Mayotte). Seven subpopulations representing seven locations with respect to the most serious threat of deforestation are recognized, of which two occur within the Forest Reserves of Mbouzi and of Sohoa. Continuing decline in AOO, habitat quality, number of locations, and number of mature individuals is expected within Grande Comore and Mayotte with the rise of urbanization. Therefore, *S. obconicus* is preliminarily assessed as "Endangered" [EN B2ab(i,ii,iii,iv,v)] within the entire archipelago.

Vernacular names: Tahila (*Service Forestier* 16769, dialect Mahoran), vavalozza (*Barthelat et al.* 344; *Mas* 98).

Notes: Up until 1956, this species was known only from the type specimen collected in 1884 in Mayotte by Léon Humblot. Subsequent specimens collected in Mayotte and Grande Comore expand its range to surrounding islands of the archipelago. Specimens from Ilots Choazil are morphologically and genetically similar to some specimens from northern Madagascar (Figs 1D, 2), which are putatively new species or hybrids. Therefore, it is possible that there is more

than one species in the Comoro Islands. The specimen *Service Forestier 16769* is said to have been collected at Outsoungui in Mayotte at 750 m elevation. However, that locality name could not be found in Mayotte or the Comoros and may be an ancient name that is no longer used. Moreover, the highest elevation on Mayotte is Benara at 660 m, much lower than the 750 m provided on the label. So, it is possible that this specimen was collected in Grande Comore where elevation reaches 2,361 m.

9. *Schrebera orientalis* Bosser & R.Rabev.

Bulletin du Muséum National d'Histoire Naturelle, séries 4, Section B, Adansonia. Botanique: Phytochimie 7(1): 61 (1985). Type: MADAGASCAR, **Province Antsiranana, Région SAVA**, environs d'Antafononana, à l'ouest d'Amboronala, entre Antalaha et Sambava, [14°04'S 50°02'E], 16 Apr. 1967, fl., *Service Forestier 27716* (holo-, P [P00062750!]; iso-, K [K000233234!], P [P00062751!, P00062752!, P00062753!], MO [MO-2971458!], TEF [TEF000362!]).

Trees 15-20 m tall, dbh unknown. New twigs gray to brown, terete to flattened, widened at the nodes, glabrous, lenticels present. Leaves persistent, imparipinnate, with 5-7 leaflets; petioles 2.7-4.5 cm, brown, terete, canaliculate above, glabrous; rachis brown, canaliculate, glabrous; leaflets ovate, 6.0-10.5 x 2.4-4.0 cm, chartaceous to subcoriaceous, slightly discolorous, darker above, glabrous, irregularly glandular-punctate on both sides, base cuneate or decurrent, margin slightly undulate, revolute near base, apex acute to acuminate, venation brochidodromous, midvein impressed above, raised below, secondary veins 10-12, conspicuous, flat above, slightly raised below; petiolules 0.8-2.2 cm. Inflorescences cymose, axillary and pseudoterminal, 7.4-8.6 cm, with more than 50 flowers; peduncles 2.6-4.5 cm, glabrous; pedicels 0-0.5 cm, glabrous; calyx 2-3.5 mm, with 4 lobes, glabrous, margin undulate; corolla color unknown but white on rehydrated sample, tubular to salverform, outside glabrous, inside with a ring of dark glandular hairs at throat, tube 6-9 mm, with 5 lobes, 2-3 mm, margin undulate; filament 1.7 mm, glabrous, anther 3-4 mm; ovary rounded, 1 x 1 mm, style 2.8 mm, stigma 1 mm, bifid, exserted. Fruits unknown.

Distribution, habitat, and phenology: *Schrebera orientalis* occurs at low-elevation humid forest, on sandy substrates, in northeastern Madagascar (Fig. 1J). It produces flowers in April.

Conservation status: *Schrebera orientalis* is known only from a single collection, representing one subpopulation and one location, which is not within a protected area. This species was last collected over 50 years ago just east of Marojejy National Park and south of the newly established Makirovana Tsihomanaomby protected area. Given that this area has been relatively well-collected in the past decades without yielding any new specimens of *S. orientalis*, it is assumed that this species is very rare or that its population has greatly declined since the time of collection. Its habitat is also subjected to ongoing threats from slash-and-burn agriculture, illegal timber logging for local consumption, exploitation of precious woods, clearing of forest understory for cultivation of cash crops, and occasional wildfires. With an AOO of 4 km² and continuing decline in AOO and habitat quality, *S. orientalis* is assigned a preliminary status of "Critically Endangered", and could be possibly extinct [CR(PE) B2ab(ii,iii)]. Indeed, *S. orientalis* is a large tree that should not be hard to miss, so it is possible that it has been overexploited beyond recovery.

Vernacular name: None recorded.

Notes: The specimen *Service Forestier 18186*, considered as a paratype of *Schrebera orientalis* (Bossler & Rabevohitra, 1985), is herein placed as the type of the newly recognized *S. littoralis*.

10. *Schrebera trichoclada* Welw.

Transactions of the Linnean Society, Botany, London, 27: 41 (1869). Lectotype (here designated): ANGOLA, Iter Angolense, **Pundo Andongo**, Jun. 1856 - 1857, fl., *Welwitsch 936* (lecto-, BM [BM000925529!], isolecto-, K [K000233241!], P [P00413206!]).

Additional material: MADAGASCAR, **Province Antsiranana, Region DIANA**, Antsiranana II, Mangoaka, Andolotsaiky, [12°19'S 49°07'E], 24 Apr. 1981, fr., *Service Forestier 30739* (P [P04065493!], TEF!); Antsiranana II, Ramena, Betahitra, [12°21'S 49°18'E], 11 Mar. 1981, fr., *Service Forestier 30742* (P [P04065494!], TEF!); Antsiranana II, Mont des Français, Ramena, Betahitra, [12°22'S 49°21'E], 12 Jun. 1981, *Service Forestier 30999* (TEF!); Diégo-Suarez, Bobaomby, Andohazompona, Windsor Castle, [12°14'S 49°10'E], 300 m, 27 Jan. 1955, fl., *Service Forestier 12740* (P [P04065472!], TEF!); Diégo-Suarez, Bobaomby, Andohazompona, Windsor Castle, [12°14'S 49°10'E], 27 Jan. 1955, fr., *Service Forestier 12742* (P [P04065481!], TEF!); Diégo-Suarez, Montagne des Français, Betahitra, [12°22'S 49°21'E], 25 May 1955, fr., *Service Forestier 14227* (P [P04065468!, P04065474!, P04065475!], TEF!); Andranovondronina, Antsisikala, Ankorovolabe, 12°09'27"S 49°12'24"E, 90 m, 13 May 2005, fr., *Guittou et al. 96* (CNARP, MO [MO-3188410!], P [P04065477!], TAN!); Andranovondronina, Antsisikala, à l'ouest d'Ampasikely, 12°11'35"S 49°12'45"E, 197 m, 13 May 2005, fr., *Ramananjahary et al. 290* (CNARP, MO [MO-3188409!], P [P04065480!], TAN!); Ankara, [12°49'S 49°01'E - 13°00'S 49°17'E], 50-409 m, 27 Nov. 1952, *Service Forestier 6211* (P, TEF!); Ouest (Nord): au sud-ouest d'Andrakaka (bordure ouest de la baie de Diégo-Suarez), [12°16'S 49°15'E], 50-75 m, 14 Nov. 1962, fr., *Service Forestier 20907* (P [P04065490!, P04065491!], TEF!); Ouest (Nord): au PK 8 de la route Diégo-Suarez à Orangéa, [12°16'S 49°25'E], 118 m, 24 Nov. 1964, fl., *Service Forestier 23238* (P [P04065486!, P04065487!, P04065488!], TEF!); Ouest (Nord): près d'Andrakaka à l'ouest de Diégo-Suarez, [12°15'S 49°21'E], 27 Feb. 1964, fl., *Service Forestier 23278* (MO!, P [P04065483!, P04065484!, P04065485!, P04065489!], TEF!); **Province Mahajanga, Region Boeny**, Ambondromamy, forêt de Befotaka, 16°22'39"S 47°10'28"E, 17 Apr. 2007, fr., *Razakamalala et al. 3373* (MO!, P [P04065476!], TAN); **Region Sofia**, environs de Mandritsara, [14°45'S 49°30'E], 700 m, 1 Sep. 1922, fl., *Perrier de la Bâthie 15044* (P [P04065478!, P04065479!], TEF!); **Province Toliara, Region Menabe**, Morondava, Bemanonga, Marofandilia, Kirindy, à 60 km NE de Morondava, 20°03'39"S 44°39'28"E, 59 m, 21 Apr. 2013, fr., *Razakamalala et al. 7455* (DOV!, MO!, P [P01071657!], TAN); Morondava, 1 km à l'ouest de Bekinana, [20°36'S 44°27'E], 19 Mar. 1956, fr., *Réserves Naturelles 160-R-190* (P [P04065473!], TEF!); Marofandilia (Kirindy), [20°08'S 44°33'E], 29 May 1980, fr., *Service Forestier 29843* (P [P04065492!], TEF!).

Shrubs or trees up to 25 m tall, dbh up to 60 cm. New twigs dark gray to light brown, terete, glabrous, lenticels present. Leaves caducous, simple, narrowly elliptic to ovate, 7.8-10.2 x 3.1-4.8 cm, papery, slightly discoloured, the lower paler, but both surfaces dull, glabrous, sometimes sparsely pubescent along lower midvein, sparsely glandular-punctate on both sides, base rounded to obtuse, margin undulate or rarely flat, apex acuminate to short acuminate, venation brochidodromous, midvein impressed above, raised below, secondary veins 7-13, very conspicuous, flat above, raised slightly below, petioles 0.9-2.1 cm, light brown, terete, canaliculate above, glabrous. Inflorescences cymose, pseudoterminal, 2.4-5.8 cm, with 4-17 flowers; peduncles 1.1-2.1 cm, glabrous, rarely pubescent; pedicels 0.3-0.6 cm, glabrous, rarely pubescent; calyx 2-3 mm, without lobes or with 4 broad undulations, glabrous, rarely pubescent, margin entire, ciliolate; corolla white tinged purple, salverform to campanulate, outside glabrous, inside with a ring of red glandulous hairs at throat, tube 11-13 mm, with 5-6

lobes, 4-7 mm, margin crenulate; filament 1.7 mm, glabrous, anther 5 mm; ovary conical, 1.5 x 1.7 mm, style 5 mm or 15 mm, heterostylous, glabrous, stigma 0.5 mm or 1 mm in short-styled and long-styled flowers, respectively, bilobed, exserted in long-styled flowers. Capsules 4.4-5.9 x 2.0-3.5 cm, yellowish to brown, clavate to pyriform, apex rounded, lenticels present. Seeds flat, winged, 2.5-4.5 x 1-1.2 cm.

Distribution, habitat, and phenology: *Schrebera trichoclada* occupies low- to mid-elevation dry forests, on lavas, limestones, and sands, from Diégo-Suarez in the north to Toliara in the south, with its highest concentration seemingly in the north (Fig. 1J). It has flowers and fruits between September and May.

Conservation status: Our assessment included 19 specimens representing 14 subpopulations and resulted in an EOO of 96,546 km² and an AOO of 64 km². Given that *Schrebera trichoclada* has a wide range from northern to southwestern Madagascar and that it may still be uncollected in some areas with suitable habitat, it is likely that the AOO is much larger than that is estimated. Its habitat is subjected to various threats, including frequent wildfires, shifting cultivation, and illegal logging for timber and for charcoal production. Fourteen locations are identified with regard to wildfires and slash-and-burn agriculture, of which three occur within protected areas (i.e., Menabe-Antanimena, Montagne d'Ambre, and Montagne des Français). With a large EOO and a good representation within protected areas, *S. trichoclada* is preliminarily assessed as "Least Concern" [LC].

Vernacular names: Vavalozza (*Service Forestier* 12740, 14227, 29843, 30742, 30999), vanaka (*Service Forestier* 30742).

Notes: The description provided here is based on Malagasy specimens, which are generally glabrous, but can sometimes be sparsely pubescent along the lower midvein. The specimens from Africa vary from glabrous to pubescent. The Malagasy specimens were once considered to be a distinct and new species (*Schrebera suarezensis* R.Capuron [ined., 1956]), but were ultimately recognized as belonging to *S. trichoclada* by Bosser & Rabevohitra (1985). Phylogenetic analyses showed a deep divergence between the Malagasy and the African *S. trichoclada* as well as between the East African and the Western-Central African members of this species (Fig. 3). It is, thus, possible that these taxa represent distinct entities in need of further taxonomic assessment.

11. *Schrebera trifoliata* Frasier, G.E. Schatz & Hong-Wa, **sp. nov.** (Fig. 8)

Diagnosis: *Schrebera trifoliata* can be easily recognized by its coriaceous, trifoliolate leaves, red flowers, and smaller fruits. It can be distinguished from other species by these characters.

Type: MADAGASCAR, **Province Toliara, Region Anosy**, Fort-Dauphin, Iabokoho, Antsotso, forêt Ivohibe, 24°34'26"S 47°11'42"E, 261 m, 1 Dec. 2005, fl., *Razakamalala et al.* 2681 (holo-, MO [MO-3188403!], iso-, P!, TAN!).

Paratypes: MADAGASCAR, **Province Toliara, Region Anosy**, Fort-Dauphin, Iabokoho, Antsotso, Bemangidy, forêt Vohibe, 24°34'10"S 47°12'37"E, 41 m, 24 May 2006, fr., *Antilahimena* 4894 (MO [MO-3188401!], P!, TAN!); Fort-Dauphin, Iabokoho, Antsotso, Bemangidy, forêt Vohibe, 24°34'09"S 47°12'23"E, 90 m, 12 Feb. 2006, fr., *Rabenantoandro et al.* 1737 (MO, P, TAN!); Fort-Dauphin, Iabokoho, Antsotso, Bemangidy, forêt Vohibe, 24°34'14"S 47°12'10"E, 280 m, 2 Apr. 2008, fr., *Rabenantoandro et al.* 1909 (MO [MO-3188404!], P!, TAN!); Fort-Dauphin, Iabokoho, Antsotso Avaratra, 24°34'35"S 47°12'28"E, 25 m, 12 Dec. 2007, fl.-fr., *Razakamalala et al.* 4029 (MO [MO-3188402!], P!, TAN!).

Shrubs to small trees up to 4 m tall, dbh unknown. New twigs gray, terete, glabrous, lenticels present. Leaves persistent, trifoliolate; petioles 1.2-2.6 cm, reddish-brown, terete, flat to canaliculate above, glabrous; rachis brown, canaliculate, glabrous; leaflets elliptic, 2.9-7.1 x 1.7-3.6 cm, coriaceous, slightly discolorous, the lower paler, glabrous, glandular-punctate on both sides, base cuneate to decurrent, margin smooth, apex rounded to retuse, venation brochidodromous, midvein impressed above, raised below, secondary veins 7-12, conspicuous, flat to slightly raised above, raised below; petiolules 0.3-1.1 cm. Inflorescences cymose, axillary and pseudoterminal, 3.2-5.2 cm, with 3-4 flowers; peduncles 0.9-1.7 cm, glabrous; pedicels 0.5-1.7 cm, glabrous; calyx 2.4-4 mm, with 4 lobes, glabrous, margin crenulate; corolla red, salverform to campanulate, outside and inside glabrous, tube 3-15 mm, with 6 lobes, 2-5 mm, margin entire; filament 1 mm, glabrous, anther 2.9 mm; ovary conical, 0.8 x 1 mm, style 16 mm, glabrous, stigma 1 mm, bilobed, exserted. Capsules 1.3-2.0 x 0.6-1.2 cm, brown, sometimes glaucous, clavate, apex rounded, lenticels absent. Seeds unknown.

Etymology: This species is named for its distinctive trifoliolate leaves.

Distribution, habitat, and phenology: *Schrebera trifoliata* occurs in low-elevation humid forests, on basement rocks, in the southeast coast of Madagascar near Fort Dauphin (Fig. 1J). It bears flowers and fruits between December and May.

Conservation status: *Schrebera trifoliata* is known from five specimens collected within a radius of 1 km. Although the specimens overlapped three adjacent grid cells, which rendered an AOO of 12 km², the EOO itself is 0.7 km² and is a more accurate measure of the known range of this species. All but one specimen occurs within the newly established Tsitongambarika protected area. However, threats such as slash-and-burn agriculture, illicit mining operations, illegal logging, and other types of wood exploitation are still reported within the protected area. Therefore, the protection afforded to this species is uncertain, particularly as it is only known from a single location with regard to the most serious threat of slash-and-burn agriculture, and its only known population is located at the edge of the protected area where anthropogenic pressure is likely to continue. As such, *S. trifoliata* is assigned a preliminary status of "Critically Endangered" [CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Vernacular name: None recorded.

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DATA AVAILABILITY

The genetic data and scripts underlying this article are available in Figshare, at <https://figshare.com/s/9f04a29df46c70a3d05d>
Quantitative morphological data are within the Supplementary Material.

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SUPPLEMENTARY MATERIAL

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Measurements from leaf, flower, and fruit used in morphometric analyses.

Table S2. Information on accessions used in phylogenetic inferences: species names, voucher information, geographic distribution, and accession numbers.

Table 1. Material analyzed for phylogenetic reconstructions

<i>Species</i>	<i>Country, State or Province, Locality</i>	<i>Specimen (Institution, Accession or Barcode)</i>	<i>Collection date</i>
	-AFRICA		
<i>Schrebra alata</i>	[Tropical Africa] - Cultivated, Göttingen BG	XX-0-GOET-14122	-
	[South Africa] - Cultivated, Kew BG	M.W. Chase 3883 (K)	-
	Zimbabwe	D.C. Plowes 1303 (NY)	1951
	South Africa, Kruger NP, Tshokwane	O. Maurin 318 (PET)	17 Sep 2005
	South Africa, Kruger NP, Pretoriuskop	O. Maurin 1221 (PET)	23 Jan 2007
<i>S. arborea</i>	Cameroon, NE Bangé	R. Letouzey 5136 (K)	25 May 1963
<i>S. trichoclada</i>	Mozambique, Sofla, Levasflor	O. Maurin 2636 (PET)	14 Jun 2010
	DR Congo, Mambasa, Ituri Forest	T.B. Hart 1544 (MO, 4398830)	26 Apr 1993
	Tanzania, Kilosa, Vuma Hill	P.J. Greenway 15382 (MO, 2218755)	9 Jul 1973
	-AMERICA		
<i>S. americana</i>	Peru, Cajamarca, Cutervo-Querocotillo	A. Weberbauer 7169 (US, 1495420)	31 Jul 1915
	Peru, Cajamarca, Lajas-Cochabamba	I.M. Sánchez Vega 5857 (MO, 3318720)	1 Nov 1991
	-ASIA		
<i>S. swietenoides</i>	Myanmar, Pegu Range	W.S. Kurz 2312 (K)	1872
	Thailand, Kanchanaburi, Si Sawat	C.F. van Beusekom 3815 (MO, 2366407)	16 Nov 1971
	-MADAGASCAR AND THE COMORO ISLANDS		
<i>S. australis</i>	Madagascar, Toliara, Bevilany	Service Forestier 22400 (P, P06774785)	13 Jan 1963
<i>S. capuronii</i>	Madagascar, Antsiranana, Ampondrabe	P. Ranirison & L. Nusbaumer 940 (K, K000197191)	21 Feb 2005
<i>S. humberitii</i>	Madagascar, Antsiranana, Fanambana-Manambery	Service Forestier 27233 (P, P06774781)	13 Dec 1966
<i>S. madagascariensis</i>	Madagascar, Antsiranana, Ambolobozokely	F. Ratovoson et al. 1116 (TAN)	23 Mar 2006
	Madagascar, Antsiranana, Montagne des Français	Service Forestier 20913 (K)	13 Feb 1962
<i>S. minor</i>	Madagascar, Toliara, Ankoba	R. Randrianaivo et al. 1757 (MO, MO-3188433)	25 Feb 2009
	Madagascar, Toliara, Tsimanampetsotsa	F. Ratovoson 1457 (MO, MO-3188435)	14 Mar 2008
<i>S. obconicus</i>	Mayotte, Ilots Choazil	C. Mas 98 (P, P00176499)	29 Apr 1999
<i>S. orientalis</i>	Madagascar, Antsiranana, Antafononana	Service Forestier 27716 (MO, MO-2971458)	16 Apr 1967
<i>S. trichoclada</i>	Madagascar, Antsiranana, Antsisikala	R. Ramananjahary et al. 290 (P, P04065480)	13 May 2005

Table 2. Best partition scheme and best-fit model per partition according to Bayesian information criterion (BIC) implemented in ModelFinder

Partition	Seq	Sites	Unique	Infor	Invar	Substitution Model
<i>matK</i> , <i>ndhF</i> , and <i>trnK</i> genes, and <i>trnL-trnF</i> spacer	29	4964	276	174	4717	K3Pu+F+R3
<i>rbcL</i> , <i>rpoC1</i> , <i>rpoC2</i> , <i>rps16</i> genes	28	9678	256	164	9458	TVM+F+I
<i>ycf1</i> gene and spacers: <i>trnQ-rps16</i> + <i>trnS-trnG</i> + <i>trnT-trnL</i>	25	8893	523	376	8365	TVM+F+R2
<i>ycf2</i>	23	6510	50	25	6479	F81+F
nrDNA	25	8005	690	0	7289	JC+I

Seq: Number of sequences

Sites: Total number of sites

Unique: Number of unique site patterns

Infor: Number of parsimony-informative sites

Invar: Number of invariant sites (for this dataset, this represents also the number of constant sites)

Table 3. Summary statistics of crown node ages for selected nodes from a sample of 500 bootstrap trees

<i>MRCA</i>	<i>Median</i>	<i>95% HPD (lower – upper)</i>
Root node	34.4	37.1 – 32.0
MRCA of <i>Schrebera swietenoides</i> and <i>S. madagascariensis</i>	30.7	33.2 – 27.5
MRCA of <i>S. trichoclada</i> and <i>S. madagascariensis</i>	28.5	30.7 – 25.9
MRCA of <i>S. alata</i> and <i>S. madagascariensis</i>	25.6	28.4 – 22.9

MRCA: most recent common ancestor

Median: median age estimated from sample of 500 bootstrap trees

95% HPD: highest posterior density interval that contains 95% of the estimates for the node age

Table 4. Biogeographic model selection in BioGeoBEARS. Best model in bold.

<i>Model</i>	<i>LnL</i>	<i>N params</i>	<i>d</i>	<i>e</i>	<i>j</i>	<i>w</i>	<i>AICc</i>	<i>AICc weight</i>
DEC	-16.18	3	2.0e-02	0.0080	0	2.76	39.62	0.03
DEC+J	-13.21	4	1.0e-12	1.0e-12	0.083	2.45	36.64	0.13
DIVALIKE	-13.47	3	1.9e-02	0.0002	0	2.91	34.19	0.44
DIVALIKE+J	-12.09	4	1.0e-12	1.0e-12	0.083	2.54	34.42	0.39
BAYAREALIKE	-21.53	3	1.4e-03	0.028	0	1.00	50.32	0.00
BAYAREALIKE+J	-15.46	4	1.0e-07	1.0e-07	0.060	0.99	41.15	0.01

LnL: log-Likelihood of the model

N params: number of free parameters estimated

d: rate of 'dispersal' (range expansion)

e: rate of 'extinction' (range contraction)

j: relative per-event weight of jump dispersal

w: exponent on manual dispersal multipliers (modifies *d, j*)

AICc: Akaike information criterion with a correction for small sample sizes

AICc weight: relative likelihood of the model divided by the sum of these values across all models

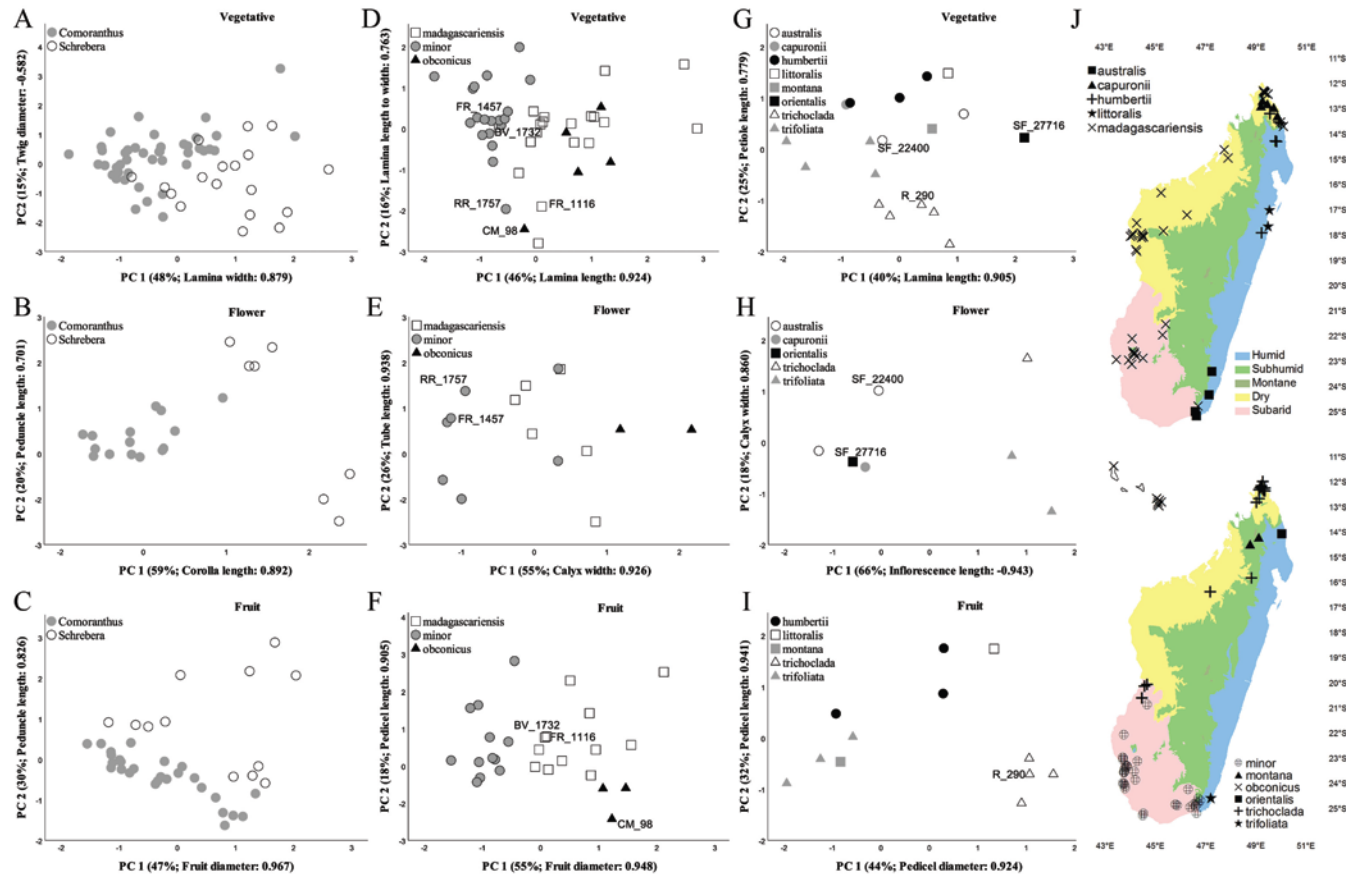


Figure 1. Principal component analyses of quantitative morphological characters of *Comoranthus* and Malagasy *Schrebera* (A-I), and their distribution in Madagascar and the Comoro Islands (J). **A-C:** patterns between *Comoranthus* and Malagasy *Schrebera*. **D-F:** patterns within *Comoranthus*. **G-I:** patterns within Malagasy *Schrebera*. Specimens used in phylogenetic inferences are noted as follows: CM_98 (*Mas* 98), FR_1116 (*Ratovoson et al.* 1116), FR_1457 (*Ratovoson* 1457), R_290 (*Ramananjahary et al.* 290), RR_1757 (*Randrianaivo et al.* 1757), SF_22400 (*Service Forestier* 22400), SF_27716 (*Service Forestier* 27716) [BV_1732 is noted as a proxy for accession *Service Forestier* 20913, which is missing from the morphological analyses, but both are morphologically similar and were collected from the same locality]. **J:** distribution of the 11 morphogroups of the *Comoranthus*-Malagasy *Schrebera* complex in Madagascar and the Comoro Islands overlaid on the five simplified bioclimatic zones of Madagascar (Schatz, 2000; after Cornet, 1974).

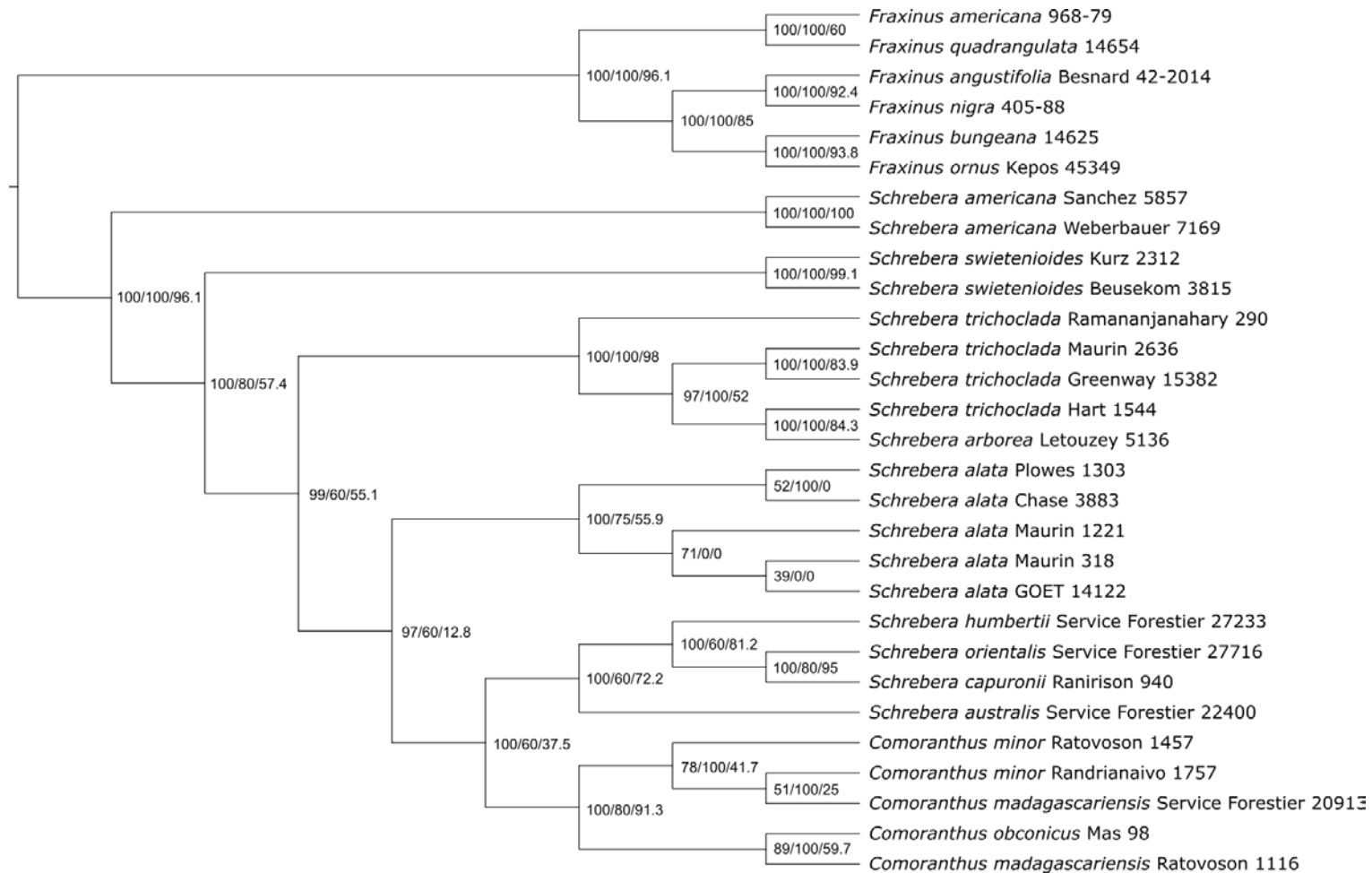


Figure 2. Cladogram based on the best ML tree found representing the relationships between the species in Schreberinae and outgroups, and the support for all clades. At each node, the three values represent: (1) the bootstrap support, (2) the gene concordance factor (gCF), and (3) the site concordance factor (sCF).

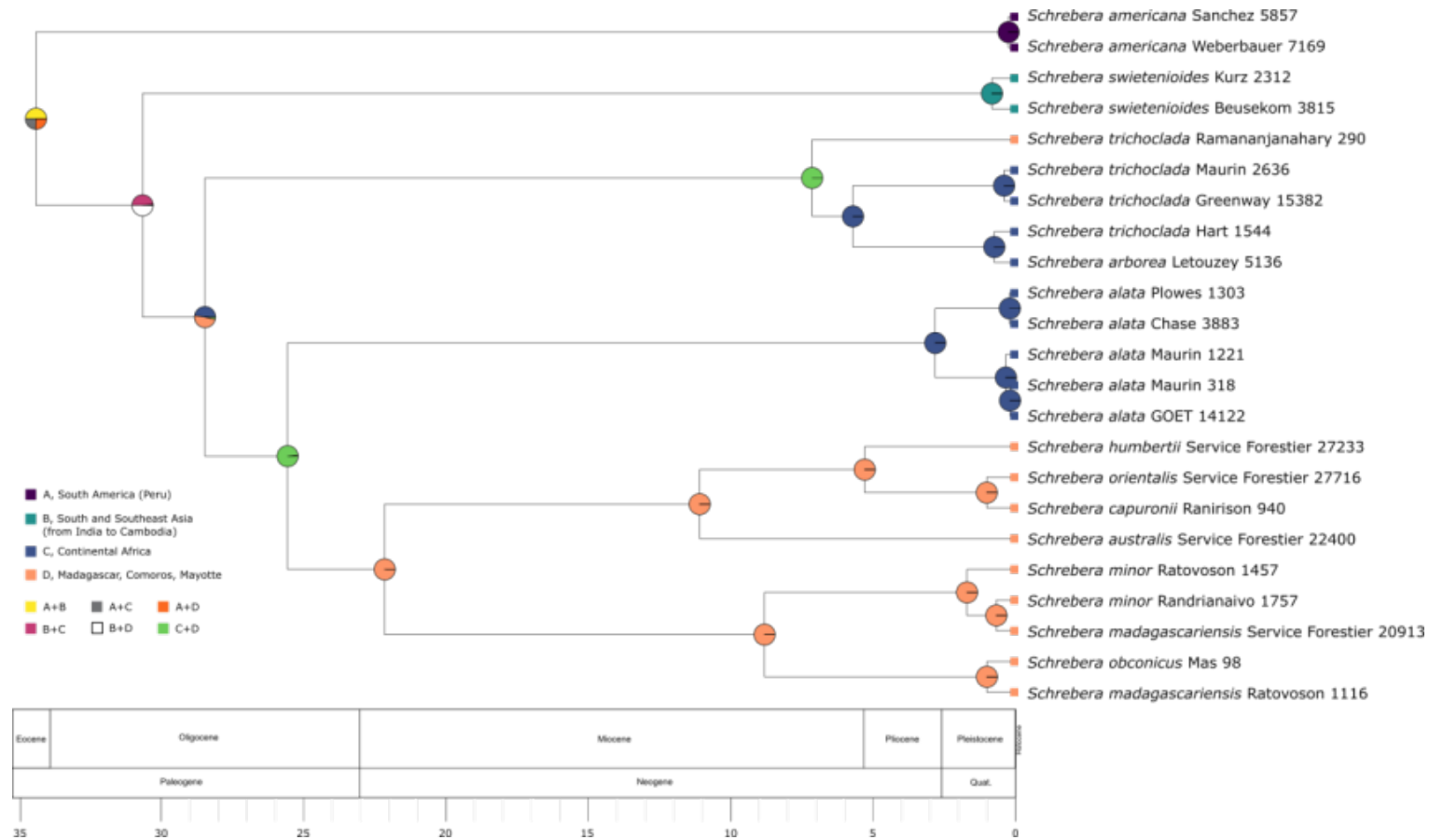


Figure 3. Summary of the biogeographic history of Schreberinae. The chronogram shown here is the dated, best ML tree from our tree search. Species names have been updated to represent the proposed nomenclatural changes here (*Comoranthus* species subsumed under *Schrebera*). At the tips, colored squares represent the distribution of each taxon, and at the nodes the pies show the estimated probability of ancestral ranges. Those node state probabilities result from the best biogeographic model for this data, DIVALIKE. Colors at the tips and nodes are explained in the legend on the lower left. The scale at the bottom represents time in millions of years from the present, and indicates the periods (bottom) and epochs (top).



Figure 4. *Schrebera australis* Frasier, G.E. Schatz & Hong-Wa. Flowering and fruiting branch [*Service Forestier* 22400].

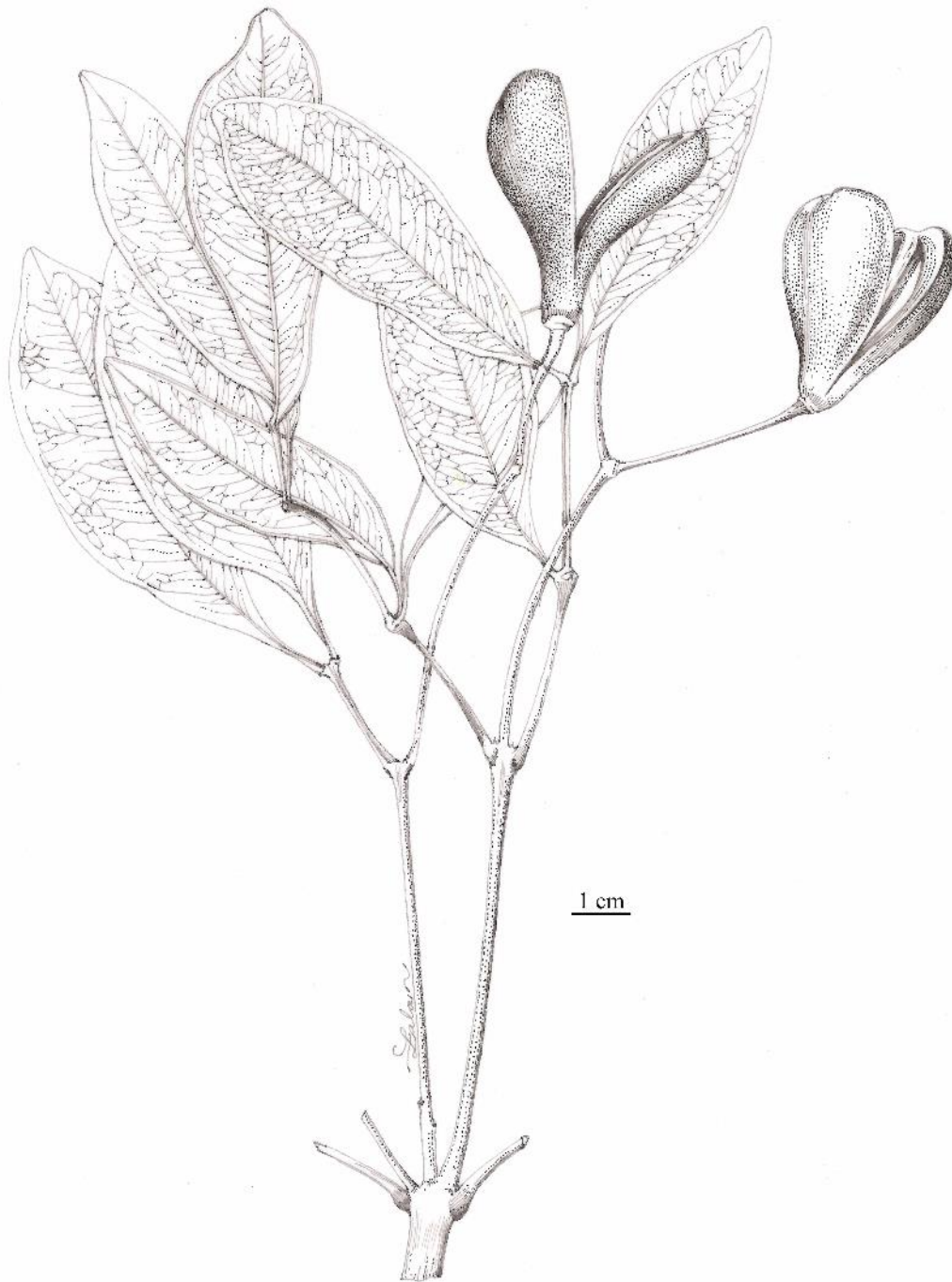


Figure 5. *Schrebera humbertii* Frasier, G.E. Schatz & Hong-Wa. Fruiting branch [*Service Forestier 27233*].

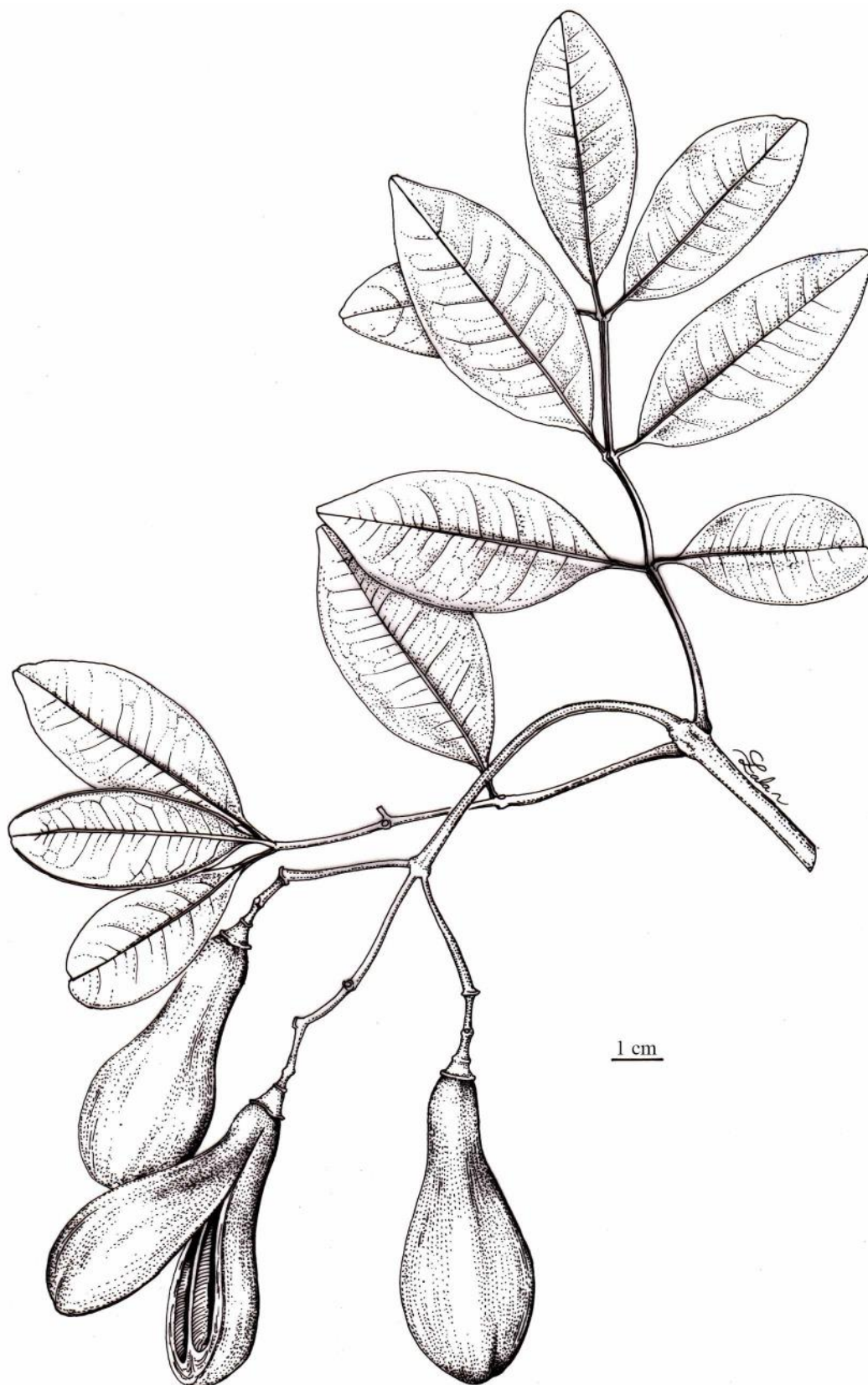


Figure 6. *Schrebera littoralis* Frasier, G.E. Schatz & Hong-Wa. Fruiting branch [*Service Forestier* 18186].

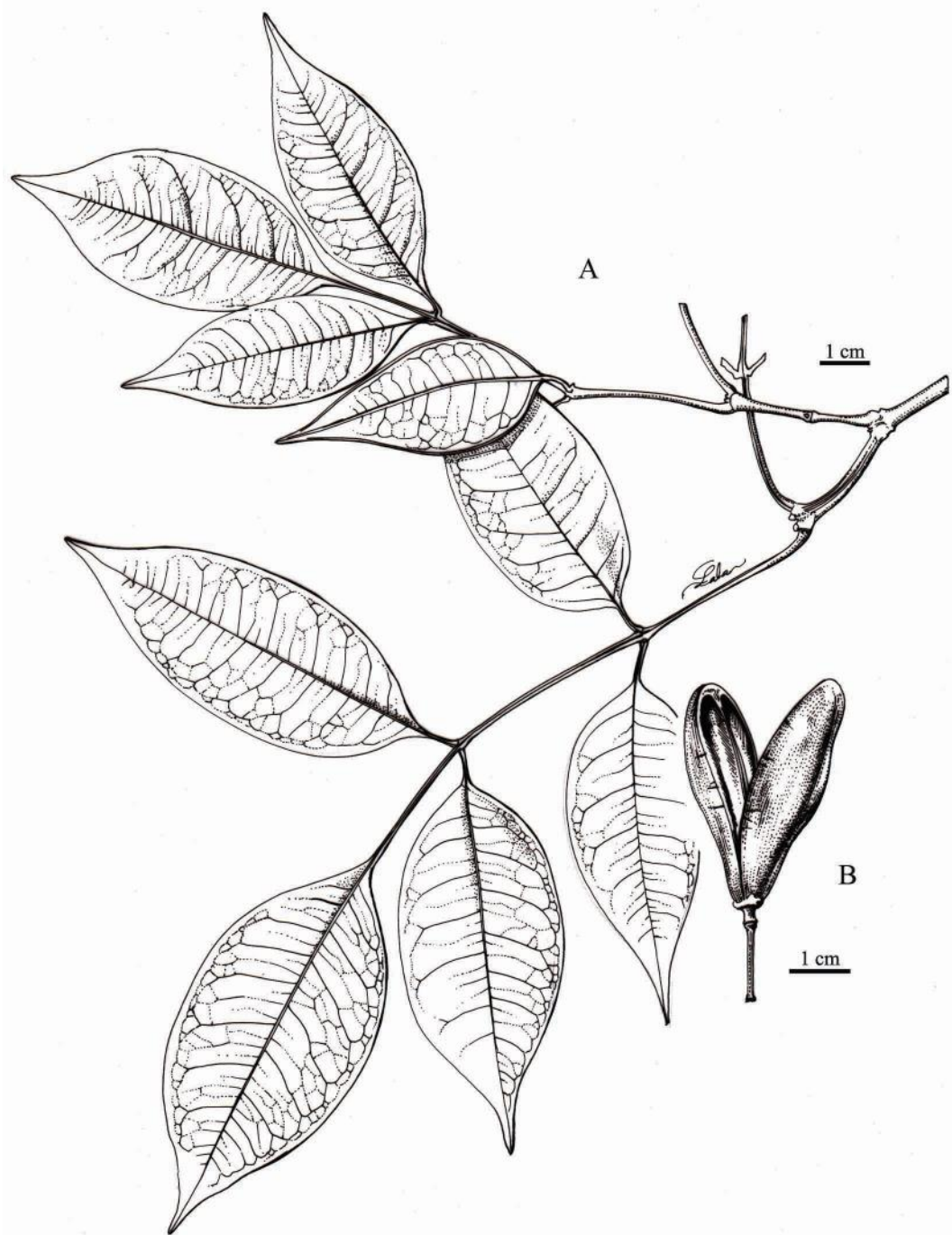


Figure 7. *Schrebera montana* Frasier, G.E. Schatz & Hong-Wa. **A.** Branch. **B.** Fruit [A & B: *Service Forestier* 974].



Figure 8. *Schrebera trifoliata* Frasier, G.E. Schatz & Hong-Wa. **A.** Fruiting branch. **B.** Fruit. **C.** Flowering branch [A & B: *Antilahimena* 4894; C: *Razakamalala et al.* 2681].