Phylogeny, Biogeography, and a Taxonomic Revision of *Rinorea* (Violaceae) from Madagascar and the Comoro Islands

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This dissertation titled
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from Madagascar and the Comoro Islands

by

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Abstract

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*Rinorea* Aublet is a pantropical genus of shrubs and small trees and is
the second most species-rich genus in the Violaceae with an estimated 225–
275 species. The species in Madagascar and the Comoro Islands have not
been revised since 1949, nor has there been an adequate understanding of
infrageneric groupings, phylogeny, and biogeography for the entire genus. The
goals of this study were: 1) taxonomic revisions of two species-rich infrageneric
groups of Malagasy and Comorian *Rinorea* (R. subsect. *Verticillatae* and the *R.
arborea* species group), 2) a revised infrageneric classification of the African
and Malagasy species, 3) phylogenetic reconstruction inferred from chloroplast
dNA sequences with genus-wide taxon sampling, and 4) biogeographic
inferences of the Malagasy species.

The revision of the genus *Rinorea arborea* group and *R.* subsect.
*Verticillatae*, resulted in nine and three new species, respectively. Forty-one
species of *Rinorea* are here recognized for Madagascar and the Comoro
Islands. A newly proposed infrageneric classification of African and Malagasy
*Rinorea*—based on morphometric and molecular phylogenetic evidence—
recognizes 11 taxonomic sections, including four new sections: *Arboreae*,
*Squamosae*, *Angustifoliae*, and *Ellipticae*. 
Phylogenetic analyses of three chloroplast regions (trnL-trnF spacer, trnL intron, and trnD-trnE spacer) provided strong branch support for a Paleotropical clade, which was further divided into two subclades: a 3-ovule clade and a 6-ovule clade. *Rinorea* subsect. *Verticillatae* showed a moderately to highly supported sister relationship to the Asian species. Biogeographic analyses confirmed at least five dispersals between Africa and Madagascar, and one between Madagascar and Asia.

The rate of endemism for Malagasy *Rinorea* is in excess of 90%. Phylogenetic and biogeographic analyses reveal that ca. 37% of species have affinities to African relatives and the remaining 63% (i.e., subsect. *Verticillatae*) are more closely related to Asian species. Several species are critically endangered or presumed extinct, while others are represented by substantial populations in protected areas.

Approved:

_____________________________________________________________

Harvey E. Ballard, Jr.

Associate Professor of Environmental and Plant Biology
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Chapter 1.

Introduction

The Genus *Rinorea*.

*Rinorea* Aublet is a pantropical genus of shrubs and small trees and is the second most species-rich genus in the Violaceae with an estimated 225–275 species. The diversity of species is mostly well known for the Neotropics, but the number of species in Asia, Madagascar, and Africa is not well understood. The most recent revision of Malagasy and Comorian *Rinorea* recognized 32 taxa (Perrier, 1949). The diversity of the African species is even less well known with estimates ranging from 110–150 (Achoundong, 1996; Wahlert, unpubl. data). In some humid and semi-deciduous forests across its range, *Rinorea* can be a locally common or abundant element in the understory and may even occur in monospecific stands (Thomas et al., 2003; Van Velzen, 2006; Wahlert, pers. obs.).

Taxonomy and Phylogeny.

As currently circumscribed, *Rinorea* is not a monophyletic group. Molecular phylogenetic studies in the family have placed *Rinorea uxpanapana* with *Hybanthus* (Feng, 2005). Also, the two species *Rinorea virgata* and *R. heteroclita* are distantly related to the core *Rinorea* clade and are to be transferred back to the earlier generic name *Dioryctandra* [synonym:
Scyphellandra] (Feng, 2005; Ballard et al., unpublished data). Other molecular phylogenies have shown the genus *Fusispermum* to be basalmost in the Violaceae, with the divergent *Rinorea apiculata* group interior to *Fusispermum*. Then, interior to the *Rinorea apiculata* group is the “core” *Rinorea*. Figure 1 summarizes the pattern of relationships that have been recovered in different molecular phylogenetic studies using both chloroplast and nuclear DNA regions (Wurdack and Davis, 2009; Tokuoka, 2007; Feng, 2005). No comprehensive phylogenetic inference has been made for the “core” *Rinorea* with taxon sampling across its range of distribution and breadth of morphological diversity. The focus of this study are the species in the “core” *Rinorea* group (references to *Rinorea* in this volume refer to the core group of *Rinorea*, while the more basal *Rinorea apiculata* group will be referred to as such).

No genus-wide infrageneric classification has been proposed for *Rinorea*. Engler (1904) erected a classification for the African and Malagasy species based primarily on characters of the androecium. This classification was expanded by Brandt (1914) and followed by de Wildeman (1920), however, there are several significant errors with this classification. For example, the morphologically dissimilar and distantly related species *Rinorea angustifolia*, *R. elliptica*, and *R. squamosa* are all placed together in *Rinorea* sect. *Ardisianthus*. Furthermore, species in the *Rinorea arborea* group were never assigned to an infrageneric taxon. Taxonomic studies reveal six infrageneric groups of *Rinorea* in Madagascar: the *Rinorea arborea* group, the *R. elliptica* group, the *R. angustifolia* group, the *R. squamosa* group, *R. subsect. Ilicifoliae* Engl., and *R. subsect. Verticillatae* Engl. Except for subsect. *Verticillatae*, which is a
Malagasy and Comorian endemic group, the other five groups contain species that also occur in Africa (Wahlert and Ballard, 2008).

The Comoro Islands have a similar representation of species groups as Madagascar, except that the Rinorea angustifolia group is conspicuously absent. In Madagascar, three species groups are represented by a single species (R. angustifolia, R. squamosa, and R. spinosa in subsect. Ilicifoliae) and a fourth group, the Rinorea elliptica group, is represented by three species: R. calycina, R. greveana, and R. pugionifera. The two remaining groups, Rinorea arborea group and R. subsect. Verticillatae, contain eight and 26 species, respectively (Chapters 3 and 4, respectively). A key to the species and species groups of Rinorea in Madagascar and the Comoro Islands is given below.

**Biogeography.**

Madagascar is one of the world’s great biodiversity hotspots with approximately 10,000–12,000 species of plants, many of which are endemic (Schatz, 2001). The diversity of Malagasy Rinorea given in Perrier (1949) suggests a rate of endemism of ca. 90%. Several factors have contributed to the floristic diversity: the tectonic history and isolation of Madagascar, a wide variety of geologic substrates, a variable topography, and climatic gradients (Yoder and Nowak, 2006). The phytogeographic affinities of the Malagasy flora have been shown to have its strongest affinity to the flora of Africa, but also other source areas, including Asia (Schatz, 1996). It is generally agreed that
long-distance dispersal to Madagascar has been the more important process in the assembly of the flora (e.g., Janssen et al., 2008). Invoking vicariance to explain shared Gondwanan floristic elements would be inconsistent with the fact that the diversification of modern flowering plant families had not yet taken place by the time Madagascar and Africa separated 158–160 Ma (e.g., Gautier and Goodman, 2003).

Recent molecular phylogenetic studies of Malagasy plant groups have provided new lines of evidence that support ongoing long-distance dispersal to Madagascar in many different plant groups. Yoder and Nowak (2006) reported that 36% of Malagasy taxa showed a sister relationship to African taxa, and that 25% showed a sister relationship to Asian taxa. Taxonomic studies of herbarium material show several Malagasy and Comorian Rinorea species to have obvious affinities to (or are conspecific with) African species. However, the opposite-leaved species of Malagasy and Comorian Rinorea are morphologically divergent and show no affinities to any other group of Rinorea.

Morphology.

In most floristic and taxonomic treatments of the Violaceae, the genus Rinorea is described as having actinomorphic flowers—but this is an entirely misleading concept. Dissection of ca. 700 flowers from species across the phylogenetic breadth and geographic range of the genus, as part of this dissertation, have shown the corolla in Rinorea to range from subequal to strongly zygomorphic (e.g., Wahlert and Ballard, 2009). In many species,
careful dissection of the flower reveals three sets of petals: an anterior petal, two lateral petals, and two posterior petals. The three sets of petals in *Rinorea* are likely homologous to the three sets of petals in other strongly zygomorphic taxa, such as *Viola*.

The three sets of petals in *Rinorea* can often be differentiated by characteristics such as petal indumentum, petal shape, folding of the petal (planar vs. conduplicate), and petal margin (entire vs. ciliate). Species with zygomorphic corollas are particularly common in Africa and Madagascar but are also found in the Neotropics and Asia (Wahlert, unpubl. data). In some other species (e.g., *R. ilicifolia*), the corolla is subzygomorphic, but the calyx is strongly zygomorphic with three sets of sepals (i.e., one anterior sepal, two lateral sepals, and two posterior sepals). Many different themes of floral symmetry can be found throughout the genus, including different combinations of zygomorphy in the calyx, corolla, and staminal tube. Careful examination of the flower is necessary to place a species in its proper infrageneric group, and symmetry can be difficult to detect in immature or over-mature flowers. Fewer than one in 100 herbarium specimens have had the flowers dissected, resulting in many misidentifications and misinterpretations of floral structure by early specialists.

The morphology of the stamens provides several characters useful in delimiting infrageneric groups. In most taxa, the filaments are fused into a staminal tube, which can have a wide variety of morphologies. In some other species, the staminal tube is rudimentary or fused only at the base. Other important characters of the stamen include position and insertion of the anthers
on the staminal tube, whether the anthers are filamented, the morphology of the staminal tube summit, and the shape and dimensions of ventral scale and dorsal anther connective scales.

The ovary in *Rinorea* is composed of three carpels, with parietal placentation of the ovules. In African and Malagasy species, the number of ovules per ovary is usually constant among closely related species and is a diagnostic character at the infrageneric level. In most African and Malagasy species, the ovary develops into an indurate, dehiscent capsule with three valves. In a few species (e.g., *R. pugionifera, R. elliptica*), the fruit is a single-seeded, fleshy, drupe-like capsule. Over the course of fruit development in some groups of *Rinorea*, some ovules abort resulting in fruits with a variable numbers of seeds per fruit. For example, in *Rinorea* subsect. *Verticillatae* from Madagascar, the ovary consistently has 6 ovules per ovary, yet mature fruits may contain 3–6 seeds per capsule.

Leaves in African and Malagasy *Rinorea* are simple and petiolate to subsessile. Among some infrageneric groups, there is convergence of leaf morphology, and species determinations of herbarium specimens without reproductive features should be considered tentative. With the sole exception of *Rinorea* subsect. *Verticillatae*, which has opposite leaves, all other species in the Paleotropics are alternate-leaved. Only two other groups in the Violaceae have opposite leaves: the *Rinorea pubiflora* group and a few species in a lineage of *Hybanthus* (= *Pombalia*), both from the Neotropics.
Field Collecting.

Two plant collecting expeditions were undertaken in Madagascar to collect leaf tissue for DNA analysis and to gather specimens for use in taxonomic revisions. Preliminary study of specimens from the Missouri Botanical Gardens (MBG) showed that the greatest number of species are in bloom from September to December. Potential collecting sites were chosen based on the likelihood of finding the most number of species in a given area. Conversations with MBG staff experienced in field collecting trips in Madagascar also helped identify collecting sites.

Two collecting trips were made in the months October–December, both in 2006 and 2007. Sites visited included the Analanamazoatra Forest in Mantadia National Park (NP) in the east, Montagne d’Ambre NP and Ankarana NP in the north, Lokobé NP on Nosy Be, the Nosy Mitsio Archipelago, Monongarivo Special Reserve in the northwest, and finally Ankarafantsika NP and environs in the west. Over both trips, 134 collections of Rinorea were made, representing ca. 12 species. A set of duplicates was left in the herbarium of the Tsimbazaza Botanical Gardens in Antananarivo, Madagascar (TAN), while other sets of duplicates were sent to Paris, France (P) and St. Louis, Missouri (MO). Some additional duplicates were taken in the field and will eventually be deposited at Kew, U.K. (K) and Leiden, the Netherlands (L).
**Research Objectives.**

The goals of this study were fourfold: 1) conduct a taxonomic revision of the two most species rich groups of Malagasy and Comorian *Rinorea*: the *Rinorea arborea* group and *R.* subsect. *Verticillatae*, 2) erect a new infrageneric classification for African and Malagasy *Rinorea*, 3) estimate the phylogeny of *Rinorea* with taxon sampling across its geographic range and breadth of morphological diversity using chloroplast DNA sequences, and 4) infer the taxonomic affinities and biogeographic histories of the Malagasy species of *Rinorea*. 
Key to the species and species groups of *Rinorea* in Madagascar and the Comoro Islands.

1. Leaves opposite............................................. *Rinorea* subsect. *Verticillatae*  
   (see Chapter 4 for key to species)

1’. Leaves alternate............................................................................................2

2. Ovules 3 per ovary...........................................................................................3

2’. Ovules 6 per ovary..........................................................................................7

3. Anthers filamented, pubescent to hirsute; fruit white or pink, becoming red, fleshy; seeds 1 per fruit; axillary and terminal buds > 0.5 cm long......................4

3’. Anthers sessile to subsessile, glabrous; fruit green to brown, indurate; seeds 3 per fruit; axillary and terminal buds < 0.5 cm long.............................................6

4. Leaf apex acute to shortly acuminat e; inflorescence 5–10 cm long; Comoro Islands.......................................................... *Rinorea calycina* (Tul.) Baill. (Figure 2)

4’. Leaf apex subacute or cuspidat e; inflorescence 2–4 cm long; Madagascar..........................................................5

5. Ovary glabrous; Mahajanga and Antsiranana Provinces.......................... *Rinorea pugionifera* H.Perrier  
   (Figure 3)

5’. Ovary pubescent; Toliara Province............ *Rinorea greveana* Baill. (Figure 4)
6. Staminal tube with a ring of cilia subtending the anthers; inflorescence a raceme-like cyme; petals strongly reflexed near the middle at anthesis.................................*Rinorea angustifolia* (Thouars) Baill. (Figure 5)

6’. Staminal tube without a ring of cilia; inflorescence most often a panicle-like cyme; petals erect, recurved, or rolled near the apex......................*Rinorea arborea* group (see Chapter 3 for a key to the species)

7. Leaf margin crenulate; inflorescence a raceme-like cyme < 2.0 cm long, with imbricate, indurate, tan-colored bracts at the base......................*Rinorea squamosa* (Boivin ex Tul.) Baill. (Figure 6)

7’. Leaf margin strongly spinose; inflorescence a narrow panicle-like cyme > 2.0 cm long, without crowded bracts at the base.........................................................*Rinorea spinosa* (Boivin ex Tul.) Baill. (Figure 7)
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Figure 1: Pattern of relationships recovered in molecular phylogenetic studies of the Violaceae and Malpighiales. As circumscribed in Wurdack and Davis (2009), Passifloraceae s.l. includes Turneraceae and Malesherbiaceae.
Figure 2: Rinorea calycina, from holotype, Boivin 3295 (P).
Figure 3: Rinorea pugionifera, from Malcomber et al. 1889 (TAN).
Figure 4: Rinorea greveana, from Morat 890 (TAN).
Figure 5: Rinorea angustifolia, from McPherson & Dumetz 14674 (TAN).
Figure 6: Rinorea squamosa, from McPherson 14715 (TAN).
Figure 7: Rinorea spinosa, from RN 2714 (TAN).
Chapter 2.

A phylogeny of *Rinorea* (Violaceae) inferred from cpDNA and a revised infrageneric classification of the African and Malagasy species

Introduction.

*Rinorea* Aublet is a pantropical genus of shrubs and small trees and is the second most species-rich genus in the Violaceae with an estimated 225–275 species. The diversity of species is mostly well known for the Neotropics (49 species; Hekking, 1988), Asia (ca. 30 species; De Muria and Ballard, unpubl. data), and Madagascar (ca. 45 species; Wahlert, unpubl. data). However, the number of species in Africa is not known with estimates ranging from 110 to 150 (Achoundong, 1996; Wahlert, unpubl. data). West Africa and Madagascar are centers of diversity for the genus, with Cameroon and Gabon being particularly species-rich (Achoundong, 1996; Thomas et al., 2003). In some humid and semi-deciduous forests in Africa and Madagascar, *Rinorea* can be a locally common or abundant element in the understory vegetation and may even occur in monospecific stands (Thomas et al., 2003; Van Velzen, 2006; Wahlert, pers. obs.).

As currently circumscribed, *Rinorea* is not a monophyletic group. Molecular phylogenetic studies in the family have placed *Rinorea uxpanapana* with *Hybanthus* (Feng, 2005). Also, the two species *Rinorea virgata* and *R. heteroclita* are distantly related to the core *Rinorea* clade and are to be transferred back to the earlier generic name *Scyphellandra* (Feng, 2005; Ballard
et al., unpublished data). Other molecular phylogenies have shown the genus *Fusispermum* to be basalmost in the Violaceae, with the divergent *Rinorea apiculata* group interior to *Fusispermum*. Then, interior to the *Rinorea apiculata* group is the “core” *Rinorea*. Figure 1 summarizes the pattern of relationships that have been recovered in different molecular phylogenetic studies using both chloroplast and nuclear DNA regions (Wurdack and Davis, 2009; Tokuoka, 2007; Feng, 2005). The focus of this study are the species in the “core” *Rinorea* group. A Neotropical origin for both *Rinorea* and Violaceae is suggested by the basal phylogenetic position of the Neotropical species of *Rinorea* and the genus *Fusispermum*, as well as the generic diversity of Violaceae in the New World (14 of 23 genera and six of eight lineages of the polyphyletic genus *Hybanthus*) (Tokuoka, 2007; Ballard, 2009; Feng, 2005). Until now, no comprehensive phylogenetic reconstruction has been produced for the core *Rinorea* with extensive taxon sampling across its geographic and morphological ranges.

No genus-wide infrageneric classification has previously been proposed for *Rinorea*. Hekking (1988) aggregated the Neotropical species into three informal groups (Apiculata, Rinorea, and Pubiflora). Taxonomic revisionary work in the Asian taxa suggests that ca. 30 species can be classified into eight morphologically coherent and distinctive groups (De Muria and Ballard, unpubl. data). Engler (1904) first proposed a classification for African *Rinorea*, which was later revised and expanded by Brandt (1914) and de Wildeman (1920). However, there are several significant problems with this classification, and it is difficult to confidently assign species to their recognized infrageneric groups.
Sorting out the taxonomy and nomenclature of the African taxa is beyond the scope of this study. Rather, a revised infrageneric classification of the African and Malagasy species will facilitate revisionary work on a group-by-group basis. The main goals of this study were: 1) to understand phylogenetic relationships in the core group of *Rinorea* based on chloroplast DNA sequences, 2) to propose a new infrageneric classification for African and Malagasy *Rinorea*, based on molecular phylogenetic and morphometric analyses, and 3) to assign each of the 293 names of African and Malagasy *Rinorea* to a particular infrageneric group—regardless of synonymy and issues of nomenclature.

**Materials and Methods.**

**Molecular Phylogeny.** *Taxon Sampling.* The use of *Fusispermum* and two species of the *Rinorea apiculata* group as outgroup taxa was based on Tokuoka (2007) and Feng (2005). Ninety-nine accessions, representing 67 unique taxa were included in the ingroup. Fifteen Neotropical species were included that represent exemplars from the three informal groups of Hekking (1988). Ten Asian accessions were included in the study, representing five of eight informal infrageneric groups with geographic sampling from southern China, Thailand, peninsular Malaysia, and Borneo. Heavy taxon sampling of African and Malagasy species included 81 accessions from each of the 11 infrageneric groups identified in preliminary morphological analyses and
described previously by earlier specialists and florists. Voucher information is given in Appendix A.

**DNA Extraction, Amplification, and Sequencing.** Genomic DNA was isolated from herbarium or fresh, silica-dried leaf tissue using the DNEasy Plant Mini Kit (Qiagen, Valencia, CA, USA.). The \( trnL \) (UAA) intron and \( trnL \) (UAA) - \( trnF \) (GAA) intergenic spacer region were amplified using the primers Tab C (5’-CGA AAT CGG TAG ACG CTA CG-3’) and Tab F (5’-ATT TGA ACT GGT GAC ACG AG-3’) (Taberlet et al., 1991). The \( trnD \) (GUC) - \( trnE \) (UUC) intergenic spacer was amplified using the primers \( trnD^{GUC} \) F (5’-ACC AAT TGA ACT ACA ATC CC-3’) and \( trnE^{UUC} \) (5’-AGG ACA TCT CTC TTT CAA GGA G-3’) (Shaw et al., 2005). Amplification of double stranded DNA used standard polymerase chain reaction (PCR) conditions. Each 25 \( \mu l \) PCR reaction contained 1–10 ng DNA, 1.0 unit AmpliTaq polymerase (Applied Biosystems, Foster City, CA, USA), 2.5 \( \mu l \) 10× buffer, 1.5 20 \( \mu l \) mmol MgCl\(_2\), 1.0 \( \mu l \) dNTPs, and 0.75 \( \mu l \) 10 mmol amplification primers. PCR amplifications for both chloroplast regions were carried out under the following conditions: an initial denaturation step (94 °C, 2 min) followed by 40 cycles of denaturation (94 °C, 30 sec), annealing (52 °C, 1 min), and elongation (72°C, 1 min), with a final extension step (72 °C, 7 min).

**Phylogenetic Analyses.** Sequences were aligned manually using BioEdit (Hall, 2007). Gaps in the alignment arising from insertions or deletions (indels) were coded using the Simple Indel Coding algorithm of Simmons and
Ochoterena (2000), as implemented in FastGap (Borchsenius, 2009).

Combinability of the two chloroplast data sets (trnL intron/trnL-trnF spacer and trnD-trnE spacer) was assessed using the Incongruence Length Difference (ILD) test (Farris et al., 1994), implemented in PAUP* v4.0b10 (Swofford, 2003) as the Partition Homogeneity Test. The test was conducted using 1,000 partition replicates, each with 10 random addition replicates, and TBR branch swapping. The best-fit model of nucleotide substitution was estimated using Modeltest (Posada and Crandall, 1998) for each of the two chloroplast partitions and the combined matrix using PAUP* v4.0b10 (Swofford, 2003). Several MP analyses were run, including: 1) DNA matrix with appended gap matrix, 2) DNA matrix without appended gap matrix, 3) DNA matrix with appended gap matrix, but with ambiguous gaps removed, 4) *Fusispermum laxiflorum* as an outgroup, and 5) *Rinorea apiculata* and *R. crenata* as outgroups. Maximum parsimony (MP) analyses were conducted on each data partition (i.e., trnL intron/trnL-trnF spacer, trnD-trnE spacer, and coded gap matrix) and a combined matrix in PAUP* v4.0b10 (Swofford, 2003) using a heuristic search strategy with TBR branch swapping, 1,000 random addition replicates, saving one tree per replicate, steepest descent off, and MULTREES in effect. All characters were equally weighted and unordered. Results were summarized in a strict consensus tree. Internal branch support of phylogenetic trees from each analysis was estimated with 1000 bootstrap (BS) replicates (Felsenstein, 1985) using a full heuristic search with TBR branch swapping, 10 random stepwise addition replicates, and MULTREES in effect.
Maximum likelihood (ML) analyses were conducted for each data partition and the combined matrix using GARLI v0.951b (Zwickl, 2006), with the GTR + $\Gamma$ + I model of nucleotide evolution, as recommended by Zwickl (2006), with base frequencies estimated by Modeltest (Posada and Crandall, 1998), and all other options set to default values. Results were summarized in a 50% majority rule tree. Branch support of ML searches was estimated using GARLI v0.951b (Zwickl, 2006), with 100 BS replicates.

Bayesian inference (BI) was conducted using MrBayes 3.1 (Huelsenbeck and Ronquist, 2001) and the GTR + $\Gamma$ + I model of nucleotide evolution. Two million generations were run to estimate probabilities using MCMC. Trees were sampled every 100 generations, with the first 40,000 trees removed from “burn in”. Posterior probabilities were plotted on a 50% majority rule tree.

**IDENTIFICATION OF INFRAGENERIC GROUPS OF AFRICAN AND MALAGASY RINOREA. Floral Dissections.** Floral dissections were made for ca. 600 herbarium specimens from MO, P, K, BM, WAG, PRE, TAN, and TEF (abbreviations from Thiers, continuously updated). Dissections were used to identify classes of androecium architecture and to score quantitative characters of the androecium for morphometric analysis. Flowers were soaked in dilute detergent solution for 30 minutes. The sepals, petals, stamens, and pistil were dissected and glued to archival-quality cotton paper, and measurements were made using a dissecting microscope with an ocular micrometer.
Morphometric Analysis. Discriminant analysis (DA) was applied to a matrix of 17 quantitative traits and four calculated ratios scored from 58 floral dissections representing the breadth of geographic distribution and morphological diversity of African and Malagasy species (all measurements made in mm). These variables were: length and width of longest sepal, length and width of shortest sepal, ratio of the shortest sepal length to the longest sepal length, ratio of the shortest sepal width to the longest sepal width, longest petal length and width, ratio of the longest petal length to the longest petal width, staminal tube height, filament length, anther length and width, dorsal connective scale length and width, ratio of dorsal connective scale length to width, ventral connective scale length and width, style length, ovules per ovary, and ovary length. Analyses were performed in Number Cruncher Statistical Software (NCSS) (Hintze, 2004).

DA was performed on three data sets: 1) the total data set with representation of all 11 infrageneric groups \((n = 58)\), 2) the set of groups with 6 ovules per ovary (Brachypetalae, Dentatae, Crassiflorae, Ilicifoliae, Squamosae, and Subintegrifoliae), but excluded subsect. Verticillatae \((n = 29)\), and 3) the set of groups with 3 ovules per ovary (Angustifoliae, Arboreae, Cycloglossae, and Ellipticae) \((n = 26)\). A priori group assignments used in the DA were based on qualitative observations of the androecium made visible in the floral dissections, as well as characteristics provided in previous taxonomic accounts. Voucher information for the specimens used in the DA are given in Appendix B.
Species Assignments to Infrageneric Taxa. A list of 293 species names of African and Malagasy Rinorea was generated by a query of the International Plant Names Index (IPNI, 2008) with the goal of assigning each name to an infrageneric taxon, regardless of synonymy or nomenclatural issues. Whenever possible, flowers from type material were dissected to confirm a species assignment to a given group. In other cases in which no flowers were available, the literature was consulted to make an assignment by one of three ways: 1) assignment was based on the classification given in Engler (1904), Brandt (1914), or de Wildeman (1920); 2) assignment was based on the species' description or illustration; or 3) the assignment was based on synonymy given a floristic treatment or other published observations (Tennant, 1963; Robson, 1960; Gray-Wilson, 1981, 1986). For example, Rinorea affinis was listed as a synonym of R. beniensis in Gray-Wilson (1986), so R. affinis was placed in Rinorea sect. Cycloglossae.

Results.

Phylogeny of Rinorea. The length of the combined aligned chloroplast data set (trnL intron/trnL-trnF spacer and trnD-trnE spacer) was 1729 base pairs. The length of the appended gap matrix used in MP analysis was 190. Results from the ILD test did not indicate significant conflict between the two chloroplast data partitions (p = 0.267) for a subset of 75 taxa, thus the two data sets were combined and analyzed as a single matrix in ML and BI analyses. The several different MP analyses all recovered trees with the same clades and
topology. Results for the MP analysis are therefore given for the analysis of the appended gap matrix and *Fusispermum laxiflorum* as an outgroup. MP analysis yielded a single tree of length 939, with a consistency index of 0.687 and a retention index of 0.857. The GTR + \( \Gamma \) + I model was selected as the best-fit model of nucleotide substitution for both chloroplast data partitions and the combined matrix. The best ML tree had a -ln likelihood score of 6411.7943. With the exception of a single clade, all five MP analyses, and the ML and BI analyses recovered the same clades and topologies and are represented by a ML 50% majority rule tree (Figures 8 and 9) and a simplified ML phylogram (Figures 10 and 11).

Phylogenetic analyses resolve the Neotropical *Rinorea apiculata* group as basal and sister to the rest of the genus, but with low branch support (< 0.5 Bayesian posterior probabilities (PP) and < 50% maximum likelihood bootstrap (MLB) and maximum parsimony bootstrap (MPB) values; Figures 8 and 10). The branch leading to the rest of the accessions sampled for the “core” *Rinorea* form a highly supported clade (1.0 PP; 100% MLB and MPB; Figures 8 and 9). Three Neotropical clades that are congruent with Hekking’s (1988) informal groups (Apiculata, Rinorea, and Pubiflora) were moderately to highly supported (Figure 10).

A Paleotropical clade was recovered with very high support (1.0 PP; 100% MLB and MPB). In the Paleotropical clade, twelve subclades were recovered, including 11 African and Malagasy clades and an Asian clade. A sister relationship between the Malagasy endemic subsection *Verticillatae* and all Asian species was moderately well supported (1.0 PP; 95% MLB; 64 %
MPB). With the exception of the placement of two accessions of *Rinorea domatiosa*, the 11 clades of African and Malagasy species were completely congruent with the 11 infrageneric groupings delimited in morphometric analyses (see below). Six clades were highly supported (> 0.95 PP; > 95% MLB and MPB): *Brachypetalae, Squamosae, Crassiflorae, Dentatae, Verticillatae,* and *Angustifoliae* (Figure 11). The remaining five clades were moderately to highly supported: *Cycloglossae* (1.0 PP; 87% MLB; 93% MPB), *Ellipticae* (0.99 PP; 80% MLB; 91% MPB), *Arboreae* (0.93 PP; 73% MLB; 77% MPB), *Subintegrifoliae* (1.0 PP; 77% MLB; < 50% MPB), and *Illicifoliae* (1.0 PP; 90% MLB; 93% MPB) (Figures 8 and 9).

Within the Paleotropical clade, the only obvious apomorphy that can be mapped onto the phylogeny is ovule number per ovary. The clade containing species with three ovules per ovary was weakly supported (1.0 PP; 53% MLB; 64% MPB), as was the clade containing species with six ovules per ovary (0.8 PP; 53% MLB; < 50% MPB) (Figure 8).

Various combinations of synapomorphic characters can be mapped on to the subclades, with the exception of the Asian clade (because of insufficient taxon sampling). Five of eight morphological groups of Asian *Rinorea* were sampled, and the morphological diversity among Asian groups is as great as that among African and Malagasy groups. Two highly supported clades show the parallel character state of opposite-leaved phyllotaxy: the Pubiflora group and *Rinorea* subsect. *Verticillatae*. Additional analysis of morphology and cytology of all groups is needed to understand the evolution and distribution of characters throughout the genus.
MORPHOMETRIC ANALYSES. In each of the three DA analyses (i.e., all 11 infrageneric African and Malagasy groups, the 6-ovule group without sect. *Verticillatae*, and the 3-ovule group), *a priori* taxon assignments were correctly classified in 100% of cases. Values of the 17 quantitative characters and the four calculated ratios are given in Appendix C.

A three dimensional scatterplot of the first three axes from DA of all 11 infrageneric groups is shown in Figure 12. The first three canonical variates (CV1, CV2 and CV3) explained 46.5%, 19.5%, and 15.7% of the total variance among the 11 infrageneric groups, respectively (Table 1). There was discrete separation of five groups (*Cycloglossae*, *Dentatae*, *Crassiflorae*, *Ilicifoliae*, and *Verticillatae*), but there was some overlap among the remaining groups (*Angustifoliae*, *Squamosae*, *Brachypetalae*, *Subintegrifoliae*, *Arboreae*, and *Ellipticae*). Staminal tube height and filament length contributed heavily to the CV1 (Table 2), along which the *Cycloglossae*, *Angustifoliae*, and *Crassiflorae* separated strongly from the rest on the basis of longer staminal tube and shorter filaments. Petal length, filament length, ventral scale width, and style length all contributed significantly to separation of *Cycloglossae* from the rest of the groups along the CV2. Filament tube height and anther length provided separation of *Ilicifoliae* and *Dentatae* from the other groups along CV3.

A scatterplot of CV1 and CV2 extracted from DA of the infrageneric groups with 3 ovules per ovary is shown in Figure 13. The four groups showed tight clustering of species within each group and complete separation among groups. The first two axes explained 88.5% and 11.1% of the total variance
among the four infrageneric groups, respectively (Table 3); the variation manifested on CV 3 was miniscule, and that axis is not portrayed or discussed. Both plotted CV axes carried modest contributions from staminal tube height and filament length (Table 3). Along CV1, the Angustifoliae are strongly distinguished from the other three groups based on well developed staminal tube and short filaments. Along CV2 the Cycloglossae and Arboreae fall into opposite positions with the Ellipticae intermediate in placement, the first group possessing the relatively shortest staminal tube and longest filaments.

A three dimensional scatterplot of the first three axes from DA of the infrageneric groups with 6 ovules per ovary (excluding Verticillatae) is shown in Figure 14. All six groups included in the analysis separated: Brachypetalae, Dentatae, Crassiflorae, Ilicifoliae, Squamosae, and Subintegrifoliae. The first three axes explained 90.2%, 4.5%, and 3.0% of the total variance among the six infrageneric groups, respectively (Table 1). Longest petal length, filament length, dorsal scale length, anther length and style length all contributed modestly to CV 1, suggesting perhaps that this axis represents an overall size component separating the Crassiflorae and Squamosae from the rest according to longer floral parts in the main but shorter filaments. Staminal tube height contributed heavily to the separation of groups along the CV2, and filament length contributed significantly to separation of groups along the CV3 (Table 4). The Squamosae are distinguished fully from the other groups along CV2 by a taller staminal tube. Along CV3, the Brachypetalae at one end of the axis are separated from the Crassiflorae, Dentatae, Ilicifoliae and Squamosae by its
shorter filaments, with the *Subintegrifoliae* taking on intermediate (and variable) values.

Over all analyses, androecial features, in particular the relative development and fine-scale features of the staminal tube, filaments, and to a lesser extent the dorsal and ventral scales and longest petal, provided key diagnostic features to confidently separate groups of African and Malagasy *Rinorea*.

**Species Assignments to Infrageneric Taxa.** Species assignments to a section were made for 214 taxa. Seventy-nine assignments (37%) were based on examination of type material. The three largest sections were sections *Dentatae*, *Brachypetalae*, and *Angustifoliae*, composed of 56, 51, and 27 species, respectively. Eleven taxa were not seen or could not be assigned to any section (Appendix D).

Given the moderately well to highly supported resolution of African and Malagasy clades recovered in phylogenetic analyses—which are also congruent with morphological groups—eleven sections are recognized for the African and Malagasy species of *Rinorea*. Four sections are newly described: 1) *Arboreae*, 2) *Angustifoliae*, 3) *Ellipticae*, and 4) *Squamosae*; six subsections are maintained and recognized at the sectional level: 1) *Dentatae*, 2) *Ilicifoliae*, 3) *Subintegrifoliae*, 4) *Crassiflorae*, 5) *Brachypetalae*, and 6) *Verticillatae*. *Rinorea sect. Cycloglossae* is maintained.

Subsections *Brachypetalae* Engl. and *Kamerunenses* Engl. are combined in sect. *Brachypetalae*. Subsections *Inaequales* Engl. and *Lobiferae*
M. Brandt were determined to be composed of taxa belonging to other groups and are hereby dismantled. A taxonomic comparison of the traditional classification and this classification is given in Table 5. Because Engler (1904) and Brandt (1914) did not typify any infrageneric taxa, lectotypes are chosen for each section.
Key to sections of African and Malagasy *Rinorea*.

1. Leaves opposite..............................................................11. *Rinorea* sect. *Verticillatae*

1’. Leaves alternate...........................................................................................2

2. Ovules 3 per ovary...........................................................................................3

2’. Ovules 6 per ovary..........................................................................................6

3. Dorsal connective scale apical, orbicular, drying white, scale margin fimbriate; staminal tube rudimentary or absent...5. *Rinorea* sect. *Cycloglossae*

3’. Dorsal connective scale apical and lateral, lanceolate-ovate, drying orange-brown, scale margin entire; staminal tube well developed.................................4

4. Inflorescence usually a panicle-like cyme.............1. *Rinorea* sect. *Arboreae*

4’. Inflorescence a raceme-like cyme.................................................................5

5. Staminal tube with a ring of cilia subtending anthers; terminal bud scale < 0.5 cm, fruit a 3-seeded indurate capsule, green to red, turning brown at maturity.................................................................2. *Rinorea* sect. *Angustifoliae*

5’. Staminal tube without a ring of cilia subtending anthers; terminal bud scale > 0.5 cm, fruit a 1-seeded fleshy berry, white, turning pink to red at maturity.................................................................7. *Rinorea* sect. *Ellipticae*

6'. Inflorescence a panicle-like cyme or narrow thyrse.................................7

7. Inflorescence a narrow thyrse; sepals clearly ribbed fanwise; staminal tube deeply sinuate between insertion of anthers, tube without a free margin or a lobed margin subtending anthers.................................8. Rinorea sect. Ilicifoliae
7'. Inflorescence a spreading panicle-like cyme; sepals veined or keeled; staminal tube continuous or notched between insertion of anthers, often with a free margin or a lobed margin subtending anthers.................................8

8. Anthers sessile or subsessile, inserted on the margin (summit) of the tube; filament (if subsessile) < 0.3 mm; margin of tube variously lobed, rarely membranous.................................................................9
8'. Anthers filamented, inserted on the inner surface of the filament tube; filaments > 0.3 mm; margin of tube clearly visible, entire or dentate to irregularly lacerate, sometimes notched.........................................................10

9. Sepals usually > 3.0 mm long, > 2.5 mm wide; petals > 6.0 mm long; dorsal connective scales > 2.0 mm long; staminal tube > 1.0 mm tall; style > 5.0 mm long.................................4. Rinorea sect. Crassiflorae
9'. Sepals usually < 3.0 mm long, < 2.5 mm wide; petals < 6.0 mm long; dorsal connective scales < 2.0 mm long; staminal tube usually < 1.0 mm tall; style < 5.0 mm long........................................3. Rinorea sect. Brachypetalae
10. Petals < 3.5 mm long; staminal tube < 1.0 mm tall; dorsal connective scales < 1.0 mm long; ventral connective scale usually 1, ovate to lanceolate, apex rounded, bifid, or irregularly lacerate; style < 2.0 mm long.................................**10. Rinorea sect. Subintegrifoliae**

10'. Petals > 3.5 mm long; staminal tube > 1.0 mm tall; dorsal connective scales > 1.0 mm long; ventral connective scales 2, linear-lanceolate, apex acute; style > 2.0 mm long........................................**6. Rinorea sect. Dentatae**
Taxonomic Treatment.


*Inflorescentia cyma paniculiformis vel racemiformis. Corolla zygomorphis petalis anticis et posticis similaribus et petalis lateralis concavis vel conduplicatis, androecium tubo staminali 0.4–1.8 mm alto, antherae sessiles summo tubi insidens, connectivum dorsale antherae lanceolatum-deltatum, 0.7–1.9 mm longum, 0.4–1.2 mm latum, ovario 3 ovulo continens, fructus capsula crassa indurata 3 semina continens et 3 valvas dehiscens.— Figure 15 E and F.

**REMARKS:** *Rinorea* sect. *Arboreae* approaches sect. *Subintegrifoliae* and sect. *Brachypetalae* but can be separated from the latter two by having three ovules per ovary. The fruits characteristic of sect. *Arboreae* are subwoody, ovoid, and the surface papillose, whereas in sects. *Subintegrifoliae* and *Brachypetalae*, the fruits are indurate, ellipsoid, ridged, and the surface smooth. Anthers are sessile in sect. *Arboreae* and filamented in *Subintegrifoliae*. Flower buds are conical in sect. *Arboreae* and ovoid to spherical in sect. *Brachypetalae*. Species in sect. *Arboreae* typically have a panicle-like cyme, but in two species from Madagascar, the lateral cymules are highly reduced and bear 1–2 flowers, giving the inflorescence a raceme-like appearance.
The *Rinorea arborea* species group has recently been revised for the African and Malagasy species and contains eight species (this volume, Chapter 3). Distributed in East Africa, the Comoro Islands, and Madagascar.


*Differt a omnibus sectionibus africanus et malacassus summo tubo staminali annulus ciliatus instructus. Inflorescentiae cyma racemiformis terminale et laterale, petalis reflexis sub anthesi, ovario 3 ovulo continens, fructus capsula indurata.* — Figure 15 G and H.

**REMARKS:** Members of *Rinorea* sect. *Angustifoliae* are immediately differentiated from all other African and Malagasy groups by the summit of the staminal tube having a ring of cilia subtending the sessile anthers. The
Inflorescence is a terminal and lateral raceme-like cyme, and the petals are most often strongly reflexed near the middle at anthesis. Species in this section have three ovules per ovary, and typically three seeds per fruit.

Other species assigned to this section by Engler (1904), Brandt (1914), and de Wildeman (1921) are removed to *Rinorea* sects. *Squamosae* and *Ellipticae*. Distributed throughout tropical Africa and Madagascar, but absent in the Comoro Islands.


REMARKS: As circumscribed here, sect. *Brachypetalae* also includes the taxa assigned to subsect. *Kamerunenses* by Engler (1904), Brandt (1914), and de Wildeman (1921). Distributed throughout tropical mainland Africa.


**4. Rinorea** sect. *Crassiflorae* (M.Brandt) Wahlert, **stat. nov.** —


**REMARKS:** Species in *Rinorea* sect. *Crassiflorae* are distinguished by their long flowers, sepals that often exceed the length of the petals, long dorsal anther connective scales, and tall, well developed staminal tubes. Distributed in central and west tropical Africa.


1914. — Lectotype (designated here): *Rinorea beniensis*. — Figure 16 A.

**REMARKS:** *Rinorea* sect. *Cycloglossae* is immediately distinguished from all other African and Malagasy groups by the white, orbicular dorsal anther connective scales with fimbriate margins. As circumscribed here, this section includes taxa assigned to *Rinorea* sect. *Macroglossae* M.Brandt subsect. *Choriandra* Engl. Distributed throughout tropical Africa.


**REMARKS:** *Rinorea* sect. *Dentatae* approaches sect. *Subintegri foliae*, but can be differentiated from the latter by its longer flowers, taller staminal tube, longer dorsal connective scales, and by the two linear ventral scales.
This is the most species-rich group identified, but a continent-wide revision is needed to determine synonymy and new species. Distributed widely throughout tropical Africa.


Differt a omnibus sectionibus africanus et malacassus fructus carnosus rubra et 1 semina continens. Inflorescentiae cyma racemiformis terminale et laterale, ovario 3 ovulo continens. — Figure 16 E and F.

**REMARKS:** *Rinorea* sect. *Ellipticae* is distinguished from all other African and Malagasy groups by its fleshy 1-seeded fruit. The ovary contains three ovules, but over the course of development, two ovules abort. It is also differentiated from sects. *Angustifoliae* and *Arboreae* by having conspicuous terminal bud scales > 1.0 cm long. Distributed in tropical East Africa, the Comoro Islands, and Madagascar.


Remarks: *Rinorea* sect. *Ilicifoliae* is distinguished from all other African and Malagasy groups by its strongly zygomorphic calyx, with tan-colored, indurate, and overlapping sepals that are clearly ribbed fanwise. The inflorescence is most often a terminal, narrow, panicle-like cyme, and the flower buds are ovoid to spherical. Several species have strongly spinose leaf margins. Distributed widely throughout tropical Africa, the Comoro Islands, and Madagascar.


_Differt a omnibus sectionibus africanus et malacassus inflorescentiae cyma racemiformis et ovario 6 ovulo continens._ — Figure 15 A and B.

**REMARKS:** *Rinorea* sect. *Squamosae* is distinguished from all other African and Malagasy groups by its raceme-like cyme and ovary containing 6 ovules. All other groups with 6 ovules per ovary have panicle-like cymes or narrow thyrses. Species in sect. *Squamosae* also have the inflorescence subtended by persistent, tan-colored, indurate, overlapping bracts—the trait for which the section is named. The species in this group share a remarkable resemblance to the *Rinorea bengalensis* group from Asia but are unrelated phylogenetically. Distributed widely throughout tropical Africa, the Comoro Islands, and Madagascar.


Distributed throughout tropical west, central, and east Africa, but absent in southern Africa, Madagascar, and the Comoro Islands.


**REMARKS:** *Rinorea* sect. *Verticillatae* is immediately separated from all other Paleotropical groups by its opposite leaves. The section has been recently revised and includes nine new species not listed below (this volume, Chapter 4). Endemic to Madagascar and the Comoro Islands.

Literature Cited


Table 1: Eigenvalues and contributed variance of each CV axis from the three discriminant analyses of the infrageneric groups of African and Malagasy *Rinorea*.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>CV</th>
<th>Eigenvalue</th>
<th>Individual contribution (%)</th>
<th>Cumulative contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All 11 groups</td>
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<td>22.358800</td>
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<td>46.5</td>
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<tr>
<td></td>
<td>2</td>
<td>9.395194</td>
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<td>66.0</td>
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<td></td>
<td>3</td>
<td>7.571177</td>
<td>15.7</td>
<td>81.8</td>
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<td>6-ovule group, excluding</td>
<td>1</td>
<td>425.529525</td>
<td>90.2</td>
<td>90.2</td>
</tr>
<tr>
<td>Verticillatae</td>
<td>2</td>
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<td>4.5</td>
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<tr>
<td></td>
<td>3</td>
<td>13.930913</td>
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<tr>
<td>3-ovule group</td>
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<tr>
<td></td>
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<td>94.944016</td>
<td>11.1</td>
<td>99.5</td>
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Table 2: Correlation of variables with CV coefficients for the DA of all 11 infrageneric groups of African and Malagasy *Rinorea*. Significant values in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>CV 1</th>
<th>CV 2</th>
<th>CV 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largest sepal length</td>
<td>-0.194871</td>
<td>0.078357</td>
<td>-0.080084</td>
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<td>Largest sepal width</td>
<td>-0.223771</td>
<td>-0.126087</td>
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<td>Shortest sepal length</td>
<td>-0.226423</td>
<td>0.135524</td>
<td>-0.153298</td>
</tr>
<tr>
<td>Shortest sepal width</td>
<td>-0.190273</td>
<td>-0.105316</td>
<td>-0.292162</td>
</tr>
<tr>
<td>Shortest sepal length:longest sepal length</td>
<td>-0.044681</td>
<td>-0.072043</td>
<td>0.097666</td>
</tr>
<tr>
<td>Shortest sepal width:longest sepal width</td>
<td>-0.003235</td>
<td>0.021271</td>
<td>0.035286</td>
</tr>
<tr>
<td>Longest petal length</td>
<td>-0.157099</td>
<td><strong>0.347218</strong></td>
<td>-0.158227</td>
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<tr>
<td>Longest petal width</td>
<td>-0.108958</td>
<td>0.157214</td>
<td>-0.146536</td>
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<tr>
<td>Longest petal length:longest petal width</td>
<td>-0.138952</td>
<td>-0.131494</td>
<td>-0.022502</td>
</tr>
<tr>
<td>Staminal tube height</td>
<td><strong>-0.359753</strong></td>
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<td><strong>0.346384</strong></td>
</tr>
<tr>
<td>Filament length</td>
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<td><strong>0.304110</strong></td>
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<td>0.041405</td>
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<tr>
<td>Anther length</td>
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<td><strong>-0.288466</strong></td>
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<tr>
<td>Anther width</td>
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<td>Ventral scale length</td>
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<td>0.047097</td>
</tr>
<tr>
<td>Ventral scale width</td>
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<td>Style length</td>
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<td><strong>0.383866</strong></td>
<td>-0.063445</td>
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<tr>
<td>Ovary length</td>
<td>-0.024434</td>
<td>0.137853</td>
<td>-0.118466</td>
</tr>
</tbody>
</table>
Table 3: Correlation of variables with CV coefficients for the DA of African and Malagasy *Rinorea* groups with 3 ovules per ovary.

<table>
<thead>
<tr>
<th>Variable</th>
<th>CV 1</th>
<th>CV 2</th>
<th>CV 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largest sepal length</td>
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<td>0.001975</td>
<td>-0.046511</td>
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<tr>
<td>Largest sepal width</td>
<td>0.000238</td>
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<tr>
<td>Shortest sepal length</td>
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<td>Shortest sepal width</td>
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<tr>
<td>Shortest sepal length:longest sepal length</td>
<td>-0.017434</td>
<td>0.014495</td>
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<tr>
<td>Shortest sepal width:longest sepal width</td>
<td>0.003316</td>
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<tr>
<td>Longest petal length</td>
<td>-0.008527</td>
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<td>0.034883</td>
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<td>Longest petal width</td>
<td>0.012268</td>
<td>0.004107</td>
<td>0.158415</td>
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<tr>
<td>Longest petal:longest petal width</td>
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<td>0.040564</td>
<td>-0.105860</td>
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<tr>
<td>Staminal tube height</td>
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<td>Filament length</td>
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<td>Ovary length</td>
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<td>0.137524</td>
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</table>
Table 4: Correlations of variables with CV coefficients for the DA of African and Malagasy *Rinorea* groups with 6 ovules per ovary, excluding sect. *Verticillatae*. Significant values in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>CV 1</th>
<th>CV 2</th>
<th>CV 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largest sepal length</td>
<td>0.073598</td>
<td>-0.051834</td>
<td>-0.005731</td>
</tr>
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<td>Largest sepal width</td>
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<td>-0.165360</td>
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<tr>
<td>Shortest sepal length</td>
<td>0.067391</td>
<td>-0.026154</td>
<td>-0.009062</td>
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<tr>
<td>Shortest sepal width</td>
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<td>0.098809</td>
<td>-0.081988</td>
</tr>
<tr>
<td>Shortest sepal length:longest sepal length</td>
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<td>0.018066</td>
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<td>Shortest sepal width:longest sepal width</td>
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<td>Longest petal width</td>
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<td>Longest petal length:longest petal width</td>
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<td>Staminal tube height</td>
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<td>Filament length</td>
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<td>Ovary length</td>
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Table 5. Comparison of Infrageneric classifications for *Rinorea* in Africa and Madagascar.
Sect. = section; § = subsection; — = taxon not recognized.

<table>
<thead>
<tr>
<th></th>
<th>Engler (1904)</th>
<th>Brandt (1914)</th>
<th>This paper</th>
</tr>
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<td></td>
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<td>sect. Cycloglossae</td>
<td>sect. Cycloglossae</td>
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<tr>
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<td>—</td>
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<tr>
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</tr>
<tr>
<td>sect. Ardisianthus</td>
<td>sect. Ardisianthus</td>
<td>—</td>
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<td>sect. Angustifoliae</td>
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<td>sect. Violanthus</td>
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<td>§ Crassiflorae</td>
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<td>sect. Arboreae</td>
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<td>§ Inaequales</td>
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<td>—</td>
<td>§ Lobiferae</td>
<td>—</td>
</tr>
</tbody>
</table>
Appendix A: List of taxa used in the chloroplast phylogeny with voucher specimen information.

*Fusispermum laxiflorum* Hekking: McPherson 10218 (MO), Panama.
Appendix B: Voucher specimens used in discriminant analysis.

holotype. *R. gracilipes*: Zenker 1244 (P), Gabon, holotype. *R. greveana:


Appendix C: The 17 quantitative values and four calculated ratios used in discriminant analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Largest Sepal length (mm)</th>
<th>Largest Sepal width (mm)</th>
<th>Shortest Sepal length (mm)</th>
<th>Shortest Sepal width (mm)</th>
<th>Ratio largest: shortest sepal length</th>
<th>Ratio largest: shortest sepal width</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. beniensis (1)</td>
<td>1.7</td>
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<td>1.2500</td>
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<td>R. ebolowensis</td>
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<td>R. talbotii (2)</td>
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<td>R. talbotii</td>
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Appendix C (continued): The 17 quantitative values and four calculated ratios used in discriminant analysis.

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Appendix C (continued): The 17 quantitative values and four calculated ratios used in discriminant analysis.

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<th>Dorsal connective scale width (mm)</th>
<th>Ratio connective scale length: width</th>
<th>Anther length (mm)</th>
<th>Anther width (mm)</th>
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Appendix C (continued): The 17 quantitative values and four calculated ratios used in discriminant analysis.

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<td>Leaf Width</td>
<td>Stem Diameter</td>
<td>Flower Diameter</td>
<td>Height</td>
</tr>
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Appendix D: Species not seen or group affiliation unknown (12 taxa).

Figure 8: Combined chloroplast ML 50% majority rule tree. Support values from BI, ML, and MP are separated by a slash (i.e., PP/MLB/MPB). Bayesian probabilities of 1.00 and bootstrap support values of 100% are indicated with “+”. Branches without support values collapse to a polytomy in the strict consensus.
Support values from BI, ML, and MP are separated by a slash (i.e., PP/MLB/MPB). Bayesian probabilities of 1.00 and bootstrap support values of 100% are indicated with “+”. Branches without support values collapse to a polytomy in the strict consensus.
Figure 10: Combined chloroplast simplified ML phylogram of Neotropical Rinorea showing the three informal groups identified in Hekking (1988). * indicates branches supported by Bayesian probabilities > 0.95, and MP and ML bootstrap values > 95%.
Figure 11: Combined chloroplast simplified ML phylogram of Paleotropical Rinorea showing the 11 sections of Rinorea in Africa and Madagascar and the Asian clade.* indicates branches supported by Bayesian probabilities > 0.95, and MP and ML bootstrap values > 95%.
Figure 12: Canonical variates analysis of the 11 infrageneric groupings of African and Malagasy *Rinorea* identified in this study.
Figure 13: Canonical variates analysis of the four African and Malagasy infrageneric groups with 3 ovules per ovary.
Figure 14: Canonical variates analysis of the six African and Malagasy infrageneric groups with 6 ovules per ovary, excluding the opposite-leaved Rinorea sect. Verticillatae.
Figure 15: Representative staminal types of Rinorea sects. Squamosae, Ilicifoliae, Arboreae, Angustifoliae, and Verticillatae.
A. sect. Squamosae; internal view; B. sect. Squamosae, external view; C. sect. Ilicifoliae, internal view; D. sect. Ilicifoliae, external view; E. Arboreae, internal view; F. Arboreae, external view; G. Angustifoliae, external view; H. Angustifoliae, internal view; I. Verticillatae, internal view; J. Verticillatae, external view. Scale bar = 1 mm.
Figure 16: Representative staminal types of *Rinorea* sects. *Cycloglossae, Crassiflorae, Brachypetalae*, and *Ellipticae*.  
Figure 17: Representative staminal type of *Rinorea* sect. *Dentatae*. A. internal view; B. external view. Scale bar = 1 mm.
Figure 18: Representative staminal type of *Rinorea* sect. *Subintegifoliae*. A. external view; B. internal view. Scale bar = 1 mm.
Chapter 3.

A revision of the *Rinorea arborea* species group (Violaceae) from Madagascar, East Africa, and the Comoro Islands

Introduction.


In the course of revising *Rinorea* from Madagascar and the Comoro Islands, many *R. arborea*-like specimens were examined that did not fit Perrier de la Bâthie’s taxonomic circumscriptions. Furthermore, multivariate morphometric analyses of the Malagasy specimens supported recognition of several additional morphologically distinctive species in the group (Wahlert and Ballard, 2008a).

The ca. 41 species of *Rinorea* in Madagascar recognized as a result of the present investigations belong to six distinctive infrageneric groups, some of which have not yet been described. Five of these groups contain species that are closely related to—or conspecific with—species in Africa (e.g., *R. arborea*, *R. elliptica*, *R. angustifolia*, *R. squamosa*, *R. spinosa*). The sixth group is the Malagasy endemic, opposite-leaved *Rinorea* subsect. *Verticillatae* Engl.
An infrageneric classification of African and Malagasy *Rinorea* was first proposed by Engler (1904) and elaborated upon by Brandt (1914) and de Wildeman (1920), but *Rinorea arborea* and related species were never placed in a recognized infrageneric taxon.

Preliminary reevaluation of morphological traits (especially floral features) in infrageneric groups in African and Malagasy *Rinorea* confirms that the *Rinorea arborea* species group comprises a well-delineated and distinctive morphological group (this volume, Chapter 2). In addition, molecular phylogenetic analysis of chloroplast DNA sequences (*trnL* intron, *trnL*-F spacer, and *trnD-trnT* spacer) resolves a well supported clade of eight accessions of species in the *R. arborea* group (93% bootstrap support; this volume, Chapter 2). Both the morphological and molecular results support the recognition of a new section in order to accommodate the species of the *R. arborea* group from Madagascar, the Comoro Islands, and East Africa (Mozambique, Tanzania, and Kenya).

**Materials and Methods.**

Quantitative and qualitative morphological data were recorded from ca. 600 herbarium specimens deposited at BM, K, MO, P, PRE, TAN, TEF, and WAG (herbarium acronyms given in Thiers, continuously updated). Floral dissections were made by soaking flowers in dilute detergent solution for 30 minutes. The sepals, petals, stamens, and pistil were then separately glued to archival-quality cotton paper, and measurements were made using a dissecting
scope with an ocular micrometer. For the Malagasy specimens without latitude/longitude data, coordinates (and sometimes elevation) were assigned post-facto using the Gazetteer to Malagasy Botanical Collecting Localities (Schatz and Lescot, 2005). For the African and Comorian specimens without latitude/longitude data, coordinates were assigned using Google Earth and other Internet-based resources. Post-facto coordinates are enclosed in square brackets. Abbreviations in the lists of exsiccatae include: RN, Réserve Naturelles; RNI, Réserve Naturelle Intégrale; and SF, Service Forestier. Vernacular names are given only for the Malagasy and Sakalava languages from Madagascar.

An explicit conservation assessment following IUCN criteria (IUCN Standards and Petitions Working Group, 2008) was conducted following the general procedure outlined by Willis et al. (2004). The utility CATS (Conservation Assessment ToolS; Moat, 2007) was used with ArcView GIS 3.2 software (Environmental Systems Research Institute, 1999) to calculate extent of occurrence (EOO) and area of occupancy (AOO). EOO and AOO ratings were qualified with additional information about distribution in protected areas, most recent collections, and in some cases, additional field observations.

**Results and Discussion.**

Examination of herbarium material from Madagascar, East Africa, and the Comoro Islands identified eight species in the *Rinorea arborea* group. *Rinorea arborea* from Madagascar was determined to be conspecific with the
same taxon from the Comoro Islands and East Africa. *Rinorea arborea* f. *sambiranensis* was found to be sufficiently differentiated from the nominate species to be recognized at the species level. *Rinorea arborea* f. *meridionalis* is a unique taxon with a discrete geographic distribution in southern Madagascar and is recognized at the species level. *Rinorea schatzii* is a new species that is closely related to *R. arborea* but is morphologically distinct and has a somewhat discrete distribution in the Marojejy region.

*Rinorea arborea* f. *occidentalis* was found to be highly variable across a large geographic area. Fifteen of the 21 syntypes given by Perrier de la Bâthie (1949) for f. *occidentalis* were examined and referred to four different taxa: two previously described species (*R. longipes* (Tul.) Baill. and *R. arborea*), *R. occidentalis*, and a new species from the Ankarafantsika region (*R. ballardii*) (Table 6). *Rinorea labatii* is a distinctive new species that differs in several character states from f. *occidentalis* and has a discrete distribution in the Namoroka region.

Scrutiny of specimens showed that there was insufficient morphological differentiation between *Rinorea longipes* and *R. viridiflora* (Tul.) Baill. to maintain them as separate species; the latter is synonymized under *R. longipes*.

Species in the *Rinorea arborea* group are differentiated primarily by the size and morphology of the petiole and leaf, indumentum of the ovary, petiole, and leaf, and the features of the inflorescence (i.e., panicle-like cyme vs. raceme-like cyme, inflorescence length, and number of flowers per lateral cymule).
The eight species in the *Rinorea arborea* group were determined to comprise a morphologically cohesive and distinctive infrageneric group in Madagascar, the Comoro Islands, and East Africa. *Rinorea* sect. *Arboreae* is a new section described here to accommodate the closely related species in the *R. arborea* group.

The following key is provided to separate the six infrageneric groups of *Rinorea* in Madagascar and the Comoro Islands. In addition to *R. sect. Arboreae* described here, three infrageneric groups identified in morphological and phylogenetic analyses remain to be described: *R. angustifolia* group, *R. elliptica* group, and *R. squamosa* group.
Key to the six infraspecific groups of *Rinorea* in Madagascar and the Comoro Islands.

1. Leaves opposite................................. *Rinorea* subsect. *Verticillatae*

1’. Leaves alternate................................................................. 2

2. Ovules 3 per ovary................................................................. 3

2’. Ovules 6 per ovary................................................................. 5

3. Anthers pubescent to hirsute; fruit white or pink, becoming red, succulent; seeds 1 per fruit; axillary and terminal buds > 0.5 cm long................. *Rinorea elliptica* group

3’. Anthers glabrous; fruit green to brown, indurate; seeds 3 per fruit; axillary and terminal buds < 0.5 cm long......................................................... 4

4. Staminal tube with a free ciliate margin subtending the anthers; inflorescence a raceme-like cyme; petals strongly reflexed near the middle at anthesis (absent in the Comoro Islands)............................................ *Rinorea angustifolia* group

4’. Staminal tube without a ciliate margin; inflorescence a panicle-like cyme; petals erect to rolled near the apex............ *Rinorea* sect. *Arboreae* Wahlert sect. nov.

5. Leaf margin crenulate; inflorescence < 2.0 cm long, with imbricate, indurate, tan-colored bracts at the base............................................ *Rinorea squamosa* group
5’. Leaf margin strongly spinose; inflorescence > 2.0 cm long, without crowded bracts at the base.................................*Rinorea* subsect. *Ilicifoliae*
Taxonomic Treatment.

*Rinorea* sect. *Arboreae* Wahlert, sect. nov.

**TYPUS** — *R. arborea* (Thouars) Baill.

*Inflorescentia cyma paniculiformis vel racemiformis. Corolla zygomorphis petalis anticis et posticis similaribus et petalis lateralibus concavis vel conduplicatis, androecium tubo staminali 0.4–1.8 mm alto, antherae sessiles summo tubi insidens, connectivum dorsale antherae lanceolatum-deltatum, 0.7–1.9 mm longum, 0.4–1.2 mm latum, ovario 3 ovulo continens, fructus capsula crassa indurata 3 semina continens et 3 valvas dehiscens.*

**DESCRIPTION.** Shrub or small tree, 2–15 m tall, evergreen to semi-deciduous; young branches glabrous or pubescent. Leaves alternate, petiolate; petioles 0.3–8.8 cm long, glabrous or pubescent, articulated at proximal end, grooved longitudinally on adaxial surface, usually with pulvini at both ends, pulvini often becoming darker in color and callused with age, 0.6–2.5 mm thick, glabrous or pubescent, petiole usually reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 0.9–3.1 × 0.5–2.0 mm, coriaceous, keeled or costate, outer surface glabrous or pubescent, margin ciliate, apex acute; lamina elliptic to broadly elliptic, lanceolate, oblanceolate, or ovate, 1.8–24.0 × 0.9–8.5 cm, herbaceous; lamina upper surface glabrous, lower surface glabrous or pubescent; primary and secondary veins glabrous on
upper surface, glabrous or pubescent on lower surface; secondary vein pairs 3–12, divergent to ascending, tertiary veins reticulate; base cuneate, rounded, or shallowly cordate, symmetrical, aequilateral or sometimes oblique; margin subentire to serrulate or serrate, rarely spinulose; apex acute, rounded, or cuspidate to shortly acuminate. Inflorescence an axillary, terminal and subterminal, panicle-like cyme (thyrsoïd), lateral cymules branched and bearing 1–15(–25) flowers, or a raceme-like cyme (botryoid) with lateral cymules unbranched and bearing 1 flower, 1.0–17.0 cm long, axis glabrous or pubescent; peduncle bracts quickly deciduous, broadly ovate, 0.9–2.5 × 0.3–4.3 mm, coriaceous, outer surface glabrous or puberulent, margin ciliate, apex rounded to truncate; pedicels (from articulation to base of flower) 0.8–3.6 mm long, glabrous or pubescent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.4–2.1 × 0.3–1.8 mm, herbaceous, outer surface glabrous or pubescent, margin entire to ciliate, apex acute to mucronate. Flowers 3.2–7.6 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, ovate to lanceolate-deltoid, 0.8–3.4 × 0.5–2.3 mm, outer surface glabrous or pubescent, margin ciliate, apex acute to rounded. Corolla zygomorphic, petals white, green-white, yellow-white, or cream-white, drying orange-brown, glabrous; anterior and posterior petals elliptic, broadly lanceolate-ovate, or lanceolate to oblanceolate, 3.1–7.4 × 1.3–3.3 mm, margin entire, apex acute to rounded, erect to rolled; lateral petals elliptic, lanceolate-elliptic, or lanceolate to oblanceolate, concave to conduplicate, 3.0–7.2 × 1.1–2.8 mm, margin entire, apex acute to rounded, erect to rolled; Stamens 2.7–4.6 mm long; staminal tube 0.4–1.8 mm tall, outer and inner surfaces glabrous,
tube rarely with a partially free, membranous flange subtending anthers; anthers sessile on summit of staminal tube, anther connectives 0.7–1.9 × 0.4–1.2 mm, glabrous; anther ventral connective scales absent, or if present, linear, ovate, or lanceolate, 0.05–0.7 × 0.05–0.3 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending one-fifth to one-half down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.1–2.2 × 0.6–1.5 mm, surface glabrous, margin entire, apex acute. Pistil 3.2–6.1 mm long; ovary ovoid, 0.6–2.1 × 0.5–1.4 mm, glabrous or pubescent; ovules 3; style 2.2–3.9 mm long, erect, filiform, straight or rarely sigmoid, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.3–2.9 cm long, 0.7–1.9 cm diameter, valve 0.5–1.2 cm wide, surface glabrous or rarely pubescent, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens often persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seeds three per capsule, 6.0–13.0 × 4.0–8.0 mm, deltoid-reniform, brown-black, shiny, glabrous.
Key to the species of *Rinorea* sect. *Arboreae*.

1. Inflorescence a raceme-like cyme with each lateral cymule bearing only 1 flower...................................................................................................................2

1'. Inflorescence a panicle-like cyme with lateral cymules bearing (1–) 2–15 (–25) flowers...........................................................................................................3

2. Petioles, ovary, lower leaf surface, and young stems pubescent, Ankarafantsika region............................................................2. *Rinorea ballardii*

2'. Petioles, ovary, lower leaf surface, and young stems glabrous, Namoroka region....................................................................................3. *Rinorea labatii*

3. Lower leaf surface and ovary pubescent, Marojejy region.................................8. *Rinorea schatzii*

3'. Lower leaf surface and ovary glabrous.......................................................................4

4. Inflorescence 1.0–9.0 cm long, lateral cymules bearing 1–7 flowers..............5

4'. Inflorescence 2.5–17.0 cm long, lateral cymules bearing 3–15 (–25) flowers..................................................................................................................7

5. Leaf lanceolate, elliptic, ob lanceolate, or rhombic, 1.8–8.0 (–12.0) cm long, petiole 0.3–2.7 cm long, Antsiranana Province.........................4. *Rinorea longipes*

5'. Leaf lanceolate or elliptic, 3.0–16.0 cm long, petiole 0.6–6.6 cm long, Mahajanga and Toliara Provinces.................................................................6
6. Leaf typically lanceolate with base rounded, Toliara Province in the vicinity of Tôlanaro (Fort Dauphin) and Analavelona..........................5. *Rinorea meridionalis*

6’. Leaf typically elliptic with base cuneate, Mahajanga Province and in the vicinity of Morondava......................................................6. *Rinorea occidentalis*

7. Petiole 4.3–8.8 cm long, 1.4–2.0 mm wide; pulvinus 2.0–2.5 mm wide; leaf 13.0–24.0 cm long, 6.0–8.5 cm wide; fruit 2.2–2.5 cm long, 1.6–2.0 cm diameter; lower Sambirano River valley region and Tsaratanana R.N.................................................................7. *Rinorea sambiranensis*

7’. Petiole 0.5–5.3 cm long, 0.5–1.5 mm wide; pulvinus 0.8–2.2 mm wide; leaf 3.5–21.0 cm long, 1.0–7.7 cm wide; fruit 1.3–2.1 cm long, widespread in northern and eastern Madagascar (Nosy Be, Ankarana, Sambirano region to Masoala Peninsula, eastern humid forests), Comoro Islands, and East Africa (Kenya, Tanzania, Mozambique).............................1. *Rinorea arborea*


**DESCRIPTION.** Shrub to tree, 2–15 m tall, stem up to 20 cm in diameter, evergreen; young branches flattened to terete in cross section, glabrous.
Leaves alternate, petiolate; petioles 0.5–5.3 cm long, 0.5–1.5 mm thick, glabrous, articulated at proximal end, grooved longitudinally on adaxial surface, usually with pulvini at both ends, pulvini becoming darker in color and callused with age, 0.8–2.2 mm thick, glabrous, petiole often reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 1.2–2.4 × 0.9–1.4 mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, often with several veins, outer surface glabrous, margin ciliate, apex acute; lamina narrowly to broadly elliptic, obelliptic, or ovate, 3.5–18.0 (–21.0) × 1.0–7.7 cm, herbaceous; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous on upper and lower surfaces; secondary vein pairs 5–12, divergent to ascending, tertiary veins reticulate; base attenuate, cuneate, rounded, or shallowly cordate, symmetrical, aequilateral or oblique; margin subentire to serrulate or serrate; apex acute to shortly acuminate or cuspidate.

Inflorescence an axillary, terminal and subterminal, panicle-like cyme (thyrsoid), 2.5–15.0 cm long, lateral cymules bearing 3–15 (–25) flowers, axis glabrous to puberulent or pubescent; peduncle bracts quickly deciduous, broadly ovate, 0.8–2.0 × 1.0–2.1 mm, coriaceous, keeled or costate, keel or costa usually terminating in a mucro, with several veins, outer surface glabrous, margin ciliate, apex rounded to truncate; pedicels (from articulation to base of flower) 1.0–3.4 mm long, glabrous, puberulent or pubescent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.8–2.0 × 0.6–1.4 mm, herbaceous, often keeled or costate, outer surface glabrous, margin ciliate, apex acute to mucronate. Flowers 4.2–6.3 mm long, flower buds conical.

Sepals subequal in size and shape, herbaceous, ovate to lanceolate-deltoid,
1.1–2.5 × 1.0–2.2 mm, outer surface glabrous to sparsely pubescent, margin ciliate, apex acute to rounded. Corolla zygomorphic, petals white, yellow-white, or cream-white, drying orange-brown, glabrous; anterior and posterior petals lanceolate-ovate to lanceolate or oblanceolate, 4.0–5.6 × 1.3–2.4 mm, margin entire, apex acute to rounded, erect to rolled; lateral petals elliptic to lanceolate or oblanceolate, concave to conduplicate, 4.0–5.5 × 1.1–2.1 mm, margin entire, apex acute to rounded, erect to rolled; Stamens 3.2–4.3 mm long; filaments connate into a continuous staminal tube, staminal tube 0.5–1.0 mm tall, outer and inner surfaces glabrous; anthers sessile on summit of staminal tube, anther connectives 0.9–1.8 × 0.5–1.2 mm, glabrous; anther ventral connective scales absent, or if present, linear or lanceolate, 0.1–0.3 × 0.1 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending ca. one-fifth to one-third down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.2–2.1 × 0.7–1.3 mm, surface glabrous, margin entire, apex acute. Pistil 3.5–5.2 mm long; ovary ovoid, 0.8–1.6 × 0.7–1.3 mm, glabrous; ovules 3; style 2.4–3.6 mm long, erect, filiform, straight or rarely sigmoid, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.3–2.1 cm long, 1.1–1.4 cm diameter, valve 0.7–1.2 cm wide, surface glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 8.0–11.0 × 4.0–8.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 19.
REMARKS. *Rinorea arborea* is variable in leaf morphology across its range. Some forms are weakly associated with geographic locality, but generally variability in leaf shape and size exists in mixed populations. Plants with obovate leaves and leaf apices shortly cuspidate are exemplified by *Perrier 5050* and *SF (Capuron) 8588* from the Masoala Peninsula south to the Fenoarivo area. Plants from the Sambava-Antalaha-Ambohitralana area have oblong leaves with serrate leaf margins and the underside of the leaf often drying to a purple color (e.g., *Perrier 2020; Hongwa et al. 11*). Some individuals from the eastern humid forests in central Madagascar have oblanceolate, drying somewhat shiny brown-green (e.g., *Rabenantoandro et al. 433; SF 16196*).

Three specimens of *Rinorea arborea* (*Gentry 11559, Humbert 22825, and Schatz & Antilahimena 4008*) have long petioles similar to *R. sambiranensis*, but they are maintained in *R. arborea* based on the overall similarity of the size and shape of the leaves.

*Rinorea arborea* co-occurs and sometimes intergrades with *R. longipes* in Ankarana Reserve, Montagne des Français, coastal areas around Vohémar, and Nosy Be. The plants from the Comoro Islands and the Nosy Mitsio island group are intermediate between *R. arborea* and *R. longipes* with ovate-lanceolate leaves, apices acuminate, and leaves drying gray-green (e.g., *Wahlert et al. 129 and 132*).

Several specimens from the Lac Alaotra region verge on *R. occidentalis*, including three syntypes of *R. arborea* f. *occidentalis: Cours 401, 488, 524, 1799, 1800, and 1962*, but given their panicle-like inflorescence and proximity to
other populations of *R. arborea*, they are assigned to the latter. The two specimens, *Anonymous s.n.*, Herbier du Jardin Botanique de Tananarive numbers 3913 and 3939, probably represent duplicates of *Cours 401* and 542, respectively.

The plants from mainland Africa are also somewhat variable in leaf size and shape but are within the range of variation for the species. Some African specimens have large leaves similar to *Rinorea sambiranensis* but lack the long petioles (e.g., *Gereau et al. 6158; Thomas 3665*).

**DISTRIBUTION AND PHENOLOGY.** In Madagascar, *Rinorea arborea* occurs in eastern humid forests and littoral forests from Iharana (Vohémar) south to Tôlanaro (Fort Dauphin), and from the Masoala Peninsula west through the Sambirano forest region to Nosy Be. It occurs in the Mitsio island group and the Comoro Islands. In mainland Africa, *R. arborea* occurs in coastal thickets and semi-deciduous forests further inland, from Kenya south to Mozambique. Across its range, *R. arborea* occurs from 0–1020 m elevation. Across its distribution, there is a wide variability in the flowering and fruiting times for *R. arborea*, but it predominately flowers between September and December and fruits from November to February. — Figures 28 and 29.

**NOMENCLATURE.** The name *Alsodeia arborea* was first published by du Petit-Thouars (1806, p. 57) and a brief diagnosis was provided, but no specimens were cited. In the treatment by Tulasne (1868, p. 309), the name was misspelled as ‘*Alsodea’ arborea* and four specimens were cited: *Thouars*
s.n., Bréon s.n., Chapelier s.n., and Bernier 181. Baillon (1886, p. 583) provided the new combination *Rinorea arborea* and cited the correctly-spelled basionym as *Alsodeia arborea*. Baillon (1886) also cited three more specimens in addition to those in Tulasne: *Boivin 1841*, and *Baron 1607 and 1609*. In his 1949 revision, Perrier de la Bâthie (who only examined collections at the Paris National Museum of Natural History) designated *du Petit-Thouars s.n.*, presumably utilizing the sheet at Paris for his description. However, there is another *du Petit-Thouars s.n.* specimen at K that very clearly represents a duplicate of the sheet at Paris. Therefore, *du Petit-Thouars s.n.* P-00592976 should be considered the holotype of *Rinorea arborea* and the sheet at K, *du Petit-Thouars s.n.* K-000231210, an isotype.

**VERNACULAR NAMES.** Fanavimaitso (*RN 10848*); hazombary (*SF 16180*); hazombato (*SF 26456*); hazomboretra (*SF 8004*); hazomdamoka (*RN2740*); hazomdomohina (*RN 3268, RN 3282*); hazomdomoina (*RN 4543*); hazompiky (*SF 26459*), hodipaso (*SF 13598*); mahanoro (*SF 13598*); marankoditra (*RN 8179*); tsibabeny (*RN 6908*).

**CONSERVATION STATUS.** The estimated EOO for *Rinorea arborea* was 3,550,610 km², and the AOO was 1,223,270 km², giving it a status of Least Concern.

**ADDITIONAL MATERIAL EXAMINED.** **Comoro Islands.** — Mohéli, Hamavounou, Lac de Boundouni, 12°22′36″S, 43°51′08″E, 53 m, 26.V.2006,
bud, Labat et al. 3700 (CNDRS, K, MO!). — Moheli, Est de lac Boundouni, [12°22'S, 43°51'E], 13.XI.1970, fl., Rakotozafy 1202 bis (P!). — Moheli, Djando, Amavouna, au dessus du lac de Boundouni, 12°22'27"S, 43°51'10"E, 90 m, 22.II.1999, Labat et al. 3197 (CNDRS, G, K!, MO!, P!).


Madagascar. — Without precise locality, bud, Baron 1609 (P!). — bud, Bréon s.n. (P!). fl., Cours 1962 (MO!, P!), [in the vicinity of Lac Alaotra?]. — bud, Chapelier s.n. (P!). — fl., Lance s.n. (P!).

P!, TAN!). — Same locality, Bardot-Vaucoulon 861 (K!, MO!, P!, TAN!). — "Fampotatrely, Ampanavoana, Vinanivao, Antalaha, Parc Masoala, 15°35’S, 50°25’E, 0–50 m, 4.IV.1996, fl., Bernard 262 (K!, MO!). — Sahaenjika, Ambodiazovola, Ampanavoana, Vinanivao, Antalaha, Parc Masoala, 15°41’33”S, 50°13’30”E, 12–100 m, 15.IX.1996, fl., Bernard 311 (MO!). — Antalaha, CR Vinanivao, Vallée d’Anaovanandrano, cours inférieur, 15°45’S, 50°10’E, 40 m, 17.IX.2003, bud, Callmander & Bohnenstengel SW 676 (MO!). — Sous-préfecture de Vohemar, commune rurale de Daraina, forêt d’Binara, 13°13’53”S, 49°35’57”E, 950 m, 25.III.2004, fl., Gautier & Ranirison LG 4696 (G, MO!). — Montagne d’Ambre National Park, at Cul de Sac ca. 200 m past Point de Vue Grande Cascade, 12°31’36”S, 49°10’20”E, 840 m, 19.IV.1993, bud, Harder et al. 1640 (MO!, TAN!). — Ankarana Special Reserve, ca. 6 km NE of Mahatsara village, on Mahatsara-Diego Suarez road, near volcanic outcrops, 12°51’01”S, 49°13’30”E, 310 m, 26.IV.1993, fl., Harder et al. 1755 (MO!, TAN!). — Vallée de la Lokoho, [14°34’S, 49°43’E], ± 300 m, fr., Humbert 22380 (K!, P!). — Vallée de la Lokoho, Nord-East, près d’Ambalavoniho, [14°34’S, 49°44’E], 75–300 m, 9–10.I.1949, Humbert & Cours 22825 (P!). — Same locality and date, Humbert & Cours 22954 (K!, P!). — Vallée inférieure de l’Androranga, affluent de la Bemarivo, Nord-East, aux environs d’Antongondriha, [14°11’30”S, 49°46’00”E], 100–250 m, 1–24.XI.1950, fl., Humbert & Capuron 23943 (K!, P!, WAG!). — Vallée inférieure de l’Androranga, affluent de la Bemarivo, Nord-East, aux environs d’Antongondriha, Mont Anjenabe, [14°17’S, 49°46’E], 300–600 m, 3–7.XI.1950, imm. fr., Humbert & Capuron 24060 (K!, P!, WAG!). — Vallée de l’Andalangy, affluent de l’Androranga, bassin de la


TAN!, WAG!). — Nosy Mitsio Archipelago, Nosy Ankarea, near old resort at base of basalt rocks, 12°50′31″S, 48°34′41″E, 0–15 m, 23.XI.2007, Wahlert et al. 129 (K!, MO! P!, TAN!, WAG!). — Nosy Mitsio Archipelago, Nosy Mitsio, Mt. Mitsio area, forest remnant near SW shore, near village of Ampanitsoha, 12°53′40″S, 48°32′35″E, 0–5 m, 25.XI.2007, bud, Wahlert et al. 132 (K!, MO! P!, TAN!, WAG!). — Antalaha, CR Vinanivao, bords de sentier, à l’entrée de Vinanivao, Péninsule Masoala, 15°52′S, 50°16′E, 40 m, 11.IX.2003, fl., Wohlhauser et al., SW493 (MO!). Fianarantsoa Province. — 15 km Sud de Farafangana, [23°01′00″S, 47°43′23″E], XII.1963, fl., Bosser 18575 (K!, TAN[2]!). — Same locality, Bosser 18743 (TAN!). — Route Farafangana-Vangaindrano, [23°00′30″S, 47°42′00″E], XII.1963, fr., Bosser 18677 (P!, TAN!). — Kianjavato, route de Mananjary, [21°22′S, 47°52′E], I.1964, fr., Bosser 18892 (K!, MO!, P!, TAN[2]!). — S. of Farafangana, in Forêt Classée near Manombo Reserve, 23°03′16″S, 47°40′28″E, 100 m, 15.XI.2001, fl., McPherson & Rabenantoandro 18429 (K!, MO!). — Between Ambalavao and Ihosy Réserve Villageoise d’Anja, 12 km from Ambalavao along RN 7, 21°51′09″S, 46°50′39″E, 1020 m, 8.XI.2003, fl., Phillipson & Rakotonandrasana 5695 (K!, MO!, WAG!). — Iabomary, 40 km au sud ouest de Farafangana, Mananivo, Farafangana, 23°03′34″S, 47°40′23″E, 0–50 m, 6.II.2001, fr., Rabenantoandro et al. 433 (MO!). — Farafangana, in Forêt Classée de Manombo, 23°04′00″S, 47°40′33″E, 42 m, 27.IX.2002, bud, Rabevohiritra et al. 4159 (MO!). — Vatomasina, Vohipeno, [21°40′30″S, 47°42′00″E], 26.XI.1952, fl., SF 6425 (P!). — Ambodinonoka, Mananjary, [20°58′30″S, 47°53′30″E, 300 m], 15.I.1955, SF 13487 (P!). — Analamiditra, Manakara, [22°09′30″S, 47°56′00″E], XI.1954, bud,
SF 13588 (P!). — Belambo, Manakara, [22°46′30″S, 47°31′10″E], 14.II.1955, 
SF 13598 (P!). — Ambodivoangy, Lakatoana, Canton Ambohinihoanana, 
District Mananjary, [21°12′00″S, 47°54′30″E], 14.II.1956, fr., SF 16180 (P!). — 
Tranoroa, Vamohora, Canton Farafangana, District Farafangana, [23°00′30″S, 
47°42′00″E], 28.V.1956, fl., SF 16194 (MO!, P!, TEF!). Mahajanga Province. — 
7–10 km E of Antsahabe, [14°46′30″S, 48°26′E], 800–900 m, 6.V.1974, Gentry 
11559 (K!, MO!, TAN!). Toamasina Province. — District d’Ambatondrazaka, 
près de Station [Lac Alaotra], [17°35′30″S, 48°32′30″E], 800 m, XI.1937, fl., 
Anonymous s.n. (P-00636138!), [Herbier du Jardin Botanique de Tananarive 
3913 = Cours 401?]. — Ambohidavakely, près de Station Lac Alaotra, District 
d’Ambatondrazaka, [17°35′S, 48°13′E], 780 m, XII.1937, fl., Anonymous s.n. 
(P!), [Herbier du Jardin Botanique de Tananarive 3939 = Cours 542?]. — Path 
from Ambatondradama to Fizoana, Masoala Peninsula, Maroantsetra, 
15°18′47″S, 50°00′09″E, 150–374 m, bud, fl., Birkinshaw et al. 502 (MO!, 
WAG!). — Ste. Marie, [16°54′S, 49°54′E, 0–45 m], 1824 or 1834, fl., Bernier 
181 (P!). — Ste. Marie de Madagascar, Lafondrou, [16°54′S, 49°54′E, 0–45 m], 
I.1848, fl., Boivin 1841 (K!, P!). — Réserve Naturelle No. 1, Tamatave, 
[17°56′S, 49°17′E], 4.XI.1953, fl., SF (Capuron) 8588 (MO[2]!, P!). — Island of 
Nosy Mangabe, 5 km S of Maroantsetra in the Bay of Antongil, 15°29′S, 
49°45′E, 150 m, Carlson 173 (MO!, TAN!). — District d’Ambatondrazaka, près 
de Station [Lac Alaotra], [17°35′30″S, 48°32′30″E], 800 m, XI.1937, fl., Cours 
401 (P!). — Ambohidavakely, près de Station Lac Alaotra, District 
d’Ambatondrazaka, [17°35′S, 48°13′E], 780 m, XII.1937, fl., Cours 488 (P- 
00537194! and P-00537144!). — Same locality, 780 m, XII.1937, fl., Cours 542
(P!). — Rivière Menaloha, [17°42′05″S, 48°27′59″E], 11.XII.1944, imm. fr.,
*Cours 1799* (MO!, P!, TAN!). — Same locality and date, *Cours 1800* (P!). —
Forêt d’Ambatosoratra, [17°23′S, 49°16′E], 1000 m, 8.I.1949, *Cours 3385* (MO!,
P!, TAN!). — Tampolo, Péninsule Masoala, Loatrozo, entre Ambodiforaha et
Andranobe, [15°41′52″S, 49°57′56″E], 200 m, 22.X.2001, *Labat & Andrianjafy*
3388 (K!, MO!). — Maroantsetra, above and N of village of Hiaraka, ESE of
Maroantsetra on NW coast of Masoala Peninsula, [15°32′S, 49°55′E], 50–75,
*Lowry et al. 4067* (MO!, TAN!). — Maroantsetra, ridge running SE of village of
Ambanizana, [15°33′31″S, 49°56′03″E], 150 m, 15.X.1986, fl., *Lowry et al. 4147*
(K!, MO!, TAN!, WAG!). — Same locality, 50 m, 18.X.1986, *Lowry et al. 4178*
(K!, TAN!, WAG!). — Environs de Fénérive, [17°23′S, 49°16′E], fl., *Perrier 5050*
(P!). — Réserve Naturelle Intégrale 3, Zahamena, au Nord Est du village
d’Andratanantsoitra, le long du fleuve l’Onibe, 17°43′S, 49°00′E, 300 m,
20.XII.1993, *Randrianjanka & Arnaud 36* (TAN!). — R.N. I, District Tamatave,
[17°56′30″S, 49°17′00″E], 21.XI.1951, *RN 3268* (P[2]!, TAN!). — R.N. I,
Ambodiriana, Tamatave, [17°56′S, 49°17′E], 18.XII.1952, *RN 4543* (MO!, P!). —
Same locality, 5.XI.1953, fl., *RN 5877* (K!, P!, TEF!). — Same locality,
21.X.1956, fl., *RN 8170* (P!). — Same locality, 27.VI.1959, fl., *RN 10848* (P!). —
Nosy Mangabe, a 520 ha island 5 km from Maroantsetra in the Bay of Antongil,
15°30′S, 49°46′E, 0–330 m, 11.X.1987, bud, fl., *Schatz 1620* (MO!, TAN!). —
Marofotsy, Marolambo, [20°06′00″S, 48°05′30″E], 31.X.1953, *SF 8004* (K!, MO!,
P!). — Same locality, 31.X.1953, *SF 9405* (K!, MO!, P!). — Ankirindro Massif,
slopes above the village Ambodivato, ca. 5 km NW of Ambinanitelo along the
Vohimaro River, 15°19′13″S, 49°33′29″E, 150 m, 20.XI.2002, imm. fr., *Schatz &
Antilahimena 4008 (MO!). — Masoala Peninsula, Ambanizana, trail along coast, 1–3 km S of Ambanizana, 15°39’S, 49°58’E, 0–10 m, 26.X.1992, fl., Schatz et al. 3338 (K!, MO!, TAN!, WAG!). — Sahamamy, Anivorano, Brickaville, [18°33’S, 48°58’E], 29.IX.1954, fl., SF 10753 (MO!, P!). — Same locality, 30.IX.1954, fl., SF 10756 (MO!, TEF!). — Amboditavolo, Lorihandava, Brickaville, [19°12’00”S, 48°53’30”E], 20.X.1954, fl., SF 12762 (P!). — Masoala Peninsula, near Andranobe, along beach, 15°40’06”S, 49°57’04”E, 2 m, 13.XI.1993, imm. fr., van Nek 2052 (TAN!). — Masoala Peninsula, S of Ambanizana, 15°38’05”S, 49°58’00”E, 50 m, 19.XI.1993, van Nek 2125 (TAN!).

Mozambique. — Sofala, Cheringoma Plateau, ca. 25 km from Inhamitanga, on Shupanga Road, 18°12’27”S, 35°19’47”E, 193 m, 9.X.2007, bud, Burrows & Wahlert 10171 (BNRH!, K!, MO!, P!, WAG!). Same locality and date, Burrows & Wahlert 10173 (BNRH!, K!, MO!, P!, WAG!). — Manica e Sofala, entre Inhamitanga e Lacerdónia, [18°11’09”S, 35°17’49”E, 130–200 m], 24.VI.1967, fr., Carvalho 978 (MO!). — Gaza, andados 10 kms do Chipenhe para Mainguelane, Floresta Muguaze, [24°59’59”S, 33°22’23”E], 29.IX.1971, fl., Correia et Marques 2269 (MO!, PRE!). — Manica e Sofala, Cheringoma, [18°30’S, 35°16’E], 17.X.1944, Mendonça 2486 (WAG!). — Zambezia, Maganja da Costa, floresta de Gobene, próx. da praia Raraga, ao km. 43 de Vila de Maganja, [17°05’S, 37°27’E], 20 m, 10.I.1968, fr., Torre & Correia 17072 (PRE!). Tanzania. — Without precise locality, 12.X.1952, fl., Carmichael 139 (MO!). — Morogoro, Ulanga District, Nambinga Forest Reserve, 15.5 km by road N or Itete, in forest W of road, 08°34’10”S, 36°29’23”E, 350 m, 29.X.1998, fr., Gereau et al. 6158 (MO!, P!). — K8, Lindi Rural District, Rondo Division,

2. *Rinorea ballardii* Wahlert, sp. nov.

*Haec species ad Rinorea occidentalis (H.Perrier) Wahlert accedit, sed floribus 1 per cymula, petiolis et ovario pubescenti, et pagina abaxiali foliorum pubescentium differt.*

DESCRIPTION. Small tree up to 4 m tall, stem up to 10 cm in diameter, often multi-stemmed at the base, semi-deciduous; young branchlets flattened to terete in cross section, densely pubescent. Leaves alternate, petiolate; petioles 0.8–3.5 cm long, 0.6–1.0 mm thick, densely pubescent, articulated at proximal end, longitudinally grooved on adaxial surface, usually with pulvini at both ends, pulvini 1.0–1.7 mm thick, pubescent, petiole usually reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 2.0–3.1 × 0.9–1.4 mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, with several veins, outer surface densely pubescent, margin ciliate, apex acute; lamina elliptic to lanceolate-elliptic, 5.4–15.5 × 1.7–4.9 cm, herbaceous; lamina upper surface sparsely pubescent, lower surfaces pubescent; primary and secondary veins sparsely pubescent on upper surface, densely pubescent on lower surface; secondary vein pairs 6–10, divergent to ascending, tertiary veins reticulate; base cuneate to rounded, symmetrical, aequilateral; margin serrulate to serrate; apex acute. Inflorescence an axillary, terminal and subterminal, raceme-like cyme (botryoid), 1.5–5.0 cm long, lateral cymules bearing 1 flower (basal cymules rarely bearing 2 flowers), axis densely pubescent; peduncle bracts eventually deciduous, broadly ovate to deltoid, 0.9–1.9 × 1.0–2.1 mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, with several veins, outer surface pubescent, margin ciliate, apex rounded to acute; pedicels (from articulation to base of flower) 1.1–2.8 mm long, pubescent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.6–1.2 × 0.4–0.7 mm, herbaceous, keeled or costate, keel or costa sometimes terminating in a mucro, often veined, outer surface pubescent, margin ciliate,
apex acute to mucronate. Flowers 4.2–5.2 mm long, flower buds conical.

Sepals subequal in size and shape, herbaceous, ovate to lanceolate-deltoid, 1.0–1.8 × 1.0–1.4 mm, outer surface glabrous or pubescent, margin ciliate or entire, apex acute to rounded. Corolla zygomorphic, petals cream-white to yellow-white, drying orange-brown, glabrous; anterior and posterior petals lanceolate to lanceolate-ovate, 3.4–5.3 × 1.8–2.5 mm, margin entire, apex acute, erect to rolled; lateral petals lanceolate to oblanceolate, concave to conduplicate, 4.2–4.9 × 1.4–1.8 mm, margin entire, apex acute, erect to rolled. Stamens 3.5–4.3 mm long, filaments connate into a continuous staminal tube, staminal tube 0.5–0.9 mm tall, outer and inner surfaces glabrous; anthers sessile on summit of staminal tube, anther connectives 1.2–1.8 × 0.7–0.9 mm, glabrous; anther ventral connective scales absent, or if present, mucronulate 0.1 mm long; anther dorsal connective scales large and conspicuous, apical and lateral, extending ca. one-fourth to entire length down the anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.7–2.0 × 0.9–1.2 mm, surface glabrous, margin entire, apex acute. Pistil 4.2–4.9 mm long; ovary ovoid, 0.9–1.9 × 1.0–1.4 mm, pubescent; ovules 3; style 2.3–3.3 mm long, erect, filiform, straight, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.9–2.3 cm long, 0.7–1.2 cm in diameter, valve 1.0–1.2 cm wide, surface sparsely pubescent, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 6.0–8.0 × 4.0–6.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 20.
DISTRIBUTION. *Rinorea ballardii* is distributed on sandy soils in the vicinity of Ankarafantsika National Park at elevations of ca. 100–350 m. The species flowers October to November and fruits November to December. — Figure 28.

VERNACULAR NAMES. Hasimpidika (*Ursch* 32).

CONSERVATION STATUS. The estimated EOO for *Rinorea ballardii* was 740 km², and the AOO was 457 km², giving it a status of Endangered. Nearly the entire range of the species is confined to PN Ankarafantsika. The species is locally abundant within the park, as well as some other adjacent unprotected areas (Wahlert, pers. obs.).

ETYMOLOGY. This species is named in honor of Harvey E. Ballard, Jr., Associate Professor of Plant Biology, Department of Environmental and Plant Biology, Ohio University, Athens, OH, USA. Ballard has contributed greatly to the taxonomy and systematics of the Violaceae.

46°48′33″E, 165 m, 8.XI.2007, fl., Wahlert et al. 110 (MO!, P!, TAN!). — Ankarafantsika National Park, along trail around Lac Ravelobe, 16°18′65″S, 46°49′13″E, 125 m, 8.XI.2007, fl., Wahlert et al. 113 (EA!, G!, K!, MO!, P!, PRE!, TAN!, WAG!). — Ankarafantsika National Park, village of Ankoririka, ca. 15 km north of Tsaramandrosoro, in the drainage of the Tsimaloto River and lemur study site, 16°15′56″S, 47°03′24″E, 210 m, 12.XI.2007, Wahlert et al. 119 (K!, MO!, P!, TAN!, WAG!).

3. *Rinorea labatii* Wahlert, sp. nov.

*Haec species ad Rinorea occidentalis (H.Perrier) Wahlert accedit sed inflorescentia racemiformi, floribus 1 per cymula, et foliis 3.2–11.5 longo × 1.6–4.3 lato differt.*

**Typus.** *Madagascar*. Mahajanga Province. — Andalasarotsy, Soalala, [16°53′11″S, 45°35′53″E, 433 m], 24.XI.1955, fl., RN 7744 (holo- P-00537118!, iso- MO3885937!, TEF!).

**Description.** Small tree, up to 7 m tall; young branches flattened to terete in cross section, glabrous. Leaves alternate, petiolate; petioles 0.6–3.1 cm long, 0.5–1.0 mm thick, glabrous, articulated at proximal end, grooved longitudinally on adaxial surface, sometimes with pulvini at both ends, pulvini 0.7–1.3 mm thick, glabrous, petiole often reflexed 5–45° (–90°) at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 0.9–1.8 × 0.5–1.3
mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, often with several veins, outer surface glabrous, margin entire to ciliate, apex acute; lamina elliptic to lanceolate-elliptic, 3.2–11.5 × 1.6–4.3 cm, herbaceous, drying gray-green; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 7–9, ascending, tertiary veins reticulate; base rounded to shallowly cordate, symmetrical, aequilateral to oblique; margin subentire to serrulate; apex acute to rounded. Inflorescence an axillary, terminal and subterminal, raceme-like cyme (botryoid), 1.5–6.5 cm long, lateral cymules bearing 1 flower, axis glabrous or rarely pubescent; peduncle bracts eventually deciduous, broadly lanceolate-ovate, 0.6–1.5 × 0.3–1.4 mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, outer surface glabrous, margin ciliate, apex rounded; pedicels (from articulation to base of flower) 1.7–3.2 mm long, glabrous or puberulent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.4–1.4 × 0.2–0.9 mm, herbaceous, often keeled or costate, outer surface glabrous or puberulent, margin ciliate, apex acute, mucronate. Flowers 3.2–5.7 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, ovate to lanceolate-deltoid, 1.4–2.6 × 0.6–2.0 mm, outer surface glabrous or rarely puberulent, margin ciliate, apex acute to rounded. Corolla zygomorphic, petals green-white, drying orange-brown, glabrous; anterior and posterior petals elliptic to lanceolate or oblanceolate, 3.8–4.8 × 1.5–2.8 mm, margin entire, apex acute, erect to rolled; lateral petals elliptic to lanceolate or oblanceolate, concave to conduplicate, 4.1–4.8 × 1.5–2.7 mm, margin entire, apex acute to rounded, erect to rolled. Stamens 3.2–4.3 mm long; staminal tube 0.6–1.2 mm tall, outer and inner surfaces glabrous;
anthers sessile on summit of staminal tube, anther connectives 0.9–1.5 × 0.4–0.9 mm, glabrous; anther ventral connective scales absent, or if present, lanceolate or linear, 0.3–0.7 × 0.1–0.2 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending ca. one-third down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.6–2.1 × 0.6–1.3 mm, surface glabrous, margin entire, apex acute. Pistil 3.4–3.9 mm long; ovary ovoid, 0.6–1.3 × 0.5–1.3 mm, glabrous, ovules 3; style 2.6–3.0 mm long, erect, filiform, straight, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.5–1.8 cm long, ca. 1.0 cm diameter, valve 0.9–1.0 cm wide, surface glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 9.0–9.3 × 5.5–7.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 21.

**DISTRIBUTION.** *Rinorea labatii* is distributed in deciduous forests in and around Namoroka National Park, at elevations of ca. 200–250 m. The species flowers September to November and fruits December to January. — Figure 27.

**VERNACULAR NAMES.** Hazompika (*RN 5622*); salohimbato (*RN 3839*); tapahy (*RN 7019*); tsilaitra (*RN 7744*).

**CONSERVATION STATUS.** The estimated EOO for *Rinorea labatii* was 353 km², and the AOO was 158 km², giving it a status of Endangered. Nearly the entire range of the species is confined to PN Tsingy de Namoroka, with a few
outlying populations. The species is mostly known from collections of RN made in the 1950s, but a single collection is from 1989.

ETYMOLOGY. This species is named in honor of Jean-Noël Labat, botanist in the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, France. His high quality botanical specimens from Madagascar and the Comoro Islands have greatly improved the accuracy of species descriptions in this revision.

PARATYPES. Madagascar. Mahajanga Province. — Namoroka, District de Soalala, Réserve No. 8, [16°22'00"S, 45°21'30"E], 15.IX.1940, fl., Decary 15770 (K!, MO!, P!, WAG!). — Same locality, 17.IX,1940, fl., Decary 15806 (K!, MO!, P!). — Boina region, 4 k SE of the village of Vilanandro, S of Soalala, 16°32'S, 45°27'E, 200 m, 23.IX.1989, fl., Du Puy et al. MB360 (P!, TAN!). — R.N. 8, Andranomavo, Soalala, [16°38'30"S, 45°36'00"E], 15.I.1952, fr., RN 3839 (MO!, P!, TAN!). — Same locality, 31.VII.1953, fl., RN 5618 (MO!, P!, TAN!, TEF!). — Same locality, 6.VIII.1953, bud, RN 5622 (P!, TEF!). — Same locality, 30.IX.1953, bud, RN 5656 (P!, TAN!, TEF!). — Same locality, 21.XI.1953, bud, RN 5682 (MO!, P!, TAN!, TEF!). — Same locality, 26.X.1954, bud, RN 6677 (P!, TEF!). — Same locality, 4.XI.1954, fl., RN 7019 (MO!, P!).


**Description.** Shrub to small tree, 1.0–7.0 m tall, stem 1–6 cm diameter, evergreen to semi-deciduous; young branchlets flattened to terete in cross section, glabrous or rarely pubescent. Leaves alternate, petiolate; petioles 0.3–2.7 cm long, 0.5–0.9 mm thick, glabrous or rarely puberulent, articulated at proximal end, longitudinally grooved on adaxial surface, pulvini wanting or occasionally present at one or both ends, 0.6–1.6 mm thick, glabrous or rarely puberulent, petiole sometimes reflexed 5–45° (–90°) at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 1.1–2.5 × 0.5–1.4 mm, coriaceous, keeled, keel terminating in a mucro, usually with several veins, outer surface glabrous, margin ciliate, apex acute, mucronate; lamina elliptic, lanceolate, oblanceolate, or rhombic, 1.8–12.2 × 1.0–5.1 cm, herbaceous; lamina upper surface glabrous, lower surface glabrous or rarely puberulent; primary vein glabrous or rarely puberulent towards base on upper surface, glabrous or rarely pubescent on lower surface, secondary veins glabrous on upper surface, glabrous or rarely pubescent on lower surface; secondary vein
pairs 3–9, divergent to ascending, tertiary veins reticulate; base cuneate, rounded, shallowly cordate, or rarely attenuate, symmetrical, aequilateral to oblique; margin subentire, crenulate-serrulate, or serrate; apex acute, acuminate, or rounded. Inflorescence an axillary, terminal and subterminal, panicle-like cyme (thyrsoid), 1.0–6.0 cm long, lateral cymules bearing 1–5 flowers, axis glabrous or puberulent; peduncle bracts eventually deciduous, broadly ovate to lanceolate-deltoid, 0.6–2.0 × 0.8–1.8 mm, coriaceous, keeled, keel terminating in a mucro, often with veins, outer surface glabrous, margin ciliate, apex rounded to acute; pedicels (from articulation to base of flower) 0.8–3.3 mm long, glabrous or puberulent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.6–2.2 × 0.4–1.8 mm, herbaceous, keeled or costate, keel or costa usually terminating in a mucro, sometimes veined, outer surface glabrous or rarely puberulent, margin ciliate, apex acute to mucronate. Flowers 3.6–6.8 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, triangular to lanceolate-ovate, 0.8–2.5 × 0.7–1.9 mm, outer surface glabrous, margin ciliate, apex rounded. Corolla zygomorphic, petals cream-white, green-white, yellow-white, or yellow-green, drying orange-brown, glabrous; anterior and posterior petals elliptic, broadly elliptic to lanceolate-ovate, 3.1–6.2 × 1.3–2.7 mm, margin entire, apex acute, erect to rolled; lateral petals elliptic or lanceolate to oblanceolate, concave to conduplicate, 3.0–5.7 × 1.1–2.3 mm, margin entire, apex acute, erect to recurved. Stamens 2.7–4.6 mm long; filaments connate into a continuous staminal tube, staminal tube 0.4–1.1 mm tall, outer and inner surfaces glabrous; anthers sessile on summit of staminal tube, anther connectives 0.7–1.8 × 0.5–
1.0 mm, glabrous; anther ventral connective scales absent, or if present, lanceolate, 0.1–0.7 × 0.1–0.5 mm; anther dorsal connective scales large and conspicuous, apical and lateral, extending ca. one-fifth to one-half down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.1–2.2 × 0.6–1.3 mm, surface glabrous, margin entire, apex acute. Pistil 3.1–5.0 mm long; ovary ovoid, 1.0–1.4 × 0.9–1.3 mm, glabrous or rarely pubescent, ovules 3; style 2.2–3.8 mm long, erect, filiform, straight or rarely sigmoid, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.2–2.0 cm long, 1.0–1.4 cm diameter, valve 0.5–1.1 cm wide, surface glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 6.0–11.0 × 4.0–7.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 22.

REMARKS. The fragmentary holotype of *Rinorea viridiflora* (Boivin 2561) was carefully scrutinized, and no character states could be found to differentiate it from *R. longipes*. The specimens SF (Capuron) 27449 and Ranirison & Nusbaumer PR 889 closely match the holotype but still fall within the range of variation of *R. longipes*. Other than the very short petioles (0.3–0.6 mm long) of these three individuals, there are no diagnostic characters to justify maintaining *R. viridiflora* as a separate species.

Typically, *Rinorea longipes* has leaves ca. 2.0–8.0 cm long × 1.0–3.0 cm wide, but several individuals have leaves up to ca. 12.0 cm long × 5.0 cm wide (e.g., Homolle 291, Rabevehitra et al. 1036, Wahlert & Rakotonasolo 9).
The specimen *Perrier 11114*, a syntype for *Rinorea arborea* f. *occidentalis* (listed as “*Perrier 1114*” in Perrier de la Bâthie 1949 and 1954), is far out of its range in Mahajanga Province, yet it is indistinguishable from the plants found at Ankarana Special Reserve. The specimen *Humbert 18837* is aberrant with a single petiole 4.8 cm long. Plants from the Daraina region have young branches and petioles pubescent (*Meyers 218, 222, and 238; McPherson 14709 and 14738; Nusbaumer et al. LN 1399)*.

The specimens *SF (Capuron) 22951* and *Rakotozafy 1491 and 1572* from Orangea Forest in Antsiranana Province have exceptionally small leaves—although somewhat immature—and may deserve taxonomic recognition if additional specimens become available. Capuron gave an exact location, but searches conducted by the author in 2006 and 2007 failed to locate any similar plants.

**DISTRIBUTION.** With the exception of *Perrier 11114, Rinorea longipes* is restricted to Antsiranana Province. It occurs in coastal forest thickets on sandy soils on the northeastern coast north of the Bemarivo River to the Orangea Forest, in humid forests at Lokobé RNI on Nosy Be, and in mountainous areas on volcanic and calcareous soils in semi-deciduous forests in Ankarana Special Reserve, Montagne des Français and in the vicinity of Daraina. It grows from sea level to 600 m elevation. *Rinorea longipes* flowers October to January and fruits December to February. — Figure 28.
**Typification.** The two *Boivin s.n.* specimens at K (K-000231202! and K-000231203!) very closely match the two *Boivin 2119 bis* sheets at P. They very likely represent the specimens *Boivin 2119 ter* cited in Tulasne (1868) and should be considered syntypes of *Rinorea longipes*.

**Conservation Status.** The estimated EOO for *Rinorea longipes* was 36058 km², and the AOO was 15957 km². It is assigned a status of Near Threatened based on the EOO and Least Concern based on the AOO. The species is widespread, occurs in protected areas, and is known from many recent collections.

Bardot-Vaucoulon 293 (P!). — Same locality, 3.XII.1990, imm. fr., Bardot-Vaucoulon 365 (P!). — Ambilobe, Matsaborimanga, Réserve Spéciale d'Ankarana, première zone de tsingy, à droite du sentier allant à Amposately, 12°55′16″S, 49°05′27″E, 130 m, 18.X.1997, Bardot-Vaucoulon & Andrianantoanina 805 (P!, TAN!). — Réserve Spéciale d'Ankarana, Ambilobe, Matsaborimanga, camp des américains, canyon deuxième, 12°55′05″S, 49°03′03″E, 110 m, 10.I.2003, fr., Bardot-Vaucoulon et al. 1123 (MO!, P!). — Nossi-Bé, [13°24′41″S, 48°18′24″E], 1849, bud, fl., Boivin s.n. (K-000231202!, K-000231203!). — Sakaramy, Montagne des Français, [12°22′00″S, 49°21′30″E], 8.XI.1944, fl., Homolle 291 (P!). — Collines et plateaux calcaires de l'Ankarana, [12°54′00″S, 49°07′48″E], 10–250 m, XII.1937–I.1938, imm. fr., Humbert 18837 (P!). — Same locality and date, fl., Humbert 18888 (BM!, P!, PRE!). — Collines et plateaux calcaires de l'Ankarana, vers Ambondrofe, [12°53′30″S, 49°12′30″E], 250 m, XII.1937–I.1938, Humbert 19050 (P!). — Collines et plateaux calcaires de l'Analamera, [12°48′00″S, 49°27′30″E], 50–400 m, I.1938, imm. fr., Humbert 19140 (P!). — Forêt d'Ambatomomo au Sud d'Anivorano Nord, [12°51′S, 49°15′E], 30.I.1960, fr., Humbert 32373 (P!). — Diego Suarez region, SE of town and SE of Ambilobe, near Darana [Daraina], on road to Vohemar (Iharana), D. Meyer's lemur study site, 14°70′S, 49°46′E, 200–250 m, 19.XII.1989, bud, McPherson 14709 (K!, MO!, TAN!). — Same locality, 20.XII.1989, fl., McPherson 14738 (K!, MO!, TAN!, WAG!). — Mantamena, part of Bekaroaka Range, 7 km NE of Daraina (Vohemar), Faritany Antsiranana, 13°08′S, 49°42′E, 112–330 m, 27.XI.1990, Meyers 218 (MO!, TAN!). — Antsahalalina, part of Bobankora Range, 12 km NE of Daraina,
Rabevohitra et al. 4203 (MO!). — Fivondronana Vohémar, Commune rurale Nosy be, forêt d’Analabe, 13°04′45″S, 49°54′17″E, 22.II.2003, imm. fr.,
Rabevohitra et al. 4495 (MO!). — Réserve Spéciale d’Ankarana, sur la piste vers le Lac Vert, 12°55′S, 49°07′E, 180 m, 22.II.1994, fr., Rahajasoa et al. 201 (K!, MO!). — Same locality, 12°54′07″S, 49°06′06″E, 180 m, 18.II.1994, fr.,
Rakotomalaza et al. 134 (K!, MO!). — Est du Diego Suarez, [12°18′38″S, 49°21′08″E, 20 m], X.1975, Rakotozafy 1491 (TAN!). — Orangea, Diego Suarez, [12°18′38″S, 49°21′08″E, 20 m], X.1978, Rakotozafy 1572 (TAN!). —
**5. Rinorea meridionalis** (H.Perrier) Wahlert stat. nov.


**DESCRIPTION.** Small tree, 3–6 m tall; young branches flattened to terete in cross section, glabrous. Leaves alternate, petiolate; petioles (0.8–) 1.7–6.6 cm long, 0.6–1.2 mm thick, glabrous, articulated at proximal end, grooved longitudinally on adaxial surface, usually with pulvini at both ends, pulvini becoming callused with age, 0.6–1.8 mm thick, glabrous, petiole usually reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 1.0–2.0 × 0.7–2.0 mm, coriaceous, keeled or costate, keel or costa terminating in a mucro, outer surface glabrous, margin ciliate, apex acute; lamina lanceolate or elliptic, 4.3–12.0 (–16.0) × 1.6–5.3 (–6.1) cm, herbaceous; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 6–10, divergent to ascending, tertiary veins reticulate; base rounded to shallowly cordate, symmetrical, aequilateral; margin serrulate to serrate; apex acute. Inflorescence an axillary, terminal and subterminal, panicle-like cyme (thyrsoïd), 2.0–9.0 cm long, lateral cymules bearing 1–7 flowers, axis glabrous to puberulent; peduncle bracts eventually deciduous, deltoid or ovate, 0.7–1.7 × 0.8–1.8 mm, coriaceous, keeled or costate, keel or costa usually terminating in a mucro, outer surface glabrous,
margin ciliate, apex acute or rounded; pedicels (from articulation to base of flower) 1.2–3.1 mm long, glabrous or pubescent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 0.8–1.9 × 0.5–1.2 mm, herbaceous, keeled or costate, keel or costa usually terminating in a mucro, outer surface glabrous, margin ciliate, apex acute to mucronate. Flowers 3.3–6.8 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, ovate to lanceolate-ovate, 1.1–3.0 × 1.0–2.3 mm, outer surface glabrous or rarely pubescent at the base, margin ciliate, apex rounded. Corolla zygomorphic, petals white or yellow-white to pale yellow-green, drying orange-brown, glabrous; anterior and posterior petals lanceolate-elliptic to lanceolate, 4.0–5.3 × 1.6–2.6 mm, margin entire, apex acute, erect to recurved; lateral petals lanceolate, concave to conduplicate, 3.7–4.7 × 1.4–1.9 mm, margin entire, apex acute, erect to recurved. Stamens 3.0–4.0 mm long; staminal tube 0.7–1.3 mm tall, outer and inner surfaces glabrous, tube sometimes with a partially free membranous flange; anthers sessile on summit of staminal tube, anther connectives 1.0–1.2 × 0.5–0.9 mm, glabrous; anther ventral connective scales absent, or if present, lanceolate, 0.1–0.2 × 0.05–0.1 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending one-fourth to one-half down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.5–1.8 × 1.1–1.3 mm, surface glabrous, margin entire, apex acute. Pistil 3.2–4.6 mm long; ovary ovoid, 0.7–1.4 × 0.5–1.1 mm, glabrous; ovules 3; style 2.5–3.1 mm long, erect, filiform, straight, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 1.6–2.0 cm long, 1.0–1.3 cm diameter, valve 0.8–1.0 cm wide, surface
glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 9.0–10.0 × 6.0–8.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 23.

**REMARKS.** Perrier treated this taxon as a forma of *Rinorea arborea*, but it is readily distinguished by its consistently lanceolate leaves, rounded leaf bases, and long slender petioles. The specimens *SF 15576* and *Humbert 19761* have slightly narrower leaves and represent a disjunct population to the west in the area of Analavelona. The specimen *Dorr et al. 3643* is far out of the range of *R. meridionalis*, but it is similar with its lanceolate leaves and slender petioles. *Randrianaivo et al. 870* approaches *R. arborea* by its thick petioles, but is assigned to *R. meridionalis* based on its leaf shape and size.

The specimen *Commerson s.n.* was tentatively placed in *Rinorea longipes* by Tulasne (1868) and Perrier (1954), but the lanceolate leaves, rounded leaf base, and slender petioles suggest a closer affinity to *R. meridionalis*. Commerson traveled near Fort Dauphin from about October–December 1770, potentially bringing him into the range of *R. meridionalis* (Dorr, 1997).

**DISTRIBUTION.** *Rinorea meridionalis* is distributed in forested areas in the mountains and river valleys in the Tôlanaro (Fort Dauphin) region, and as an outlying population in the vicinity of Analavelona, at elevations of 100–1200 (–
1900) m. *Rinorea meridionalis* flowers October to December and fruits November to December. — Figure 27.

**VERNACULAR NAMES.** Hazondimoa, ampodimoa (*RN 3417*); hazondomohy (*RN 5969*); hazondomohina (*RN 8195*), pepolahihala (*SF 15576*).

**CONSERVATION STATUS.** The estimated EOO for *Rinorea meridionalis* was 98639 km², and the AOO was 44461 km². It is assigned a status of Near Threatened based on the EOO and Least Concern based on the AOO. The species is mostly confined to unprotected littoral forests on sands in the Fort Dauphin region. However, the species is well known from several recent collections.


**DESCRIPTION.** Shrub to small tree, 2–4 m tall, semi-deciduous; young branchlets terete to flattened in cross section, glabrous or sometimes puberulent. Leaves alternate, petiolate; petioles 0.6–4.2 cm long, 0.5–1.1 mm thick, glabrous or sometimes pubescent at distal end, articulated at proximal end, longitudinally grooved on adaxial surface, usually with pulvini at both ends, pulvini becoming darker in color and callused with age, 0.7–1.4 mm thick, glabrous or pubescent, petiole sometimes reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 1.3–3.1 × 0.5–1.7 mm, coriaceous, keeled, keel terminating in a mucro, outer surface glabrous or pubescent, margin ciliate, apex acute; lamina elliptic or obelliptic, 3.0–15.0 × 1.3–5.2 cm, herbaceous; lamina upper and lower surfaces glabrous; primary vein glabrous on upper surface, glabrous or rarely puberulent on lower surface; secondary veins glabrous; secondary vein pairs 6–10, divergent to ascending, tertiary veins reticulate; base cuneate, rounded, or shallowly cordate, symmetrical, aequilateral to oblique; margin crenate-serrulate to serrate; apex acute. Inflorescence an axillary, terminal and subterminal, reduced paniculate cyme (thrysoid), 1.5–8.5 cm long, lateral cymules bearing 1–3 (–4) flowers, axis
glabrous, puberulent or pubescent; peduncle bracts eventually deciduous, broadly ovate, 0.7–2.5 × 0.5–1.8 mm, coriaceous, keeled, keel sometimes terminating in a mucro, often with several veins, outer surface glabrous or pubescent, margin ciliate, apex rounded or truncate, sometimes mucronate; pedicels (from articulation to base of flower) 1.2–3.6 mm long, pubescent or rarely glabrous; bractlets subtending lateral cymules persistent, deltoid to lanceolate-deltoid, 0.7–2.1 × 0.3–1.0 mm, herbaceous, usually keeled or costate, outer surface glabrous or pubescent, margin ciliate, apex acute. Flowers 3.5–5.6 (–7.6) mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, broadly ovate to lanceolate-deltoid, 1.0–3.4 × 0.5–2.0 mm, outer surface glabrous or puberulent, margin entire to ciliate, apex rounded. Corolla zygomorphic, petals yellow-white, drying orange-brown, glabrous; anterior and posterior petals elliptic, lanceolate-elliptic, or oblanceolate, 3.2–5.2 (–7.4) × 1.7–2.1 (–3.3) mm, margin entire, apex acute, erect to recurved; lateral petals elliptic to lanceolate, concave to conduplicate, 3.2–5.3 (–7.2) × 1.4–1.9 (–2.8) mm, margin entire, apex acute to rounded, erect to rolled; Stamens 3.0–4.6 mm long; filaments connate into a continuous staminal tube, staminal tube 0.5–1.8 mm tall, outer and inner surfaces glabrous; anthers sessile on summit of staminal tube, anther connectives 0.8–1.5 × 0.6–1.1 mm, glabrous; anther ventral connective scales absent; anther dorsal connective scales large and conspicuous, mostly apical, but sometimes extending ca. one-fifth to one-third down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.2–2.2 × 0.8–1.5 mm, surface glabrous, margin entire, apex acute. Pistil 3.4–4.7 (–6.1) mm long;
ovary ovoid, 0.7–1.2 (–2.1) × 0.6–1.2 mm, glabrous; ovules 3; style 2.2–3.9 mm long, erect, filiform, straight, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, ca. 1.3–1.7 cm long, ca. 1.0–1.1 cm diameter, valve ca. 0.6–0.9 cm wide, surface glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit; seed 6.0–10.0 × 5.0–8.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 24.

REMARKS. Perrier de la Bâthie (1949) listed 21 syntypes for *Rinorea arborea* f. *occidentalis*, which are referred to four different taxa in this revision (Table 6). The plants from Toliara Province, in the vicinity of Morondava (Humbert 11363, Keraudren-Aymonin et Aymonin 25947, and Randrianaivo et al. 461), are somewhat divergent and may represent a new species. Differing character states include 1(2) flower per lateral cymule, flowers up to 7.6 mm long, and staminal tube with a partially free flange subtending anthers, the flange irregularly lacerate and scarious. Additional collections with mature leaves are needed to completely evaluate the distinctiveness of these three specimens.

In the Ankarafantsika region, *Rinorea occidentalis* co-occurs with *R. ballardii* in a few locations. Some specimens of *R. occidentalis* (Wahlert et al. 112 and 117) resemble *R. ballardii* by the puberulent petioles and abaxial leaf surfaces, but are assigned to the former.
DISTRIBUTION. *Rinorea occidentalis* is distributed in western Madagascar in seasonally dry, semi-deciduous forests, at elevations of 56–600 m. *Rinorea occidentalis* flowers September to December and fruits November to February. — Figure 27.

VERNACULAR NAMES. Hazompasy (*Labat et al. 2167*).

CONSERVATION STATUS. The estimated EOO for *Rinorea occidentalis* was 64441 km², and the AOO was 31334 km². It is assigned a status of Near Threatened based on the EOO and Least Concern based on the AOO. *Rinorea occidentalis* is widely distributed across western Madagascar, in both protected and unprotected areas, and is represented by several recent collections.

152 (MO!, P!, TAN!, WAG!). Toliara Province. — Entre Morondava et le prolongement sud du Bemaraha, 20°04'S, 44°38'E, vers 300 m, X.1933, fl., Humbert 11363 (K!, P[2]!, TAN!). — Environs de Morondava, est de Mahabo, [20°06'S, 44°37'E], 5.XII.1970, fl., Keraudren-Aymonin et Aymonin 25947 (P[2]!). — Fivondronana Belo sur Tsiribihina, Commune de Bemarivo, Fokontany Mangotroky, à 16 km au Nord-Est de Belo sur Tsiribihina, 19°36'28"S, 44°35'30"E, 100 m, 28.XI.1999, fl., Randrianaivo et al. 461 (MO!).


DESCRIPTION. Shrub to small tree, 2–8 m tall, evergreen; young branches flattened to terete in cross section, glabrous. Leaves alternate, petiolate; petioles 3.5–8.8 cm long, 1.4–2.0 mm thick, glabrous, articulated at proximal end, grooved longitudinally on adaxial surface, with pulvini at both ends, pulvini becoming darker in color and callused with age, 2.0–2.5 mm thick, glabrous, petiole infrequently reflexed 5–40° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 2.2–3.0 × 1.2–1.8 mm, coriaceous, keeled or costate, outer surface glabrous, margin ciliate, apex acute; lanceolate-elliptic to oblong-elliptic, rarely ovate, 13.0–24.0 × 6.0–8.5 cm, herbaceous; lamina
upper and lower surfaces glabrous; primary and secondary veins glabrous on upper and lower surfaces; secondary vein pairs 9–11, divergent to ascending, tertiary veins reticulate; base cuneate to rounded, symmetrical, (sub)aequilateral; margin serrulate to serrate; apex acute. Inflorescence an axillary, terminal and subterminal, well-branched panicle-like cyme (thyrsoid), 7.0–17.0 cm long, lateral cymules branched and bearing 3–several flowers, axis glabrous or rarely puberulent; peduncle bracts quickly deciduous, broadly ovate, 1.2–2.3 × 2.9–4.3 mm, coriaceous, keeled, keel terminating in a mucro, often with several veins, outer surface glabrous to puberulent, margin ciliate, apex rounded to truncate; pedicels (from articulation to base of flower) 1.7–3.0 mm long, glabrous to puberulent; bractlets subtending lateral cymules persistent, ovate to lanceolate-deltoid, 1.1 × 0.6–0.8 mm, herbaceous, often keeled or costate, outer surface glabrous or puberulent, margin ciliate, apex acute to mucronate. Flowers 5.1–6.5 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, broadly ovate to deltoid, 1.2–2.2 × 1.1–2.1 mm, outer surface glabrous to puberulent, margin ciliate, apex acute to rounded. Corolla zygomorphic, petals white, drying orange-brown, glabrous; anterior and posterior petals lanceolate-elliptic, 5.0–5.6 × 1.7 mm, margin entire, apex acute, erect to reflexed; lateral petals lanceolate, concave to conduplicate, 4.8–5.1 × 1.6 mm, margin entire, apex acute, recurved to rolled. Stamens 4.3 mm long; staminal tube 0.7 mm tall, outer and inner surfaces glabrous; anthers sessile on summit of staminal tube, anther connectives 1.6–1.7 × 1.0 mm, glabrous; anther ventral connective scales lanceolate, 0.3 × 0.2 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending ca. one-fourth down
the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 2.0 × 0.9 mm, surface glabrous, margin entire, apex acute. Pistil 4.6 mm long; ovary ovoid, 1.3 × 1.1 mm, glabrous; ovules 3; style 3.1 mm long, erect, filiform, straight, glabrous. Fruit a thick-walled hard capsule, dehiscent along three straight sutures, ellipsoid, 2.2–2.5 cm long, 1.6–2.0 cm diameter, valve 1.0–1.2 cm wide, surface glabrous, papillose, young fruit green, turning brown at maturity; calyx, corolla, and stamens persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 8.0–13.0 × 7.0–8.0 mm, deltoid-reniform, brown-black, shiny, glabrous. — Figure 25.

**REMARKS.** *Rinorea sambiranensis* is similar to *R. arborea* but is distinguished by long leaves and petioles, and large fruits and seeds. The specimen *Wohlhauser et al. SW744* verges on *R. arborea* but is assigned to *R. sambiranensis* based on its large fruits. Some specimens of *R. arborea* from Ankarana Special Reserve with broadly ovate leaves and long petioles are superficially similar to *R. sambiranensis* but otherwise more closely resemble *R. arborea* and are assigned to the latter (e.g., *Leeuwenberg et al. 14383*).

**DISTRIBUTION.** *Rinorea sambiranensis* occurs in humid rainforests and mesic semi-deciduous forests in the lower Sambirano River valley, the lower slopes of the Tsaratanana massif, and coastal forests surrounding Ambaro Bay between Beramanja and Maherivaratra. *Rinorea sambiranensis* flowers in October and fruits between November and June. — Figure 27.
VERNACULAR NAMES. Hazondamokana (Schatz & Antilahimena 4008); tsibabe (Ravololonanahary et al. 28).

CONSERVATION STATUS. The estimated EOO for *Rinorea sambiranensis* was 3837 km², and the AOO was 1218 km². It is assigned a status of Endangered based on the EOO and Vulnerable based on the AOO. The species is distributed in primarily unprotected areas but does occur in Tsaratanana RNI. *Rinorea sambiranensis* is also known from a few recent collections.

ADDITIONAL MATERIAL EXAMINED. Madagascar. Antsiranana Province. — Tsaratanana Reserve, Fivondronana Ambanja, Commune Ambodimanga Ramena, Fokontany Antsahabe, 13°52′37″S, 48°51′02″E, 547 m, 15.XI.2001, fr., Antilahimena et al. 811 (MO!, TAN!). — 1 km west of Mandrizavona, Fokontany Antsahabe, Firaisana Ambodimanga, Fivondronana Ambanja, 13°48′02″S, 48°44′50″E, 440 m, 6.X.1998, fl., imm. fr., Birkinshaw et al. 523 (K!, MO!, WAG!). — Tsaratanana RNI, River Antsaharatsy, 13°48′53″S, 48°47′29″E, 800 m, 14.IV.2000, fr., Birkinshaw et al. 665 (MO!). — Ambilobe, Beramanja, Anketra, forêt de Kalabenono, bas de pente et bord de rivière, 13°38′09″S, 48°40′08″E, 316 m, 18.XII.2006, fr., Callmander et al. 525 (K!, MO!). — Diana, Ambilobe, Beramanja, Anketra, village le plus proche Antanambao-Belinta, versant nord-ouest du Kalabenono, sur la rivière Androkaroka longeant vers l’ouest, 13°38′38″S, 48°40′07″E, 520 m, 24.VI.2007, fr., Rakotovao et al. 3795 (MO!). — Forêt d’Ambato, Ambanja, 13°26′12″S, 48°44′18″E, 0–60 m,
22.VI.1996, fr., Ranaivojaona et al. 78 (M!). — Fivondronana Ambilobe, Commune Tanambao-Marivorahona, Fokontany Ananjaka, village plus proche Ankatsaka à 45 min (par voiture) de Tanambao-Marivorahona sur la Route Nationale 6, croisement à 15 km d’Ambilobe, forêt d’Andasibe à pied du village d’Ankatsaka, 13°06’00”S, 49°10’07”E, 155 m, 6.XI.2004, imm. fr., Randrianaivo et al. 1094 (MO!). — Ambato Forêt, Domaine de Sambirano, Firaisana Ambanja, Fivondronana Ambanja, 13°26′53″S, 48°33′36″E, 500–800 m, 21.VI.1996, fr., Ravololonanahary et al. 28 (MO!, TAN!). — Near the bridge over River Ramena, on road ca. 15 km south of Ambanja, at the village of Ambodidimaka, 13°46′17″S, 48°28′19″E, 24 m, 8.XI.2006, Wahlert & Rakotonasolo 18 (K!, MO!, P!, TAN!). — Ambilobe, Commune rurale Beramanga, Chaîne Galoka, Mont Galoka, Fokontany Anketrabe-Belinta, 13°35′52″S, 48°42′48″E, 270 m, 18.II.2005, fr., Wohlhauser et al. SW 744 (MO!).

8. **Rinorea schatzii** Wahlert, sp. nov.

*Haec species ad Rinorea arborea (Thouars) Baill. inflorescentia paniculiformi affinis sed petiolis et ovario pubescenti et pagina abaxiali foliorum pubescentium differt.*

**Typus.** Madagascar. Antsiranana Province. — Eastern Domain, Reserve Integrale Massif de Marojezy, just N of the village of Manderra which lies on the edge of the reserve and is 5 km N of Manantenina which lies 42 km
by road NE of Andapa on Hwy 36 (Andapa-Sambava), remnant lowland forest, 14°27'S, 49°50'E, 100–200 m, 19.IX.1987, fl., Schatz et al. 1556 (holo-,
MO[3592271]; iso-, K!, TAN!, WAG!).

**DESCRIPTION.** Shrub to small tree, 2–10 m tall, evergreen; young branches flattened to terete in cross section, puberulent to pubescent. Leaves alternate, petiolate; petioles 0.7–3.3 cm long, 0.8–1.5 mm thick, puberulent to pubescent, articulated at proximal end, grooved longitudinally on adaxial surface, often with pulvini at both ends, pulvini becoming callused with age, 1.0–2.0 mm thick, pubescent, petiole often reflexed 5–90° at one or both ends; stipules quickly deciduous, free, lanceolate-deltoid, 2.5–2.8 × ca. 1.2 mm, coriaceous, keeled, keel terminating in a mucro, outer surface pubescent, apex acute; lamina elliptic to obelliptic, 7.0–20.0 × 2.5–6.6 cm, herbaceous; lamina upper surface glabrous, lower surface pubescent; primary and secondary veins glabrous on upper surface, pubescent on lower surface; secondary vein pairs 7–10, divergent to ascending, tertiary veins reticulate; base attenuate to cuneate, symmetrical, aequilateral or slightly oblique; margin subentire to serrulate; apex acute to shortly acuminate or cuspidate. Inflorescence an axillary, terminal and subterminal, panicle-like cyme (thyrsoi d), 2.0–10.0 cm long, lateral cymes branched and bearing 1–7 flowers, axis pubescent; peduncle bracts quickly deciduous, ovate or lanceolate-deltoid, 1.4–2.1 × 1.2–2.2 mm, coriaceous, keeled, keel usually terminating in a mucro, outer surface puberulent, margin ciliate, apex rounded; pedicels (from articulation to base of flower) 1.1–2.2 mm long, pubescent; bractlets subtending lateral cymes
persistent, ovate to lanceolate-deltoid, 1.3–2.0 × 0.8–1.5 mm, herbaceous, usually keeled or costate, outer surface pubescent, margin ciliate, apex acute to mucronate. Flowers 4.0–5.3 mm long, flower buds conical. Sepals subequal in size and shape, herbaceous, ovate-deltoid, 1.7–2.4 × 1.5–2.0 mm, outer surface pubescent, margin ciliate, apex rounded. Corolla zygomorphic, petals white to yellow, drying orange-brown, glabrous; anterior and posterior petals broadly lanceolate-elliptic or oblanceolate, 4.2–5.4 × 1.9–2.5 mm, margin entire, apex acute, erect to rolled; lateral petals lanceolate to oblanceolate, concave to conduplicate, 4.1–5.1 × 1.6–2.2 mm, margin entire, apex acute, erect to rolled. Stamens 3.6–3.9 mm long; staminal tube 0.7–0.9 mm tall, outer and inner surfaces glabrous, tube sometimes with a partially free flange, flange margin irregularly lacerate, membranous; anthers sessile on summit of staminal tube, anther connectives 1.1–1.9 × 0.7–0.8 mm, glabrous; anther ventral connective scales ovate to lanceolate, 0.05–0.2 × 0.05–0.2 mm; anther dorsal connective scales large and conspicuous, apical and lateral extending ca. one-fourth down the length of anther connectives, lanceolate-deltoid, scarious, drying orange-brown, 1.6–2.1 × 1.1–1.2 mm, surface glabrous, margin entire, apex acute. Pistil 4.3–5.0 mm long; ovary ovoid, 0.9–1.1 × 0.7–0.9 mm, pubescent, ovules 3; style 3.2–3.6 mm long, erect, filiform, straight or slightly sigmoid, glabrous. Fruit not seen. — Figure 26.

REMARKS. *Rinorea schatzii* is similar to *R. arborea* but is a distinctive pubescent species with a more or less discrete distribution in the Marojejy region.
DISTRIBUTION. *Rinorea schatzii* occurs in humid rainforests in Marojejy National Park and Anjanaharibe-Sud Special Reserve at an elevation of 100–200 m. The species flowers September to October. — Figure 27.

VERNACULAR NAMES. Hazompiky (*SF 26495*).

CONSERVATION STATUS. The estimated EOO for *Rinorea schatzii* was 494 km², and the AOO was 140 km², giving it a status of Endangered. However, the species occurs in two protected areas and is represented by a few recent collections.

USES. Used as a support for *Vanilla* vines (*Miller et al. 3314*); small construction (*SF 26495*).

ETYMOLOGY. This species is named in honor of George E. Schatz, Curator of Botany, Missouri Botanical Garden, St. Louis, MO, USA. Schatz has collected widely throughout the world and has contributed greatly to the knowledge of the Malagasy flora with his book, *Generic Tree Flora of Madagascar* (Schatz, 2001).

PARATYPES. **Madagascar.** Antsiranana Province. — Hills N of Mandena, between Mandena and the Reserve Integral de Marojejy, 14°27–28’S, 49°17–18°E, 100–200 m, 30.IX.1988, fl., *Miller et al. 3314* (K!, MO!, TAN!, WAG!). —
Maroamibi, Sambava, [14°25’S, 49°47’E], 22.X.1956, fl., *RN 7946* (P!). —

Ambohimitsinjo, Sambava, [14°18’S, 49°43’E], 15.IX.1957, fl., *RN 9080* (P!,
TEF!). — Same locality, [14°18’S, 49°43’E], 16.VIII.1957, bud, *RN 9102* (MO!,
P!, TAN!, TEF!). — Soahitra, Andrahanjo, Ambohimitsinjo, Sambava,
[14°18’30”S, 49°43’E], 22.X.1967, *SF 26495* (P!).
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Annual meeting of the American Society of Plant Taxonomists.


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<td>Cours 408 (P!)</td>
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Figure 19: Rinorea arborea, from Bosser 18575 (TAN).
Figure 20: Rinorea ballardii, from RN 7947 (P).
Figure 21: Rinoera labatii, from Du Puy et al. MB360 (TAN).
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Figure 23: Rinorea meridionalis, from McPherson 14447 (TAN).
Figure 24: Rinorea occidentalis, from Leeuwenberg 14383 (TAN).
Figure 25: Rinorea sambiranensis from Perrier 15225 (P).
Figure 26: Rinorea schatzii from Schatz et al. 1556 (MO).
Figure 27: Distribution of *Rinorea meridionalis*, *R. occidentalis*, *R. sambiranensis*, *R. labatii*, and *R. schatzii*.

Key: *Rinorea meridionalis* (▽); *R. occidentalis* (Ο); *R. sambiranensis* (●); *R. labatii* (▼); *R. schatzii* (■).
Figure 28: Distribution of *Rinorea arborea*, *R. ballardii*, and *R. longipes*.

Key: *Rinorea arborea* (▼); *R. ballardii* (●); *R. longipes* (●).
Figure 29: Distribution of *Rinorea arborea* in mainland Africa.
Chapter 4.

A revision of *Rinorea* subsection *Verticillatae* Engl. (Violaceae) from Madagascar and the Comoro Islands

Introduction.

*Rinorea* Aublet is a pantropical genus of shrubs and small trees and is the second most species-rich genus in the Violaceae, with an estimated 225–275 species. The most recent treatment of the genus in Madagascar recognized 27 species and five infraspecific taxa (Perrier, 1949).

The species of *Rinorea* in Madagascar belong to six distinctive infrageneric groups (this volume, Chapter 2). Five of these groups contain species that are closely related to—or conspecific with—species in Africa (i.e., *Rinorea* subsect. *Ilicifoliae* Engl., *R. arborea* group, *R. squamosa* group, *R. angustifolia* group, and *R. elliptica* group). The sixth group is the Malagasy and Comorian endemic, opposite-leaved *Rinorea* subsect. *Verticillatae* Engl. (Wahlert and Ballard, 2008). *Rinorea* subsect. *Verticillatae* was erected by Engler (1904) but not recognized in Brandt (1914) or De Wildeman (1920). Multivariate morphometric and molecular phylogenetic analyses demonstrate *Rinorea* subsect. *Verticillatae* to be a distinctive and well supported infrageneric taxon (this volume, Chapter 2).

Among Old World taxa, the species in *Rinorea* subsect. *Verticillatae* are instantly recognizable by their opposite leaves. Molecular phylogenetic analysis reveals *R.* subsect. *Verticillatae* to share a most recent common ancestor with
Asian taxa, however, no morphological synapomorphies have yet been discovered that would link these two groups. Biogeographic inferences suggest an origin involving the most recent common ancestor of the *Verticillatae* and eight Asian morphological groups (De Muria and Ballard, unpubl.) via long distance dispersal to Madagascar (this volume, Chapter 5).

Perrier (1949) recognized 17 taxa in *Rinorea* subsect. *Verticillatae*, but many additional specimens examined for this study did not fit any previously described species. Indeed, subsect. *Verticillatae* is by far the most species-rich infrageneric taxon of *Rinorea* in Madagascar.

**Materials and Methods.**

Morphological data were scored for ca. 60 quantitative and qualitative characters from herbarium specimens deposited at K, MO, P, and WAG (herbarium acronyms given in Thiers, continuously updated). Floral dissections were made by soaking flowers in dilute detergent solution for 30 minutes. The sepals, petals, stamens, and pistil were then separately glued to archival-quality cotton paper, and measurements were made using a dissecting scope with an ocular micrometer.

For the Malagasy specimens without latitude/longitude data, geographic coordinates (and sometimes elevation) were assigned post-facto using the Gazetteer to Malagasy Botanical Collecting Localities (Schatz and Lescot, 2005) and are enclosed in square brackets. For the Comorian specimens without latitude/longitude data, coordinates were assigned using Google Earth
and other Internet-based resources. Abbreviations in the lists of exsiccatae include: Fiv., Fivondronana; Fir., Firaïsana; Fkt., Fokontany; RN, Réserve Naturelles; RNI, Réserve Naturelle Intégrale; SF, Service Forestier.

An explicit conservation assessment following IUCN criteria (IUCN Standards and Petitions Working Group, 2008) was conducted following the general procedure outlined by Willis et al. (2004). The utility, CATS (Conservation Assessment ToolS; Moat, 2007) was used with ArcView GIS 3.2 software (Environmental Systems Research Institute, 1999) to calculate extent of occurrence (EOO) and area of occupancy (AOO). EOO and AOO ratings were qualified with additional information about distribution in protected areas, most recent collections, and in some cases, additional field observations.

Results.

After examination of type specimens and an additional ca. 350 specimens of *Rinorea* subsect. *Verticillatae*, it was determined that all 17 of Perrier’s taxa constitute morphologically well defined species, often with discrete distributions or habitat preferences. Two infraspecific taxa (*R. pauciflora* f. *sempervirens* and f. *latidentata*) are distinctive but are maintained at the level of forma given the paucity of available collections and lack of evidence concerning potential clines connecting extreme forms to recognized, well-characterized taxa. Nine new species are described. In addition to a key to the species of *Rinorea* subsect. *Verticillatae*, descriptions for 26 taxa are provided below.
Key to the species of *Rinorea* subsect. *Verticillatae*.

1. Inflorescences distinctly pedunculate, peduncle usually > 5.0 mm........2

1’. Inflorescences subsessile, peduncle usually < 5.0 mm...........................9

2. Primary and secondary veins clearly sunken on upper leaf surface, and raised on lower leaf surface.................................................................3

2’. Primary and secondary veins not sunken or raised..............................4

3. Inflorescences < 1.5 cm long, Zhamena region......................10. *Rinorea coursii*

3’. Inflorescences > 1.5 cm long, Moramanga region (Perinet, Mantadia, Analamanazoatra)............................................................7. *Rinorea bullata*

4. Leaf bases clearly auriculate, Antsiranana Province and Comoro Islands..........................................................5. *Rinorea auriculata*

4’. Leaf bases attenuate-cuneate.................................................................5

5. Terminal bud scales pubescent; leaf lanceolate, Vatomandry region...........................................23. *Rinorea ternifolia*

5’. Terminal bud scales glabrous or rarely puberulent; leaf elliptic or obelliptic..........................................................6

6. Pedicels < 1.5 mm, Boina region, Mahajanga Province.............11. *Rinerea diversifolia*
6’. Pedicels > 1.5 mm.....................................................................................................7

7. Terminal buds < 2.0 mm long, Vatomandry region........1. *Rinorea allorgeae*
7’. Terminal buds conspicuous, > 2.0 mm..............................................................8

8. Petioles 2.0–8.5 mm, Analavelona region........3. *Rinorea analavelensis*
8’. Petioles 4.0–17.0 mm long, Comoro Islands........15. *Rinorea monticola*

9’. Anther dorsal connective scales large and conspicuous..............................10

10. Petioles and terminal buds puberulent to pubescent.................................11
10’. Petioles and terminal buds glabrous............................................................14

11. Leaves 0.7–2.6 cm long, Mangoro River basin at ca. 500 m.................................14. *Rinorea microphylla*
11’. Leaves 1.5–9.5 cm long..................................................................................12

12. Sepals < 2.0 mm long.........................................................................................13
12’. Sepals > 2.0 mm long... Forêt d’Analafondro, Sahafary Plateau, Antsiranana Province.................................21. *Rinorea sahafarensis*

13. Leaf apex subacute, upper and lower leaf surface pubescent at the base, Zombitsy and Ankarakantsika regions.............................6. *Rinorea boinensis*
13'. Leaf apex cuspidate or shortly acuminate, lower leaf surface puberulent, Nosy Mitsio Island, Antsiranana Province.......................

25. Rinorea verticillata

14. Sepals > 3.0 mm..................................................................................................................15

14'. Sepals < 3.0 mm..................................................................................................................17

15. Leaves > 4.0 cm wide, apex cuspidate, Île St. Marie and adjacent coastal areas on the mainland..........................................................20. Rinorea rubra

15'. Leaves < 4.0 cm wide, apex subacute, acute, shortly cuspidate, or acuminate........................................................................................................16

16. Petioles 2.5–14.0 mm long, leaves obovate to oblanceolate, pedicel < 7.0 mm long, Masoala Peninsula..................................................2. Rinorea ambanizanensis

16'. Petioles 8.0–32.0 mm long, leaves broadly elliptic to obovate, pedicel > 7.0 mm long, Sambava region, Antsiranana Province......22. Rinorea sambavensis

17. Leaf bases broadly rounded, Maningotry, Fort Dauphin region........................................................................................................8. Rinorea capuronii

17'. Leaf bases cuneate or attenuate-cuneate.................................................................18

18. Stamens > 3.1 mm tall........................................................................................................19

18'. Stamens < 3.1 mm tall........................................................................................................20
19. Leaves obovate to obelliptic or elliptic; sepals 1.5–2.1 mm long; in the region of R.S. Ivohibe and P.N. Andringitra.................................9. Rinorea cornigera
19’. Leaves lanceolate, elliptic or oblanceolate; sepals 0.9–1.7 mm long; Moramanga region (Perinet, Mantadia, Analanamazoatra)................24. Rinorea urschii

20. Stamens < 2.1 mm, leaves broadly lanceolate, Vohemar region, Antsiranana Province.................................................................26. Rinorea vohemarensis
20’. Stamens > 2.1 mm, leaves elliptic to broadly elliptic, rarely obovate........21

21. Petioles up to 8.0 mm long..................................................................................................................22
21’. Petioles < 4.0 mm long..........................................................................................................................23

22. Leaves elliptic to broadly elliptic; sepals < 1.5 mm long, ovate-deltoid; Fort Dauphin region, usually on sands..............................12. Rinorea mcphersonii
22’. Leaves obovate; sepals > 1.5 mm long, ovate to suborbicular; Fenoarivo (?) region..............................................................17. Rinorea pauciflora

23. Leaves broadly ovate, up to 4.7 cm wide; confluence of the Mananara and Mandrare Rivers, between Andohahela and Elakelaka, Mt. Apiky below Mahamavo.................................................................18. Rinorea pauciflora f. latidentata
23’. Leaves elliptic, < 3.0 cm wide...........................................................................................................24

24. Stamen < 2.2 mm long; anther ventral connective scales < 0.2 mm long; pedicel < 1.4 mm long; Bemaraha.................................4. Rinorea antsalovensis
24’. Stamen > 2.4 mm long; anther ventral connective scales > 0.4 mm long; pedicel > 2.0 mm long..............................25

25. Leaves 1.6–5.0 cm long, 0.6–2.0 cm wide; pedicel < 4.0 mm long; confluence of the Mananara and Mandrare Rivers....13. *Rinorea mandrarensis*

25’. Leaves 3.5–8.5 cm long, 1.4–3.0 cm wide; pedicel > 4.0 mm long; Beampingaratra Massif.........................19. *Rinorea pauciflora f. sempervirens*
Taxonomic Treatment.

1. *Rinorea allorgeae* Wahlert sp. nov.

*Haec species ad Rinorea diversifolia H.Perrier accedit, sed caule pubescente, folio obelliptico, apex acuminato differt.*

**Typus.** — Madagascar, Toamasina Province: Allorge & Rakotozafy 2640, Vatomandry, [19°02'00"S, 48°56'15"E], bud, fr., 14.XI.2001 (holo-, P[00272293]).

**Description.** Shrub; young branches flattened in cross section, puberulent. Leaves opposite, anisophyllous; petioles 0.5–3.0 mm long, glabrous; stipules caducous, free, linear, 0.4–0.8 × 0.15–0.3 mm, outer surface glabrous, margin ciliate, apex acute, horned or mucronate; terminal bud scales foliaceous, lanceolate-linear, 0.6–2.0 mm long, glabrous, margin ciliate, apex acute, mucronate, often curved; lamina obelliptic, 1.9–9.0 × 1.0–3.0 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–5, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin serrulate-crenulate, revolute; apex acuminate. Inflorescence a terminal cyme, 1.0–2.5 cm long, axis glabrous, peduncle 3.4–15.0 mm long, peduncle subtended by two persistent bud scales; pedicels 2.2–4.2 mm long, glabrous; pedicel bractlets caducous, highly reduced, triangular to broadly ovate, 0.2–0.4 × 0.3–0.4 mm, glabrous, keeled,
margin entire or ciliate, apex rounded. Flowers 3.6–4.0 mm long. Sepals unequal, ovate-deltoid, 1.2–2.2 × 0.8–1.5 mm, glabrous, margin entire, apex subacute to rounded. Petals subequal, lanceolate to ovate, 3.5–4.3 × 1.5–2.0 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin ciliate towards the base, apex rounded, erect. Stamens 2.2–2.5 mm long; staminal tube 0.8–0.9 mm tall, outer and inner surfaces glabrous, with a dentate or lacerate margin subtending anthers; anthers subsessile to filamente, filaments 0.1–0.5 mm long, glabrous, anther connectives 0.7 × 0.5 mm, base of anthers pubescent; anther ventral connective scales linear-lanceolate, deeply bilobed, 0.25–0.4 × 0.1–0.2 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.0–1.2 × 0.8–1.0 mm, surface glabrous, margin entire, apex rounded. Pistil 2.9–3.5 mm long; ovary ovoid, 0.8–1.2 × 0.6 mm, glabrous; style 1.9–2.2 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 6.0–7.0 mm long, ca. 4.0 mm diameter, surface glabrous, with raised reticulate veins, valves unequal, 1.8–2.0 mm wide, capsule dehiscing along three straight sutures; fruit bearing remnants of style; seed 2.7–2.8 × 2.2–2.5 mm, subspherical-ovoid, yellow-tan, smooth, glabrous. — Figure 30.

**Distribution and Phenology.** *Rinorea allorgeae* is distributed in eastern humid rainforests between Toamasina and Farafangana. The species flowers in October and fruits in November. — Figure 58.
CONSERVATION STATUS. *Rinorea allorgeae* was last collected in 2001. There were not enough collections to calculate EOO, and the AOO was estimated at < 4000 km². The species is assigned Near Threatened based on the AOO.

ETYMOLOGY. This species is named in honor of Lucile Allorge, an authority of ethnobotany of Madagascar.

PARATYPES. — **Madagascar, Fianarantsoa Province:** SF (Capuron) 23677, Forêt d’Amporoforo (entre Farafangana et Vohipeno), [22°29’00”S, 47°47’30”E], fl., imm. fr., 22.X.1964 (P!, MO!).

2. *Rinorea ambanizanensis* Wahlert sp. nov.

*Frutex. Lamina obovata vel oblanceolata, 3.2–10.0 cm longa, 1.7–3.8 cm lata, apice acuminata, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.5–14.0 mm longo. Inflorescentiae terminale, cymosae, 1.0–1.5 cm latae. Calyx 3.1–4.5 mm longo, glabro. Corolla 4.1–4.8 mm longo. Fructus ellipsoideus, ca. 9.5 mm longus; semine ovoideo.*

**TYPUS. — Madagascar, Toamasina Province:** Zjhra & Hutcheon 157, Masoala Peninsula, forest surrounding research station at Andronabe on western coast, 15°39’30”S, 49°57’30”E, 0–600 m, fl., 9.II.1992 (holo-, MO!, iso-, K!).
DESCRIPTION. Shrub, up to 2.5 m tall; young branches flattened in cross section, glabrous to puberulent. Leaves opposite, anisophyllous; petioles 2.5–14.0 mm long, glabrous; stipules caducous, not seen; terminal bud scales conical, foliaceous, linear-lanceolate, 0.5–2.8 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina obovate to oblanceolate, 3.2–10.0 × 1.7–3.8 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin low-serrate to serrulate-crenulate, revolute; apex acuminate. Inflorescence a terminal cyme, less than 1.5 cm long, axis glabrous or puberulent, peduncle 1.0–3.5 mm long, peduncle subtended by two persistent bud scales; pedicels (2.7–) 4.0–6.5 mm long, glabrous; pedicel bractlets persistent, ovate-deltoid to subulate, 0.7–1.6 × 0.4–0.8 mm, glabrous, keeled, margin ciliate, apex acute, mucronate. Flowers 4.1–5.6 mm long. Calyx zygomorphic, sepals strongly unequal, lanceolate, 3.1–4.5 × 1.1–1.7 mm, usually keeled, glabrous, margin ciliolate, apex subacute to acute, mucronate or horned. Petals unequal, lanceolate, 4.1–4.8 × 0.9–1.0 mm, outer surface glabrous, inner surface pubescent, margin entire or ciliate, apex acute, erect to recurved. Stamens 2.9–3.1 mm long; staminal tube 0.7–0.9 mm tall, outer and inner surfaces glabrous, with a dentate or irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.2–0.4 mm long, anther connectives 0.9–1.1 × 0.9 mm, base of anthers pubescent; anther ventral connective scales lanceolate, apex acute, bifid, or truncate, 0.45–0.5 × 0.2–0.4 mm; anther dorsal connective scales large and conspicuous, apical,
lanceolate, scarious, white, 1.0–1.1 × 0.6 mm, surface glabrous, margin entire, apex acute. Pistil 3.2–3.8 mm long; ovary ovoid, 1.0–1.1 × 0.6 mm, glabrous; style 2.1–2.5 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, ca. 9.5 mm long, ca. 4.0 mm diameter, surface glabrous, with raised reticulate veins, valves unequal, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 3.6–4.0 × 3.0–3.2 mm, ovoid, light brown, smooth, glabrous. — Figure 31.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea ambanizanensis* is distributed in humid rainforests in the Masoala Peninsula, at elevations of 0–600 m. The species flowers in February and fruits September through December. — Figure 57.

**CONSERVATION STATUS.** *Rinorea ambanizanensis* is known from six recent collections (1989–1996); four are from the protected PN Masoala, and two (*Morat et al. 8583 and 8593*) may have been collected from PN Mananara. The estimated EOO was < 5000 and AOO was < 500, thus a provisional conservation assessment of Endangered is given for *R. ambanizanensis*. However, if more collections are gathered from both Masoala and Mananara, then the status of the species may be closer to Vulnerable.

**ETYMOLOGY.** This species is named for the village of Ambanizana, near the type locality on the Masoala Peninsula.


Description. Shrub ca. 1–2 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 2.0–8.5 mm long, glabrous; stipules caducous, not seen, leaving a scar at the base of bud scale; terminal bud scales conspicuous, conical, foliaceous, lanceolate-linear, twisted, 2.3–8.0 mm long, glabrous, margin entire, apex acute, mucronate; lamina ob lanceolate, 2.5–11.0 × 1.1–3.5 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 6–8,
ascending, tertiary veins reticulate; base attenuate, symmetrical, subaequilateral; margin serrate; apex subacute to shortly acuminate. Inflorescence a terminal compound or panicle-like cyme, (1.5–) 2.5–6.0 cm long, axis glabrous, peduncle 12.0–33.0 mm long, peduncle subtended by two conspicuous persistent bud scales; pedicels 1.9–3.5 mm long, glabrous; pedicel bractlets eventually deciduous, triangular-ovate, 0.8–1.3 × 0.6–1.0 mm, keeled or costate, glabrous, margin ciliate, apex acute, mucronate. Flowers 3.8–4.8 mm long, flower buds conical. Sepals unequal, lanceolate-deltoid, 0.9–2.2 × 0.6–1.2 mm, keeled or costate, glabrous, margin ciliate, apex rounded to acute. Petals subequal, lanceolate, 3.8–5.0 × 1.3–1.7 mm, outer surface glabrous, inner surface sparsely pubescent near the middle, margin entire to ciliate, apex subacute to rounded, erect. Stamens 2.4–3.4 mm long; staminal tube 1.0–1.2 mm tall, outer and inner surfaces glabrous, tube summit with a membranous, irregularly toothed flange subtending anthers; anthers subsessile, filaments 0.05–0.3 mm long, anther connectives 0.5–0.8 × 0.5–0.7 mm, base of anthers pubescent; anther ventral connective scales bifid or deeply lobed, 0.4–0.6 × 0.15–0.3 mm; anther dorsal connective scales large and conspicuous, apical, rhombic-ovate, scarious, white, 1.0–1.6 × 0.8–1.4 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 3.3–4.3 mm long; ovary ovoid, 0.8–1.5 × 0.6–0.8 mm, glabrous; style 2.1–2.8 mm long, erect, fluted in cross-section, straight, tapered or clavate, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 1.5–2.2 cm long, 0.8 cm diameter, surface glabrous, with raised reticulate veins, valves subequal, 2.0–5.0 mm wide, the back of each valve somewhat thickened, capsule dehiscing along three straight sutures;
calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 5.2–5.6 × 4.7–5.5 mm, ovoid-tetrahedral, shiny brown, smooth, glabrous, (1)2 seeds per valve. — Figure 32.

REMARKS. In the protologue, Perrier (1949) listed two syntypes for Rinorea analavelensis: Humbert 14203 and Humbert 14247. The latter was annotated by Perrier as a “type” and was therefore chosen as the lectotype. Another specimen, Humbert 19761, has cuttings of both Rinorea analavelensis (middle and right) and R. arborea cf. f. occidentalis H.Perrier (on the left) on the same sheet.

DISTRIBUTION AND PHENOLOGY. Rinorea analavelensis is primarily distributed in the Analavelona Massif with an outlying population in the Andringitra Massif in Fianarantsoa Province, at an elevation of 950–1300 m. The species flowers from February through April and fruits June–December. — Figure 57.

CONSERVATION STATUS. Rinorea analavelensis does not currently grow in any protected areas, but it continues to be represented by recent collections (e.g., Rakotovao & Randriantafika 1049). The estimated EOO was < 5000 and AOO was < 500, and a status of Endangered is applied to the species.

ADDITIONAL MATERIAL EXAMINED. Madagascar, Fianarantsoa Province. — RN 4843, RN 5, Vohitsaoka, Ambalavao, 22°17’S, 46°50’E, bud, 26.XII.1952

4. **Rinorea antsalovensis** Wahlert sp. nov.

*Frutex. Lamina elliptica, 2.1–5.0 cm longa, 0.9–1.6 cm lata, apice acuto, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.0–4.0 mm longo. Inflorescentiae terminale, cymosae, 1.0 cm longo. Calyce 1.7–2.5 mm longo, glabro. Corolla 4.2–4.3 longo.*

**Typus.** — Madagascar, Mahajanga Province: *Leandi & Saboureau 3043*, Antsingy, vers Andobo, sentier vers l’est vers 6–7 km, [18°39’S, 44°44’E],
300 m, bud, fl., 5–8.II.1960 (holo-, P[00537091]!, iso-, K[000253957]!, MO[3857208]!, WAG!).

DESCRIPTION. Shrub; young branches flattened in cross section, puberulent. Leaves opposite, anisophyllous; petioles 2.0–4.0 mm long, glabrous; stipules caducous, free, lanceolate-ovate, 0.6–0.8 × 0.4–0.5 mm, outer surface glabrous, keeled, margin ciliate, apex acute, horned or mucronate; terminal bud scales foliaceous, lanceolate-linear, 0.7–2.2 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina elliptic, 2.1–5.0 × 0.9–1.6 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin serrulate, revolute; apex subacute to acute. Inflorescence a terminal cyme, less than 1.0 cm long, axis puberulent, peduncle 0.5–1.7 mm long, peduncle subtended by two persistent bud scales; pedicels 0.8–1.4 mm long, glabrous; pedicel bractlets persistent, lanceolate-deltoid, 0.6–0.9 × 0.4–0.6 mm, glabrous, keeled, margin ciliate, apex acute, horned. Flowers 4.2–4.3 mm long. Sepals unequal, lanceolate-deltoid, 1.7–2.5 × 0.9–1.2 mm, glabrous, keeled, margin ciliate, apex acute, horned. Petals subequal, lanceolate, 4.2–4.3 × 0.9–1.0 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin entire, apex acute, erect. Stamens 2.1–2.2 mm long; staminal tube 1.1–1.2 mm tall, outer and inner surfaces glabrous, with a dentate, free margin subtending anthers; anthers subsessile, filaments 0.15–0.25 mm long, anther connectives 0.5–0.6 × 0.5–0.6 mm; anther ventral connective scales 2, ligulate-linear, 0.1–
0.2 × 0.05 mm; anther dorsal connective scales reduced, apical, ovate or variable, scarious, white, 0.2–0.3 × 0.2 mm, surface glabrous, margin entire to lacerate. Pistil 2.2–2.8 mm long; ovary ovoid, 0.7–0.9 × 0.5–0.7 mm, glabrous; style 1.8–2.0 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 33.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea antsalovensis* is only known from the Bemaraha Massif, at elevations of ca. 300 m. The species flowers in February. — Figure 57.

**CONSERVATION STATUS.** There were not enough collections to assign a conservation status to *Rinorea antsalovensis*. While it was collected from a now-protected area (PN Bemaraha), the species has not been collected in the last 50 years.

**ETYMOLOGY.** The species is named after the Bemaraha Massif.


**DESCRIPTION.** Shrub up to ca. 3 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous, subsessile; petioles up to 3.0
mm long, glabrous; stipules caducous, free, lanceolate, 0.9–2.3 × 0.7–1.0 mm, herbaceous, outer surface glabrous, margin entire, base cordate to auriculate, apex mucronate; terminal bud scales conspicuous, conical, foliaceous, lanceolate, conduplicate, 2.6–6.0 mm long, glabrous, margin entire, apex acute, mucronate; lamina pandurate to oblanceolate, gray-green, 4.2–12.0 × 1.9–4.5 (–5.0) cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 5–9, ascending, tertiary veins reticulate; base shallowly cordate to auriculate (rounded), symmetrical, oblique; margin subentire to low-serrate, revolute; apex rounded to subacute. Inflorescence a terminal compound or panicle-like cyme, 1.5–5.0 cm long, axis glabrous, peduncle 9.0–29.0 mm long, peduncle subtended by two conspicuous persistent bud scales; pedicels 1.7–3.2 mm long, glabrous; pedicel bractlets quickly deciduous, lanceolate-deltoid, 1.0–1.7 × 0.6–1.0 mm, herbaceous, keeled, glabrous, margin entire to ciliate, apex acute, mucronate. Flowers 4.1–6.0 mm long, flower buds conical. Calyx zygomorphic; sepals unequal, lanceolate-deltoid or ovate, 2.7–4.8 × 0.7–1.9 mm, keeled, outer surface glabrous, inner surface glabrous or sparsely pubescent, lateral sepals usually conduplicate, margin entire to ciliate, apex acute, mucronate. Corolla subzygomorphic; petals subequal, lanceolate-deltoid, 4.1–5.5 × 1.2–1.6 mm, white, outer surface glabrous, inner surface glabrous or pubescent near the middle, margin entire, ciliate towards the base, apex acute, erect, upper third of petals often becoming darker in color. Stamens 2.5–2.8 mm long; staminal tube 0.5–1.1 mm tall, outer and inner surfaces glabrous, vestiges of filaments visible in the tube; anthers sessile to filamented on summit of staminal tube, filaments
(if present) 0.05–0.1 mm long, anther connectives 0.7–1.1 × 0.4–0.8 mm, glabrous; anther ventral connective scales 1 or 2, lanceolate, 0.3–0.4 × 0.15–0.2 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.0–1.3 × 0.6–1.1 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 3.0–5.0 mm long; ovary ovoid, 0.7–1.2 × 0.6–1.0 mm, glabrous; style 2.3–3.6 mm long, erect, fluted in cross-section, straight, tapered or clavate, glabrous, apex often becoming darker in color. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid to subglobose, 6.5–7.3 mm long, 5.3–5.5 mm diameter, surface glabrous, with raised reticulate veins, tan to brown-green, valves subequal, 2.0–2.8 mm wide, the back of each valve with a thickened ridge, capsule dehiscing along three straight sutures between ridges; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 3.6–4.0 × 1.9–2.8 mm, ovoid, yellow-tan, wrinkled, glabrous, (1)2 seeds per valve. — Figure 34.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea auriculata* is distributed at various stations in Antsiranana Province (Ankarana, Sahafary, Sakaramy), in Mahajanga Province (primarily in the Bemaraha Massif), and the Comoro Islands (Mayotte), at elevations of ca. 100–200 m. *Rinorea auriculata* flowers October through April, and occasionally in July; two specimens were fruiting in December. — Figure 58.
CONSERVATION STATUS. Based on the EOO (213,046 km²) and AOO (78,444 km²) estimates, Rinorea auriculata is the only species in subsect. Verticillatae with a conservation status of Least Concern.

VERNACULAR NAMES. Kimbanala, (RN 7741); lolobenioahariva (RN 5677); sarilehaky (RN 8789).


DESCRIPTION. Shrub, 2–3 m tall; young branches flattened in cross section, pubescent. Leaves opposite, anisophyllous; petioles 2.0–6.0 mm long, pubescent; stipules caducous, free, ovate, 0.3–0.5 × 0.2 mm, outer surface pubescent, margin ciliate, apex acute, horned or mucronate; terminal bud scales foliaceous, lanceolate-linear, 0.5–3.0 mm long, pubescent, margin ciliate, apex acute, mucronate; lamina elliptic, or less often lanceolate-elliptic or obelliptic, 1.5–6.0 × 0.7–2.2 cm; lamina upper and lower surfaces glabrous, but pubescent at the base; primary and secondary veins glabrous, but sparsely pubescent at the base; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin serrulate to serrate, revolute; apex subacute. Inflorescence a terminal cyme, less than 1.0 cm long, axis pubescent, peduncle 0.5–2.5 mm long, peduncle subtended by two persistent bud scales; pedicels 1.0–2.0 mm long, glabrous; pedicel bractlets persistent, triangular to subulate, 0.4–0.9 × 0.3–0.5 mm, glabrous to sparsely pubescent, keeled, margin entire to ciliate, apex acute, mucronate. Flowers 3.0–4.0 mm long. Sepals subequal, ovate-deltoid, 0.9–1.9 × 0.7–1.6 mm, glabrous, keeled, margin entire to ciliolate, apex acute to rounded, usually mucronate. Petals subequal, lanceolate, 3.5–4.1 × 1.0–1.3 mm, outer surface glabrous, inner surface glabrous to sparsely pubescent in the upper half, margin entire, apex acute, erect. Stamens 2.3–2.7 mm long; staminal tube 0.6–1.0 mm tall, outer and inner surfaces glabrous, with a membranous, dentate, free margin subtending anthers; anthers subsessile, filaments 0.05–0.4 mm long, anther connectives 0.5–0.7 × 0.4–0.6 mm; anther ventral connective scales linear-lanceolate, apex subacute or deeply bilobed, 0.3–0.5 × 0.1–0.2 mm;
anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.8–0.9 × 0.5–0.6 mm, surface glabrous, margin entire, apex rounded. Pistil 2.5–3.5 mm long; ovary ovoid, 0.6–1.0 × 0.5–0.7 mm, glabrous; style 1.9–2.6 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 35.

DISTRIBUTION and PHENOLOGY. *Rinorea boinensis* is disjunctly distributed in the Ankarafantsika region and the Analavelona Massif, at elevations of 150–975 m. Most specimens examined show *Rinorea boinensis* to be in bud February through April, with a single flowering specimen in April. — Figure 58.

CONSERVATION STATUS. The estimated EOO of *Rinorea boinensis* was 30,162 km² and the AOO was 23,000 km²; the species is assigned a status of Near Threatened.


**DESCRIPTION.** Small tree up to 6 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous, subsessile; petioles 1.0–6.0 mm long, glabrous; stipules caducous, not seen; terminal bud scales lanceolate-deltoid, 3.0–5.7 mm long, conspicuous, white to tan, keeled, outer surface glabrous, margin entire, apex acute, mucronate; lamina oblanceolate, 3.4–13.0 × 1.8–6.0 cm, lower surface drying purple-green to purple-brown; lamina upper and lower surfaces glabrous; primary and secondary veins sunken on upper leaf surface and raised on lower leaf surface, glabrous; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base attenuate or cuneate(rounded), symmetrical, aequilateral to oblique; margin subentire to low-serrate, revolute; apex cuspidate, shortly acuminated, or acute. Inflorescence a terminal and subterminal panicle-like cyme, 1.5–13.5 cm long, lateral cymes bearing 1–10 flowers, axis glabrous to sparsely puberulent, pedunculate, peduncle 5.0–58.0 mm long, subtended by bud scales; pedicels 2.0–4.0 mm long, glabrous; pedicel bractlets subtending lateral cymes eventually deciduous, lanceolate-deltoid, 0.9–2.5 × 0.8–1.0 mm, herbaceous, keeled, glabrous, margin ciliate, apex acute, mucronate. Flowers 3.6–5.0 mm long, flower buds conical. Sepals subequal, deltoid-ovate, 1.1–1.5 × 0.6–1.0 mm,
outer surface glabrous, margin ciliate, apex rounded. Petals subequal, lanceolate, 3.0–4.1 × 1.4–1.7 mm, white, outer surface glabrous, inner surface sparsely pubescent near the middle, margin entire, ciliate towards the base, apex acute, erect. Stamens 2.1–3.3 mm long; staminal tube 0.6–1.1 mm tall, outer and inner surfaces glabrous; anthers sessile to filamented, inserted on the inner surface of staminal tube and subtended by a membranous, dentate or irregularly lacerate flange, filaments (if present) 0.1–0.3 mm long, anther connectives 0.5–0.7 × 0.3–0.5 mm, base of anthers often pubescent; anther ventral connective scales variable, either 1 scale lanceolate-deltoid with apex bifid or deeply 2-lobed, or 2 scales linear, 0.3–0.8 × 0.1–0.3 mm; anther dorsal connective scales large and conspicuous, apical, deltoid-ovate, scarious, white, 1.0–1.6 × 0.8–1.0 mm, surface glabrous, margin entire, apex subacute. Pistil 2.5–4.0 mm long; ovary ovoid, 1.0–1.4 × 0.6–1.0 mm, glabrous; style 1.5–2.6 mm long, erect, fluted in cross-section, straight, tapered, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid to subglobose, 7.8–8.0 mm long, 5.0–6.0 mm diameter, green, drying dark reddish-brown, glabrous, valves subequal, 2.2–3.7 mm wide, the back of each valve with a thickened ridge, ridge corrugated or ribbed transversely, capsule dehiscing along three straight sutures between ridges; calyx and corolla persistent at base of maturing fruit, fruit sometimes bearing remnants of style; seed 3.6–4.7 × 2.7–3.6 mm, obovoid to irregularly shaped, orange-brown to tan, glabrous, 0–2 seeds per valve. — Figure 36.
REMARKS. In the protologue, Perrier (1949) listed two syntypes for *Rinorea bullata*: *Baron 6012* and *Perrier 6061* [sic], actually 5061. The latter was annotated by Perrier as a “type” and was therefore chosen as the lectotype.

DISTRIBUTION AND PHENOLOGY. *Rinorea bullata* is distributed in rainforests in the Perinet-Analamazoatra region, at elevations of 900–1000 m. The species flowers November through December and fruits in February. — Figure 58.

CONSERVATION STATUS. *Rinorea bullata* is known from several recent collections in two protected areas: PN Mantadia and RS Analamazaotra. However, the species is assigned a status of Critically Endangered based on estimates of EOO and AOO.

**8. Rinorea capuronii** Wahlert sp. nov.

*Frutex. Lamina elliptica, (4.2–) 6.5–8.2 cm longa, (1.6–) 3.3–4.4 cm lata, apice acuminato, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.3–3.5 mm longo. Inflorescentiae terminale, cymosae, 1.5 cm longo. Calyce 0.9–1.5 mm longo, glabro. Corolla 4.5–4.7 longo.*

**Typus.** — Madagascar. Toliara Province. *SF (Capuron) 27990*, Environs sud du col du Maningotry, au N.W. de Fort-Dauphin, [24°42′00″S, 46°44′30″E], bud, fl., 16.XI.1967 (holo-, P[no accession number]!).

**Description.** Shrub; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 2.3–3.5 mm long, glabrous; stipules caducous, not seen, leaving white, oval scars at base of terminal buds; terminal
bud scales conical, foliaceous, linear-lanceolate, 1.4–2.7 mm long, glabrous, margin entire, apex acute, mucronate; lamina lanceolate-ovate, (4.2–) 6.5–8.2 × (1.6–) 3.3–4.4 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 8–10, divergent to ascending, tertiary veins reticulate; base rounded, symmetrical, aequilateral; margin serrulate to serrate, subrevolute; apex acuminate. Inflorescence a terminal and subterminal cyme, less than 1.5 cm long, axis glabrous, peduncle 2.0–4.0 mm long, peduncle subtended by two persistent bud scales; pedicels 4.5–6.0 mm long, glabrous; pedicel bractlets persistent, subulate, 0.4–0.7 × 0.4–0.6 mm, glabrous, keeled, margin entire to ciliolate, apex acute, mucronate. Flowers 4.5–4.7 mm long. Sepals unequal, ovate, 0.9–1.5 × 0.8–1.3 mm, glabrous, keeled, margin ciliate, apex subacute, mucronate. Petals unequal, lanceolate, 4.5–4.7 × 1.6–1.8 mm, outer surface glabrous, inner surface sparsely pubescent, margin ciliolate, apex rounded, erect to recurved. Stamens 3.5 mm long; staminal tube 0.6 mm tall, outer and inner surfaces glabrous, with an irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.1 mm long, anther connectives 0.8 × 0.6 mm, base of anthers pubescent; anther ventral connective scales lanceolate, apex subacute, 0.8 × 0.3 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate, scarious, white, 1.2 × 0.9 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 3.6 mm long; ovary ovoid, 1.0 × 0.6 mm, glabrous; style 2.7 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 37.
REMARKS. A highly distinctive species known only from a single collection.

DISTRIBUTION AND PHENOLOGY. *Rinorea capuronii* is known only from the Beampingaratra Massif, at elevations of ca. 500–600 m. The species flowers in November. — Figure 57.

CONSERVATION STATUS. *Rinorea capuronii* is known from a single collection, which is over 40 years old. It is not known whether or not it was collected from the protected area PN Andohahela, but recent satellite imagery shows the Beampingaratra Massif to contain large areas of primary vegetation. There were insufficient collections for estimation of EOO and AOO.

ETYMOLOGY. This species is named in honor of René Capuron (1921–1971), prolific plant collector in Madagascar and author of *Essai d'introduction à l'étude de la flore forestière de Madagascar* (Dorr, 1997). Two other Capuron collections are the types of *Rinorea sahafarensis* Wahlert and *Rinorea vohemarensis* Wahlert (this study).

DESCRIPTION. Shrub to small tree, 1.5–7 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 3.0–9.0 mm long, glabrous; stipules caducous, free, linear-lanceolate, 0.6–1.5 × 0.15–0.2 mm, outer surface glabrous, margin ciliate, apex acute, mucronate; terminal bud scales foliaceous, linear-lanceolate, 1.0–4.8 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina obovate to obelliptic or elliptic, 2.0–7.0 × 0.9–3.2 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base cuneate, symmetrical, aequilateral; margin low-serrate to serrulate-crenulate, revolute; apex acuminate. Inflorescence a terminal cyme, 1.0–1.5 cm long, axis glabrous, peduncle 1.5–4.0 mm long, peduncle subtended by two persistent bud scales; pedicels 2.5–4.0 mm long, glabrous; pedicel bractlets caducous, lanceolate-ovate to subulate, usually scariosus, 0.8–1.5 × 0.6–0.9 mm, glabrous, keeled, margin ciliate, apex rounded, mucronate. Flowers 3.8–6.0 mm long. Sepals unequal, ovate-deltoid, 1.5–2.1 × 1.3–1.5 mm, glabrous, keeled, margin ciliolate, apex subacute, mucronate. Petals subequal, narrowly lanceolate, 4.2–5.2 × 1.0–1.2 mm, outer surface glabrous, inner surface pubescent in the middle, margin entire, apex acute, erect. Stamens 3.2–3.5 mm long; staminal tube 0.9–1.0 mm tall, outer and inner surfaces glabrous, with an irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.05–0.2 mm long, glabrous, anther connectives 0.9–1.0 × 0.5 mm, base of anthers sparsely pubescent; anther ventral connective scales linear-lanceolate, apex bifid or deeply bilobed, 0.6–0.8 × 0.25–0.4 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate, scariosus, white, 1.5–1.7 × 0.8–1.0 mm,
surface glabrous, margin entire, apex rounded. Pistil 3.4–3.9 mm long; ovary ovoid, 0.7–0.8 × 0.5–0.6 mm, glabrous; style 2.6–3.2 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, ca. 9.0–11.0 mm long, ca. 4.0 mm diameter, surface glabrous, with raised reticulate veins, capsule dehiscing along three straight sutures; fruit bearing remnants of style; seed ca. 3.0 × 2.5 mm, subspherical, yellow-tan, smooth, glabrous. — Figure 38.

**Distribution and Phenology.** *Rinorea cornigera* is distributed in the Andringitra Massif, at elevations of 700–1200 m. It flowers and fruits November through December. — Figure 56.

**Conservation Status.** *Rinorea cornigera* is known from several recent collections from both unprotected and protected areas (PN Andringitra and PS Pic d'Ivohibe). The EOO estimate of 2923 km² gives the species a status of Endangered, whereas the AOO estimate of 722 km² places the species in Vulnerable status.

**Additional Material Examined.** **Madagascar. Fianarantsoa Province:** — *Lewis et al.* 827, Andringitra, Camp I, ca. 45 km S of Ambalavao, east bank of Iantara River, along Ambalamanenjana-Ambatomboay trail, edge of Andringitra Reserve, 22°13’20”S, 47°01’29”E, 720 m, fl., fr., 15–21.XI.1993 (MO!). — *Messmer et al.* NM 575, 9 km ESE d'Ivohibe, 6.5 km SE d'Angodongodona, corridor forestier entre la Réserve Spéciale d’Ivohibe et la Parc National
10. *Rinorea coursii* Wahlert sp. nov.

*Frutex vel arbor. Lamina obovata vel oblanceolata, 4.9–10.0 cm longa,* 2.8–4.1 cm lata, apice rotundato vel subacutato, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.5–6.0 mm longo. *Inflorescentiae terminale,* cymosae, 1.5 cm longo. *Calyce 1.0–1.6 mm longo, glabro. Corolla 3.7–4.8 longo.*

**TYPUS.** — Madagascar. Toamasina Province, *Cours 2006*, Forêt d’Analamihilana, [17°43’30”S, 48°27’05”E], 850 m, bud, fl., 27.XII.1944 (holo-, P[00537100]!, iso-, P[00537101]!).

**DESCRIPTION.** Shrub or small tree up to 5 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 2.5–6.0 mm long, glabrous; stipules caducous, not seen; terminal bud scales linear-lanceolate, 1.0–1.6 mm long, outer surface pubescent, margin ciliate, apex acute, mucronate; lamina obovate to oblanceolate, 4.9–10.0 × 2.8–4.1 cm;
lamina upper and lower surfaces glabrous; primary and secondary veins sunken on upper leaf surface and raised on lower leaf surface, glabrous; secondary vein pairs 4–7, ascending, tertiary veins reticulate; base attenuate-cuneate, subsymmetrical, aequilateral to oblique; margin low-serrate to serrulate, revolute; apex rounded to subacute. Inflorescence a terminal cyme, less than 1.5 cm long, axis glabrous to puberulent, peduncle 10.0–20.0 mm long, peduncle subtended by two persistent bud scales; pedicels 3.0–5.2 mm long, glabrous; pedicel bractlets ovate, 3.0–5.2 × 0.4–0.9 mm, keeled, pubescent, margin ciliate, apex rounded, mucronate. Flowers ca. 5.0 mm long. Sepals unequal, ovate to lanceolate-deltoid, 1.0–1.6 × 0.7–1.3 mm, usually keeled, outer surface glabrous, margin ciliate, apex acute to rounded. Petals unequal, lanceolate, 3.7–4.8 × 1.1–1.4 mm, outer surface glabrous, inner surface sparsely pubescent near the upper half, margin entire, apex subacute, erect. Stamens 2.6–2.9 mm long; staminal tube 0.7–1.0 mm tall, outer and inner surfaces glabrous, with a dentate margin subtending anthers; anthers subsessile, filaments 0.15–0.25 mm long, anther connectives 0.7–1.0 × 0.6–0.7 mm, base of anthers pubescent; anther ventral connective scales variable, lanceolate or irregular, 0.2–0.3 × 0.1–0.25 mm; anther dorsal connective scales large and conspicuous, apical, deltoid-ovate, scarios, white, 0.9–1.1 × 0.8 mm, surface glabrous, margin entire, apex subacute to rounded. Pistil 2.9–4.1 mm long; ovary ovoid, 0.8–1.2 × 0.5–0.7 mm, glabrous; style 2.0–3.1 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 39.
REMARKS. The paratypes, *Herbier du Jardin Botanique de Tananarive* (s.collector) 3844, and *Herbier du Jardin Botanique de Tananarive* (s.collector) 3877, may represent isotypes. They are a very close match to the holotype and were probably collected in the same locality as *Cours 2006*.

DISTRIBUTION AND PHENOLOGY. *Rinorea coursii* is distributed in Forêt d’Analamihilana, and is expected in Zahamena. It flowers in December. — Figure 57.

CONSERVATION STATUS. The species is known only from three collections made in 1944. Much deforestation has occurred in the region around Lac Alaotra, including recent mechanized industrial-scale logging in the Zahamena region (Schatz, pers. comm.). There were insufficient data to calculate EOO and AOO.

ETYMOLOGY. This species is named in honor of Gilbert Cours Darne (born 1909), agronomist and botanist, primarily in Madagascar, where he served in a variety of positions, including Director of the Agriculture Station at Alaotra, Ambatondrazaka, Madagascar and Inspecteur Général, Office de la Recherche Scientifique et Technique, O.R.S.T.O.M. (Dorr, 1997).

PARATYPES. — Madagascar. Toamasina Province: — *Herbier du Jardin Botanique de Tananarive* (s.collector) 3844, without precise locality [vicinity of Lac Alaotra?], bud, fl., s.date (P[00537097]!). — *Herbier du Jardin Botanique de*
Tananarive (s.collector) 3877, without precise locality, [vicinity of Lac Alaotra?], bud, s.date (P[00537098]!).


**DESCRIPTION.** Shrub, up to 2 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 1.5–5.0 mm long, glabrous; stipules caducous, free, lanceolate-deltoid or linear, 0.9–1.2 × 0.3–0.4 mm, outer surface glabrous, margin ciliate, apex acute, horned; terminal bud scales conical, foliaceous, lanceolate-linear, 0.8–2.2 mm long, glabrous, margin entire, apex acute, mucronate; lamina elliptic, rarely obelliptic, 3.0–8.0 × 1.1–2.7 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 4–7, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin serrulate to serrate, revolute; apex subacute. Inflorescence a terminal cyme, less than 1.0 cm long, axis glabrous or puberulent, peduncle 4.0–11.0 mm long, peduncle subtended by two persistent bud scales; pedicels 0.5–1.6 mm long, glabrous or puberulent; pedicel bractlets eventually deciduous, triangular, 0.4–0.7 × 0.3–0.4 mm, glabrous, margin entire, apex acute. Flowers 2.5–3.2 mm long. Sepals unequal, ovate-deltoid, 1.2–2.0 × 0.7–1.4 mm, glabrous, margin entire, apex acute. Petals subequal, lanceolate, 2.2–2.7 × 1.0–1.5 mm, outer surface glabrous,
inner surface sparsely pubescent in the upper half, margin entire, apex acute, erect. Stamens 2.2–2.5 mm long; staminal tube 0.6 mm tall, outer and inner surfaces glabrous, with a membranous, irregularly lacerate, free margin subtending anthers; anthers subsessile, filaments 0.1–0.3 mm long, anther connectives 0.6–0.7 × 0.5–0.6 mm, base of anthers pubescent; anther ventral connective scales linear-lanceolate, deeply bilobed to the base of scale, 0.4–0.5 × 0.1–0.2 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.0–1.1 × 0.8–0.9 mm, surface glabrous, margin entire, apex subacute. Pistil 2.2–2.5 mm long; ovary ovoid, 0.5–0.6 × 0.5–0.6 mm, glabrous; style 1.3–2.0 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 40.

**DISTRIBUTION AND PHENOLOGY.** The type locality of *Rinorea diversifolia* is in the region between Maevatanana and Andriba, with an outlying population in the Bemaraha Massif, at elevations up to ca. 300 m. The type specimen of *Rinorea diversifolia* was in flower in August, while the only other specimen assigned to the species (*SF (Capuron) 26116*) was in bud in October. — Figure 56.

**CONSERVATION STATUS.** *Rinorea diversifolia* is known from two collections. The region around the type locality has been highly degraded, and no collections have been made from the location in over 100 years. The other collection, *SF (Capuron) 26116*, was made in 1966 in the region of PN Bemaraha.
ADDITIONAL MATERIAL EXAMINED. Madagascar. Mahajanga Province: —
SF (Capuron) 26116, Forêt dans RNI No. IX, Berano, Canton Antsalova, District
Antsalova, [18°44’S, 44°44’E], bud, 17.X.1966 (P!).

12. Rinorea mcphersonii Wahlert sp. nov.

Frutex. Lamina elliptico vel late-elliptico, 2.0–8.7 cm longa, 0.8–4.6 cm
lata, apice rotundato vel subacutato, basi cuneata, adaxialiter et abaxialiter
glabra; petiolo 1.0–8.0 mm longo. Inflorescentiae terminale, cymosae, 1.0 cm
longo. Calyce 0.8–1.5 mm longo, glabro. Corolla 2.9–3.7 longo. Fructus
ellipsoideus, 8.0–9.5 mm longus; semine subsphaerico-ovoideo.

TYPUS. — Madagascar. Toliara Province, McPherson & Dumetz 14335,
Fort Dauphin (Tôlanaro) region; NE of city, in region called Mandena, beyond
Botanical Garden and QIT camp, in forest remnants near coastal lake, 24°57’S,
47°00’E, 25 m, fl., fr., 31.X.1989 (holo-, MO[3766316]!, iso-, K!, TAN!).

DESCRIPTION. Shrub, up to 3 m tall; young branches flattened in cross
section, glabrous or puberulent. Leaves opposite, anisophyllous; petioles 1.0–
8.0 mm long, glabrous; stipules eventually deciduous, free, lanceolate-deltoid,
0.2–0.8 × 0.3–0.7 mm, outer surface glabrous, margin ciliate, apex acute,
horned or mucronate; terminal bud scales conical, foliaceous, linear-lanceolate,
0.6–2.2 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina
elliptic to broadly elliptic, 2.0–8.7 × 0.8–4.6 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 4–6, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin low-serrate to serrulate or serrate, revolute; apex subacute to rounded. Inflorescence a terminal and subterminal cyme, less than 1.0 cm long, axis glabrous or puberulent, peduncle 1.0–4.0 mm long, peduncle subtended by two persistent bud scales; pedicels 1.7–2.8 mm long, glabrous; pedicel bractlets persistent, triangular to subulate, 0.6–0.9 × 0.3–0.5 mm, glabrous, keeled, margin ciliate, apex acute, mucronate. Flowers (2.7–) 3.2–4.5 mm long. Sepals unequal, ovate-deltoid, 0.8–1.5 × 0.9–1.1 mm, usually keeled, glabrous, margin ciliate, apex acute to rounded, mucronate. Petals unequal, lanceolate, 2.9–3.7 × 1.1–1.8 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin entire to ciliate, apex subacute, erect to recurved. Stamens 2.1–2.6 mm long; staminal tube 0.6–1.0 mm tall, outer and inner surfaces glabrous, often with a membranous, dentate or irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.05–0.2 mm long, anther connectives 0.4–0.7 × 0.4–0.6 mm, base of anthers pubescent; anther ventral connective scales linear-lanceolate or lanceolate, apex subacute, bifid, or deeply bilobed, 0.25–0.6 × 0.1–0.2 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.8–1.1 × 0.6–0.9 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 2.5–3.1 mm long; ovary ovoid, 0.6–1.1 × 0.5–0.8 mm, glabrous; style 1.7–2.4 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 8.0–9.5 mm long, 3.7–5.0
mm diameter, surface glabrous, with raised reticulate veins, valves unequal, 1.1–2.9 mm wide, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 2.5–3.5 × 2.4–3.0 mm, subspherical-ovoid, dark brown or yellow-tan with brown maculae, smooth, glabrous, 1 (–2) seeds per valve. — Figure 41.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea mcphersonii* is distributed in sands in littoral forests and low mountains in the Fort Dauphin region, at elevations of 0–300 m. The species flowers and fruits October through March. — Figure 56.

**CONSERVATION STATUS.** *Rinorea mcphersonii* is represented by many recent collections, but from a rather small geographic area. Several populations have been extirpated by the QIT mining activities in the region. The estimated EOO was 686 km² and AOO was 346 km², and the species is therefore placed in Endangered status.

**ETYMOLOGY.** This species is named in honor of Gordon Duane McPherson (born 1947), plant collector, curator at Missouri Botanical Gardens, St. Louis, MO, USA, and specialist in Euphorbiaceae (Dorr, 1997).

**PARATYPES.** — **Madagascar.** Toliara Province: — *D’Arcy & Rakotozafy 15365*, Reserve Forestier Mandena, ca. 7 km N of Fort Dauphin, [24°58’S, 46°59’E], 10 m, bud, 10.V.1983 (MO!). — *D’Arcy & Rakotozafy 15368*, Same

**DESCRIPTION.** Shrub or small tree; young branches flattened in cross section, glabrous to puberulent. Leaves opposite, anisophyllous; petioles 2.3–4.0 mm long, glabrous; stipules eventually deciduous, free, lanceolate-deltoid, 0.4–1.3 × 0.5–0.8 mm, outer surface glabrous, keeled, margin ciliate, apex acute, horned or mucronate; terminal bud scales conical, foliaceous, lanceolate-linear, 0.9–2.3 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina elliptic, 1.6–5.0 × 0.6–2.0 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–5, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin subentire, low-serrate, or serrulate, revolute; apex subacute to rounded. Inflorescence a terminal cyme, less than 1.0 cm long, axis puberulent, peduncle 1.5–4.2 mm long, peduncle subtended by two persistent bud scales; pedicels 2.0–4.0 mm long, glabrous; pedicel bractlets persistent, triangular to subulate, 0.5–0.9 × 0.5–0.7 mm, glabrous, keeled, margin ciliate, apex acute, mucronate. Flowers 3.5–4.5 mm long. Sepals unequal, ovate-deltoid, 1.2–2.0 × 0.8–1.5 mm, glabrous, keeled, margin ciliate, apex acute, mucronate. Petals subequal, lanceolate, 3.4–3.6 × 1.5–1.7 mm, outer surface glabrous, inner surface
sparsely pubescent in the upper half, margin entire to ciliate, apex acute, erect. Stamens 2.4–2.5 mm long; staminal tube 0.7–0.9 mm tall, outer and inner surfaces glabrous, with a membranous, dentate or irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.05–0.3 mm long, anther connectives 0.7 × 0.4 mm; anther ventral connective scales linear-lanceolate or lanceolate, 0.4–0.5 × 0.15 mm, apex subacute, bifid, or deeply bilobed; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.8 × 0.7–0.8 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 2.9–3.7 mm long; ovary ovoid, 0.8–1.5 × 0.6 mm, glabrous; style 2.0–2.3 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 7.5–9.0 mm long, 0.4–0.5 mm diameter, surface glabrous, with raised reticulate veins, valves unequal, 1.2–3.5 mm wide, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 2.6–3.6 × 1.8–2.6 mm, subspherical-ovoid, brown, smooth, glabrous, usually 1 (–2) seeds per valve. — Figure 42.

**Distribution and Phenology.** *Rinorea mandrarensis* is distributed in the Mananara River drainage in the Andohahela region, at elevations of 400–900 m. The species flowers and fruits in January and February. — Figure 58.

**Conservation Status.** *Rinorea mandrarensis* is known from two collections made in 1934. Populations of the species may still persist in PN
Andohahela. There were insufficient data to conduct estimates of EOO and AOO.

**ADDITIONAL MATERIAL EXAMINED.** Madagascar. Toliara Province: — Humbert 13769, Bassin de reception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l’Andohahela et l’Elakelaka, entre Ampahiso et Mahamavo, [22°32’30”S, 46°29’50”E], 400–800 m, bud, fl., imm. fr., I–II.1934 (P[00537172]!), syntype.


**DESCRIPTION.** Shrub, ca. 1 m tall; young branches flattened in cross section, pubescent. Leaves opposite, anisophyllous; petioles 1.5–4.0 mm long, glabrous to sparsely puberulent; stipules eventually deciduous, free, lanceolate-deltoid, 0.8–1.8 × 0.6–0.9 mm, outer surface glabrous to pubescent, keeled, margin ciliate, apex rounded to acute, mucronate; lamina oblanceolate or elliptic, 0.7–2.6 × 0.5–1.2 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–5, ascending, tertiary veins reticulate; base attenuate, symmetrical, aequilateral; margin low-serrulate, mature revolute towards the base; apex rounded to subacute. Inflorescence a terminal cyme bearing 1–3 flowers, peduncle 1.0–3.0 mm long, pubescent; bracts subtending inflorescence ovate, 0.3–0.6 × 0.4–0.7 mm,
glabrous or sparsely puberulent, keeled, margin ciliate, apex acute, mucronate; pedicels 2.2–3.2 mm long, glabrous; Flowers 3.9–5.0 mm long, flower buds conical. Sepals subequal, ovate, 0.6–1.6 × 0.5–0.8 mm, keeled, outer surface glabrous, margin ciliate, apex rounded to acute, mucronate. Petals subequal, lanceolate-elliptic, 3.9–4.3 × 1.0–1.3 mm, white, outer surface glabrous, inner surface sparsely pubescent near the middle, margin entire, ciliate towards the base, apex rounded to acute, erect to rolled. Stamens 1.8–3.3 mm long; staminal tube 0.7–0.8 mm tall, outer and inner surfaces glabrous; anthers filamentoed on summit of staminal tube, filaments 0.15–0.3 mm long, anther connectives 0.6–0.8 × 0.3–0.5 mm, pubescent at the base; anther ventral connective scales 1, linear or lanceolate, 0.7–0.8 × 0.1–0.2 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.2–1.6 × 0.7–0.9 mm, surface glabrous, margin entire, apex subacute. Pistil 3.3–4.0 mm long; ovary ovoid, 0.7–1.0 × 0.4–0.6 mm, glabrous; style 2.3–2.7 mm long, erect, fluted in cross-section, straight or bent, tapered or clavate, glabrous. Fruit not seen. — Figure 43.

REMARKS. Known only from the holotype.

DISTRIBUTION AND PHENOLOGY. The type locality of *Rinorea microphylla* is the upper basin of the Sahadranomby River, a tributary of the Mangoro River, at elevations of ca. 500 m. The single collection of *Rinorea microphylla* was in flower in September. — Figure 56.
CONSERVATION STATUS. There were insufficient collections to estimate EOO and AOO. Satellite imagery in the region of the type collection, made in 1911, shows extensive deforestation. Perrier (1949) noted the species may be extinct.


Lectotype (designated here): Boivin s.n., Comoros, Anjouan, [12°13’S, 44°26’E], bud, [1850, acc. Tulasne, 1868], P[030605]!; isolectotypes: P[030606]! and K[000253947]! *Rinorea monticola* M.Brandt (Bot. Jahrb. Syst. 51, 117. 1913) is a later homonym and is an illegitimate name under Article 53.1 of the Code.

DESCRIPTION. Shrub to small tree, 1–7 (–12) m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 4.0–17.0 mm long, glabrous; stipules caducous, free, lanceolate-deltoid, 0.9–2.5 × 0.3–1.1 mm, outer surface glabrous, margin ciliate, apex acute, mucronate, leaving a scar at the base of bud scale; terminal bud scales conspicuous, conical, foliaceous, lanceolate-linear, twisted, 1.6–4.6 mm long, glabrous or puberulent, margin entire, apex acute, mucronate; lamina oblanceolate, obovate, or elliptic, 4.7–15.5 × 1.6–5.2 (–7.0) cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 5–8, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, subaequilateral; margin serrulate to serrate, rarely subentire,
revolute; apex subacute, shortly acuminate, or cuspidate. Inflorescence a terminal and subterminal cyme, 1.0–4.5 cm long, axis glabrous, peduncle 2.5–5.5 (–15.0) mm long, peduncle subtended by two conspicuous persistent bud scales; pedicels 1.5–2.7 mm long, glabrous; pedicel bractlets eventually deciduous, triangular-ovate, 0.7–0.9 × 0.6–0.9 mm, glabrous, margin ciliate or entire, apex acute, mucronate. Flowers 2.0–4.0 mm long. Sepals unequal, lanceolate-deltoid, 0.8–2.0 × 0.6–1.3 mm, usually keeled, glabrous, margin entire to ciliolate, apex rounded to acute, often with a horn or mucro. Petals subequal, lanceolate, 2.9–3.2 × 0.9–1.5 mm, outer and inner surfaces glabrous or rarely sparsely puberulent, margin entire to ciliolate, apex rounded, erect to recurved. Stamens 2.0–2.6 mm long; staminal tube 0.5–1.0 mm tall, outer and inner surfaces glabrous; anthers subsessile, filaments 0.05–0.2 mm long, anther connectives 0.5–0.9 × 0.4–0.5 mm; anther ventral connective scales ovate, sometimes bilobed, 0.2 × 0.15 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.7–1.1 × 0.6–0.7 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 2.4–3.5 mm long; ovary ovoid, 0.6–1.1 × 0.6–0.7 mm, glabrous; style 1.5–2.0 mm long, erect, fluted in cross-section, straight, tapered, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 8.5–16.0 mm long, ca. 0.4–0.8 mm diameter, surface glabrous, with raised reticulate veins, valves subequal, 1.0–3.4 mm wide, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 3.3–4.5 × 3.2–4.2 mm, spherical-subtetrahedral, yellow-tan, smooth, glabrous, 2 seeds per valve. — Figure 44.
DISTRIBUTION AND PHENOLOGY. *Rinorea monticola* is distributed throughout the Comoro Islands, at elevations of 500–1200 m. It flowers August through May and fruits throughout the year. — Figure 56.

CONSERVATION STATUS. The calculated EOO for *Rinorea monticola* was 23,152 km², and the AOO was 12893 km². These estimates give the species a status of Near Threatened to Least Concern. The species is represented by several recent collections from forest reserves (Sohoa and Benara).


**DESCRIPTION.** Shrub 1–2 m tall; young branches flattened in cross section, glabrous to sparsely puberulent. Leaves opposite, anisophyllous;
petioles 1.0–3.0 mm long, glabrous or rarely pubescent; stipules caducous, not seen; terminal bud scales lanceolate-linear, concave, 1.1–2.6 mm long, often keeled, glabrous to pubescent, margin entire or ciliate, apex acute, mucronate; lamina broadly oval-elliptic or rarely oblanceolate, 3.3–10.3 × 1.1–4.3 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous on upper and lower leaf surfaces; secondary vein pairs 5–8, divergent to ascending, tertiary veins reticulate; base cuneate to attenuate, symmetrical, subaequilateral; margin serrate, revolute; apex cuspidate to acuminate. Inflorescence a terminal and lateral compound cyme, less than 1.0 cm long, axis glabrous to sparsely pubescent, peduncle 1.0–2.5 mm long, subtended by bud scales; pedicels 1.5–3.5 mm long, glabrous to sparsely pubescent; pedicel bractlets triangular-ovate, 0.3–0.5 × 0.2–0.5 mm, keeled, glabrous to pubescent, margin ciliate, apex truncate, rounded, or acute, mucronate. Flowers 3.5–4.0 mm long, flower buds conical. Sepals unequal, lanceolate-deltoid or ovate, 1.2–2.0 × 0.7–1.1 mm, carnose, costate or keeled, outer surface glabrous, margin ciliate, apex acute, often mucronate. Petals subequal, lanceolate, 3.2–3.7 × 0.8–1.4 mm, outer surface glabrous, inner surface glabrous, but with a tuft of hairs towards the apex, margin entire, ciliate towards the base, often revolute, apex acute, erect. Stamens 1.0–2.0 mm long; staminal tube 0.7–1.2 mm tall, outer and inner surfaces glabrous; anthers subsessile, filaments 0.03–0.2 mm long, anther connectives 0.6–0.7 × 0.3–0.5 mm, base of anthers pubescent; anther ventral and dorsal connective scales absent. Pistil 2.1–2.7 mm long; ovary ovoid, 0.5–1.0 × 0.6 mm, glabrous; style 1.6–1.7 mm
long, erect, fluted in cross-section, straight, tapered, glabrous. Fruit not seen. — Figure 45.

REMARKS. Tulasne (1886: 319) and Perrier (1949: 324) incorrectly cite Richard 968 as “Richard 368”.

DISTRIBUTION AND PHENOLOGY. *Rinorea mutica* is distributed on Nosy Mitsio and in the Sambirano River valley, at elevations of 20–300 m. It flowers August through May. — Figure 57.

CONSERVATION STATUS. The estimated EOO and AOO for *Rinorea mutica* were < 100 km², giving it a Critically Endangered status. However, the species commonly occurs in the well protected PN Lokobé on Nosy Be.


Lectotype (designated here): du Petit Thouars s.n., Madagascar, without locality, fl., s.date, P[030609]!; isolectotypes: K!, P[030610]!

DESCRIPTION. Shrub; young branches flattened in cross section, puberulent. Leaves opposite, anisophyllous; petioles 3.5–8.0 mm long, glabrous; stipules caducous, not seen; terminal bud scales foliaceous, lanceolate-linear, 1.0–1.8 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina obovate, 2.0–7.0 × 1.3–2.8 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 2–4, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin subentire to low-serrate, revolute; apex rounded.

Inflorescence a terminal cyme, less than 1.0 cm long, axis puberulent, peduncle 1.0–2.0 mm long, peduncle subtended by two persistent bud scales; pedicels 2.3–4.0 mm long, glabrous; pedicel bractlets persistent, ovate, 0.9–1.0 × 0.7–0.8 mm, glabrous, keeled, margin ciliate, apex rounded, usually mucronate.

Flowers 3.8–4.5 mm long. Sepals unequal, ovate to suborbicular, 1.5–2.1 × 1.7–2.3 mm, glabrous, margin ciliate, apex rounded. Petals unequal, lanceolate,
3.5–3.7 × 1.3–2.1 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin entire to ciliate, apex subacute, erect to recurved. Stamens 2.8–3.1 mm long; staminal tube 0.8–1.2 mm tall, outer and inner surfaces glabrous; anthers subsessile, filaments 0.1–0.4 mm long, anther connectives 0.7–0.8 × 0.4–0.5 mm; anther ventral connective scales ovate-lanceolate, 0.5–0.6 × 0.15–0.3 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.1 × 0.9–1.0 mm, surface glabrous, margin entire, apex rounded. Pistil 3.7 mm long; ovary ovoid, 1.0 × 0.7 mm, glabrous; style 2.6 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 46.

REMARKS. Known only from the type material. Perrier (1949) associated collections from the Fort Dauphin region (Baron 3062, 3085 and 3117; Elliot 2506) with the species represented by Thouars s.n., but the latter is not a close match to the specimens from Fort Dauphin. The many collections examined from the Fort Dauphin area are assigned to Rinorea mcpersonii Wahlert.

DISTRIBUTION AND PHENOLOGY. It is known that Thouars collected both in Fort Dauphin from 1792–1793, and the Fenoarivo area on the central coast from 1795–1796 (Dorr, 1997). The Thouars s.n. collection may represent a collection from Fenoarivo. It is possible that the type of Rinorea pauciflora was collected from a now-extirpated coastal thicket or littoral forest from the Fenoarivo area.
**Conservation Status.** The type locality is not known, and thus a conservation status could not be calculated.


**Description.** Shrub to small tree; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles 2.5–4.0 mm long, glabrous; stipules eventually deciduous, free, lanceolate-deltoid, 1.0–1.5 × 0.6–1.0 mm, outer surface glabrous, keeled, margin ciliate, apex acute, horned or mucronate; terminal bud scales conical, foliaceous, lanceolate-linear, 1.7–4.0 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina elliptic to broadly elliptic, (4.0–) 5.0–9.0 × (1.2–) 2.5–4.7 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 5–7, ascending, tertiary veins reticulate; base cuneate, symmetrical, aequilateral; margin serrate, revolute; apex subacute. Inflorescence a terminal cyme, less than 1.0 cm long, axis puberulent, peduncle 2.0–4.0 mm long, peduncle subtended by two persistent bud scales; pedicels 2.2–4.5 mm long, glabrous; pedicel bractlets eventually deciduous, triangular to subulate, 0.7–0.9
× 0.6–1.0 mm, glabrous, margin ciliate, apex acute, mucronate. Flowers 3.7–4.6 mm long. Sepals unequal, ovate-deltoid, 1.4–2.0 × 1.4–1.8 mm, glabrous, margin ciliate, apex rounded, mucronate. Petals subequal, lanceolate, 4.0–4.2 × 1.7–2.1 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin entire to ciliate, apex subacute to rounded, erect. Stamens 2.8 mm long; staminal tube 1.0 mm tall, outer and inner surfaces glabrous; anthers subsessile, filaments 0.1 mm long, anther connectives 0.6 × 0.5 mm; anther ventral connective scales lanceolate, apex bifid, 0.5 × 0.2 mm; anther dorsal connective scales large and conspicuous, apical, ovate, scarious, white, 1.1 × 1.0 mm, surface glabrous, margin entire, apex rounded. Pistil 3.3 mm long; ovary ovoid, 0.9–1.0 × 0.8 mm, glabrous; style 2.3–2.5 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, ca. 10.0 mm long, ca. 0.5 mm diameter, surface glabrous, valves unequal, 2.6–3.5 mm wide, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed not seen. — Figure 47.

REMARKS. Known only from the type material. Perrier originally described this taxon as a forma, but he annotated the sheets and referred to the taxon as a variety in his floristic treatment (Perrier 1954). *Rinorea pauciflora f. latidentata* appears on the basis of the single collection to merit species rank, but it is maintained at the rank of forma until more collections become available to confirm its distinctions.
DISTRIBUTION AND PHENOLOGY. *Rinorea pauciflora* f. *latidentata* was collected very close to the type locality of *Rinorea mandrarensis*, and is only known from the Mananara River drainage in the Andohahela region, at elevations of 400–900 m. *Rinorea pauciflora* f. *latidentata* flowers January through February. — Figure 58.

CONSERVATION STATUS. Populations of the species may still persist in PN Andohahela. There were insufficient data to conduct estimates of EOO and AOO.


DESCRIPTION. Shrub; young branches flattened in cross section, glabrous to puberulent. Leaves opposite, anisophyllous; petioles 2.0–3.0 mm long, glabrous; stipules eventually deciduous, free, lanceolate-deltoid, 0.5–2.0 × 0.5–0.8 mm, outer surface glabrous, margin ciliate, apex acute, horned or mucronate; terminal bud scales foliaceous, lanceolate, 1.4–2.3 mm long, glabrous, margin ciliate, apex acute, mucronate; lamina elliptic, 3.5–8.5 × 1.4–3.0 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–4, ascending, tertiary veins reticulate;
base cuneate-attenuate, symmetrical, subaequilateral; margin low-serrate to serrulate, revolute; apex subacute. Inflorescence a terminal and subterminal cyme, less than 1.0 cm long, axis puberulent, peduncle 1.0–3.0 mm long, peduncle subtended by two persistent bud scales; pedicels 4.0–5.1 mm long, glabrous; pedicel bractlets persistent, triangular to subulate, 0.8–1.2 × 0.5–0.7 mm, glabrous, keeled, margin ciliate, apex acute to rounded, mucronate. Flowers 4.2–4.9 mm long. Sepals unequal, ovate, 1.3–1.8 × 0.9–1.5 mm, keeled, glabrous, margin ciliate, apex acute to rounded, mucronate. Petals unequal, lanceolate, 4.0–4.5 × 1.2–1.4 mm, outer surface glabrous, inner surface pubescent in the upper half, margin entire to ciliate, apex subacute, erect. Stamens 2.8–3.1 mm long; staminal tube 0.7–0.8 mm tall, outer and inner surfaces glabrous; anthers subsessile, filaments 0.1–0.2 mm long, anther connectives 1.0 × 0.4–0.5 mm; anther ventral connective scales lanceolate, apex acute or bifid, 0.4–0.6 × 0.15 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 1.0–1.5 × 0.7–1.0 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 3.1–3.5 mm long; ovary ovoid, 0.7–0.8 × 0.6–0.7 mm, glabrous; style 2.3–2.7 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 48.

REMARKS. Known only from the type material. Perrier originally described this taxon as a forma, but he annotated the sheets and referred to the taxon as a variety in his floristic treatment (Perrier 1954). Rinorea pauciflora f. sempervirens may merit elevation to the rank of species if additional specimens
confirm its distinctions from related taxa, but it is maintained at the rank of forma until more collections become available.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea pauciflora* f. *sempervirens* is only known from the Beampingaratra Massif, at elevations of 1100–1500 m. *Rinorea pauciflora* f. *sempervirens* flowers in October. — Figure 57.

**CONSERVATION STATUS.** Populations of the species may still persist in PN Andohahela. There were insufficient data to conduct estimates of EOO and AOO.


**DESCRIPTION.** Shrub, up to 4 m tall; young branches flattened in cross section, glabrous. Leaves opposite, anisophyllous; petioles (4.0–) 9.0–28.0 mm long, glabrous; stipules caducous, not seen; terminal bud scales conical, foliaceous, linear-lanceolate, 3.0–5.5 mm long, glabrous, margin entire to ciliate, apex acute, mucronate; lamina obovate to oblanceolate, 7.0–18.0 × (2.5–) 4.4–7.0 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 4–6, ascending, tertiary veins reticulate; base cuneate, unsymmetrical, aequilateral to oblique; margin low-serrate to
serrate, revolute; apex cuspidate. Inflorescence a terminal cyme, less than 2.0 cm long, axis glabrous to puberulent, peduncle 2.0–5.0 mm long, subtended by two persistent bud scales; pedicels 4.2–6.0 mm long, glabrous; pedicel bractlets caducous, triangular, lanceolate-deltoid, or subulate, 0.9–2.2 × 0.6–1.1 mm, glabrous, keeled or costate, margin entire to ciliolate, apex acute, mucronate. Flowers 5.5–6.2 mm long. Calyx zygomorphic, sepals strongly unequal, lanceolate or ovate, 3.6–5.5 × 1.5–2.2 mm, sometimes keeled, glabrous, margin entire to ciliolate, apex acute, sometimes horned or mucronate. Petals unequal, lanceolate, 4.5–5.4 × 1.3–1.8 mm, outer surface glabrous, inner surface pubescent, margin entire to ciliolate, apex acute, erect to recurved. Stamens 3.4–3.9 mm long; staminal tube 0.9–1.4 mm tall, outer and inner surfaces glabrous, with a dentate, lobed, or irregularly lacerate margin subtending anthers; anthers subsessile, filaments 0.15–0.3 mm long, anther connectives 0.9–1.2 × 0.5–0.8 mm, base of anthers with long hairs; anther ventral connective scales lanceolate, apex rounded or truncate, 0.7–1.1 × 0.5 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate, scarious, white, 1.7–1.8 × 0.9–1.0 mm, surface glabrous, margin entire, apex acute. Pistil 3.5–4.3 mm long; ovary ovoid, 0.9–1.3 × 0.7–1.0 mm, glabrous; style 2.2–3.0 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 49.

**Distribution and Phenology.** *Rinorea rubra* is distributed on Île Saint-Marie and on the mainland in the region around Foulpointe, at elevations of ca. 20–150 m. It flowers December through April. — Figure 56.
CONSERVATION STATUS. The estimated EOO of *Rinorea rubra* was 1891 km², and the AOO was 501 km². These assessments give the species a status of Endangered or Vulnerable. However, the region of the type locality on Île Saint-Marie has been deforested, and Perrier (1949) wrote that the species may be extinct there. It may persist on the mainland in the protected PN Mananara but was last collected there in 1967.


*Frutex. Lamina elliptico-ovato, 2.2–4.0 cm longa, 0.8–1.8 cm lata, apice rotundato vel subacutato, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.5–8.0 mm longo. Inflorescentiae terminale, cymosae, 1.0 cm longo. Calyce 2.0–3.1 mm longo, glabro. Corolla 4.3–4.6 longo.*

**TYPUS.** — Madagascar, Antsiranana Province: SF (Capuron) 24529, Forêt d’Analafondro, au pied Sud-Est du plateau de Sahafary, bassin inférieur
DESCRIPTION. Shrub; young branches flattened in cross section, puberulent to pubescent. Leaves opposite, anisophyllous; petioles 2.5–8.0 mm long, puberulent; stipules caducous, free, lanceolate-deltoid, 0.5–0.7 × 0.3–0.4 mm, outer surface glabrous or pubescent, keeled, margin entire to ciliate, apex acute, mucronate or horned; terminal bud scales foliaceous, lanceolate-linear, 1.2–4.5 mm long, pubescent, apex acute, mucronate; lamina elliptic-ovate, 2.2–4.0 × 0.8–1.8 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 4–7, ascending, tertiary veins reticulate; base cuneate, symmetrical, aequilateral; margin serrulate, revolute; apex subacute to rounded. Inflorescence a terminal cyme, less than 1.0 cm long, axis puberulent, peduncle 2.2–5.0 mm long, peduncle subtended by two persistent bud scales; pedicels 1.0–2.0 mm long, glabrous; pedicel bractlets persistent, ovate-deltoid, 0.7–0.9 × 0.6–0.8 mm, puberulent, margin entire, apex acute, mucronate. Flowers 4.2–5.2 mm long. Sepals unequal, lanceolate-deltoid, 2.0–3.1 × 1.4–1.8 mm, outer surface glabrous, inner surface sparsely puberulent, keeled, margin entire, apex subacute to acute, mucronate. Petals subequal, lanceolate, 4.3–4.6 × 1.2–1.6 mm, outer surface glabrous, inner surface glabrous or rarely sparsely pubescent in the upper half, margin entire, apex acute, erect. Stamens 2.6–2.7 mm long; staminal tube 1.0–1.1 mm tall, outer and inner surfaces glabrous, margin more or less entire; anthers nearly sessile, filaments less than 0.05 mm long, anther connectives 0.8 × 0.6 mm,
base of anthers with a few hairs; anther ventral connective scales lanceolate, 0.2 × 0.4 mm, apex rounded to irregular; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.9–1.0 × 0.7–0.8 mm, surface glabrous, margin entire, apex rounded. Pistil 3.3 mm long; ovary ovoid, 0.8–0.9 × 0.6–0.7 mm, glabrous; style 2.3–2.4 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 50.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea sahafarensis* is only known from the Analafondro Forest, at the foot of the Sahafary Plateau, at elevations of ca. 50 m. The species flowers in February. — Figure 58.

**CONSERVATION STATUS.** *Rinorea sahafarensis* is known from a single collection made in 1966. There were insufficient collections for estimation of EOO and AOO.

**ETYMOLOGY.** This species is named for the type locality, in the region around Sahafary Plateau.

**22. Rinorea sambavensis** Wahlert sp. nov.

*Frutex. Lamina late-elliptico vel obovato, (3.1–) 5.2–9.5 cm longa, (1.0–) 2.1–3.9 cm lata, apice subacutato, acutato, vel breviter cuspidato, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 8.0–32.0 mm longo. Inflorescentiae
Terminale, cymosae, 1.0–2.0 cm longo. Calyce 2.9–4.2 mm longo, glabo.

Corolla 4.5–5.4 longo.

Typus. — Madagascar, Antsiranana Province: Lowry & Rabenantoandro

5197, Amjombavola (= Ambatobiribiry), ca. 10 air-km N of Sambava,
14°10′55″S, 50°05′14″E, fl., 9.V.2000 (holo-, K!, iso-, MO!, P!, TAN!).

Description. Shrub, up to 2 m tall; young branches flattened in cross
section, glabrous. Leaves opposite, anisophyllous; petioles 8.0–32.0 mm long,
glabrous; stipules caducous, not seen; terminal bud scales conical, foliaceous,
linear-lanceolate, 1.9–4.0 mm long, glabrous, weakly keeled, margin ciliate,
apex acute, mucronate; lamina broadly elliptic to obovate, (3.1–) 5.2–9.5 ×
(1.0–) 2.1–3.9 cm; lamina upper and lower surfaces glabrous; primary and
secondary veins glabrous; secondary vein pairs 5–6, ascending, tertiary veins
reticulate; base cuneate, symmetrical to unsymmetrical, aequilateral to oblique;
margin subentire to low-serrate, revolute; apex subacute, acute, or shortly
cuspidate. Inflorescence a terminal cyme, less than 2.0 cm long, axis sparsely
puberulent, peduncle 2.3–3.2 mm long, subtended by two persistent bud scales;
pedicels 8.7–11.0 mm long, glabrous; pedicel bractlets eventually deciduous,
lanceolate-deltoid or subulate, 1.0–1.6 × 0.8–1.3 mm, glabrous, keeled, margin
ciliate, apex acute, mucronate. Flowers 6.5–7.1 mm long. Calyx zygomorphic,
sepals strongly unequal, lanceolate or ovate, 2.9–4.2 × 1.5–2.7 mm, sometimes
keeled, glabrous, margin ciliolate, apex acute or rounded, mucronate. Petals
unequal, lanceolate, 4.5–5.4 × 1.3–1.8 mm, outer surface glabrous, inner
surface pubescent, margin entire to ciliolate, apex acute, erect to recurved. Stamens 3.3 mm long; staminal tube 1.1 mm tall, outer and inner surfaces glabrous, with a dentate margin subtending anthers; anthers subsessile, filaments 0.1–0.2 mm long, anther connectives 0.8–1.0 × 0.7–0.9 mm, base of anthers with a few hairs; anther ventral connective scales lanceolate, apex bifid, 0.6 × 0.2 mm; anther dorsal connective scales large and conspicuous, apical, ovate, scarious, white, 1.5 × 1.0 mm, surface glabrous, margin entire, apex acute. Pistil 4.6 mm long; ovary ovoid, 1.1 × 1.0 mm, glabrous; style 3.2 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 51.

**Distribution and Phenology.** *Rinorea sambavensis* is only known from the area north of Sambava, at elevations of ca. 0–150 m. The species flowers in May. — Figure 57.

**Conservation Status.** *Rinorea sambavensis* is known from a single collection made in 2000. There were insufficient collections for estimation of EOO and AOO.

**Etymology.** This species is named after the town near the type locality.

Sevazy, au S.W. de Vatomandy, \([19°27'S, 48°41'E]\), bud, fl., fr., X.1921, P[030620]!; isoelectotype: P[030621]!

**DESCRIPTION.** Shrub; young branches flattened in cross section, pubescent. Leaves opposite, anisophyllous; petioles 2.0–3.0 mm long, pubescent; stipules caducous, free, linear, ca. 0.4 × 0.1 mm, outer surface glabrous, apex acute, mucronate; terminal bud scales foliaceous, lanceolate-linear, 0.5–1.3 mm long, pubescent, apex acute, mucronate; lamina lanceolate, 1.0–4.7 × 0.6–2.4 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–5, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, aequilateral; margin serrulate-crenulate, revolute; apex acute. Inflorescence a terminal cyme, 1.5–2.0 cm long, axis sparsely pubescent, peduncle 10.0–15.0 mm long, peduncle subtended by two persistent bud scales; pedicels 2.0–2.8 mm long, glabrous; pedicel bractlets caducous, highly reduced, triangular, ca. 0.15 × 0.15 mm, glabrous, keeled, margin ciliate, apex acute. Flowers 3.5–4.1 mm long. Sepals unequal, ovate, 1.1–1.6 × 0.7–1.1 mm, glabrous, margin ciliate, apex rounded. Petals unequal, lanceolate, 3.5–4.0 × 1.5–1.6 mm, outer surface glabrous, inner surface pubescent, margin ciliate, apex acute to subacute, erect. Stamens 2.6–2.7 mm long; staminal tube 0.6–0.7 mm tall, outer and inner surfaces glabrous, with a densely ciliate margin subtending anthers; anthers filamented, filaments 0.2–0.5 mm long, pubescent, anther connectives 0.5–0.6 × 0.5–0.6 mm, base of anthers pubescent; anther ventral connective scales linear-lanceolate, 0.5–0.6 × 0.1 mm, apex acute or bifid; anther dorsal connective scales large and
conspicuous, apical, lanceolate-ovate, scarious, white, 1.0–1.3 × 0.7–0.8 mm, surface glabrous, margin entire, apex rounded. Pistil 2.8–3.3 mm long; ovary ovoid, 0.8–1.0 × 0.6–0.7 mm, glabrous; style 2.0–2.4 mm long, erect, fluted in cross-section, straight, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, ca. 8.0 mm long, ca. 4.0 mm diameter, surface glabrous, with raised reticulate veins, valves unequal, ca. 2.0 mm wide, capsule dehiscing along three straight sutures; fruit bearing remnants of style; seed ca. 3.0 × 3.0 mm, subspherical-ovoid, dark brown or yellow-tan, smooth, glabrous. — Figure 52.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea ternifolia* is only known from the area around Sevazy, in the vicinity of Vatomandry, at elevations of ca. 0–100 m. The species flowers and fruits in October. — Figure 58.

Conservation Status. The type collection of *Rinorea ternifolia*, made in 1921, comes from a heavily deforested region. There were insufficient collections for estimation of EOO and AOO.

DESCRIPTION. Shrub up to 3.0 m tall; young branches flattened in cross section, pubescent or glabrous. Leaves opposite, anisophyllous; petioles 2.0–6.0 mm long, glabrous; stipules eventually deciduous, free, lanceolate-deltoid, 1.0–2.6 × 0.5–0.6 mm, outer surface glabrous, keeled, margin ciliate, apex acute; lamina lanceolate, elliptic, or oblanceolate, 1.7–5.5 (–7.0) × 0.9–2.5 (–3.5) cm, lower surface drying purple-green to purple-brown; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 4–6, ascending, tertiary veins reticulate; base attenuate-cuneate or attenuate-rounded, decurrent onto petiole, symmetrical, subaequilateral; margin low-serrate to serrate, revolute; apex acute to shortly acuminate. Inflorescence a terminal and subterminal cyme, 1.0–1.5 cm long, axis puberulent or glabrous, peduncle 1.2–2.5 mm long; pedicels 2.4–5.0 mm long, glabrous; pedicel bractlets eventually deciduous, lanceolate-ovate, 0.7–1.0 × 0.3–0.9 mm, keeled, keel terminating in a mucro, glabrous, margin ciliate, apex acute to rounded. Flowers 4.0–5.0 mm long, flower buds conical. Sepals subequal, ovate or deltoid, 0.9–1.7 × 0.8–1.2 mm, keeled, keel terminating in a mucro or short horn, glabrous, margin ciliate, apex rounded to acute. Petals subequal, lanceolate, 3.1–4.3 × 1.0–1.3 mm, outer surface glabrous, inner surface pubescent, margin entire, ciliate towards the base, apex acute to rounded, erect to recurved. Stamens 3.1–3.5 mm long; staminal tube 0.8–1.0 mm tall, outer and inner surfaces glabrous, tube summit membranous, usually toothed, with a single tooth between anthers; anthers subsessile, filaments 0.1–0.2 mm long, anther connectives 0.7–0.9 × 0.3–0.4 mm, base of anthers pubescent; anther ventral connective scales linear-lanceolate, often bifid or deeply divided, white,
0.7–0.8 × 0.1–0.15 mm; anther dorsal connective scales large and conspicuous, apical, lanceolate, scarious, white, 1.6–2.3 × 0.8–1.0 mm, surface glabrous, margin entire, apex rounded to subacute. Pistil 3.1–4.0 mm long; ovary ovoid, 0.6–1.0 × 0.5–0.6 mm, glabrous; style 2.2–3.2 mm long, erect, fluted in cross-section, straight, clavate, glabrous. Fruit a three-parted, indurate capsule, dehiscent, ellipsoid, 6.5–9.0 mm long, surface glabrous, with reticulate veins, valves subequal, 2.0–3.4 mm wide, the back of each valve somewhat thickened, capsule dehiscing along three straight sutures; calyx and corolla persistent at base of maturing fruit, fruit bearing remnants of style; seed 2.4–3.0 × 2.0–3.0 mm, subspherical-tetrahedral, yellow-tan with light brown maculæ, smooth, glabrous, usually 1 seed per valve. — Figure 53.

**Distribution and Phenology.** *Rinorea urschii* is distributed in the Perinet-Analamazoatra region, at elevations of 800–1000 m. The species flowers and fruits October through December. — Figure 56.

**Conservation Status.** The estimated EOO of *Rinorea urschii* was 7997 km² and AOO was 4574 km², giving it a status of Vulnerable to Near Threatened. However, the species has been recently collected from the protected areas PN Mantadia and RS Analamazaotra.

**Additional Material Examined.** Madagascar. Toamasina Province: — Cours 2846, d’Amboditafonana à Ankosy, [19°58’00”S, 48°03’30”E], fl., 11.X.1945 (MO!, P!). — Lam & Meeuse 5374, Analamazaotra, [18°56’S,
48°26′E], bud, 11.XI.1938 (P!). — *Lorence 1897*, Route Nationale no. 2, at 20
km west of Perinet, [18°56′57″S, 48°29′45″E], 950 m, bud, 29.X.1978 (K!, MO!).
— *Raharilala et al. 71*, Forêt d’Anjozorobe, à l’Est du village d’Anjosahabe, forêt
à l’Ouest d’Anfatrapeo, à environ 12 km à l’Est d’Anjozorobe, près du village de
Ravoandriana, 18°23′S, 47°57′E, 1300–1500 m, fr., 29.X.1993 (K!, M!). — *SF
1710*, Ambatondrazaka, [17°50′S, 48°25′E], bud, 11.X.1950(?) (P!). — *SF
(Capuron) 22066*, Vestige forestier à Ankarahara, PK 100 de la route
Tananarive-Moramanga, rive gauche du Mangoro, [18°54′S, 48°09′E, 800 m],
fl., 1.XI.1962 (P!). — *Skema et al. 223*, P.N. Mantadia, Circuit Chute Sacree, on
first path to the right, up hill, ca. 50 m, 18°49′32″S, 48°26′05″E, 986 m, sterile,
12.X.2006 (K!, MO!, P!, PRE!, TAN!). — *Skema et al. 228*, Same locality and
date, sterile (K!, MO!, P!, PRE!, TAN!). — *Wahlert et al. 64*, P.N. Mantadia,
Circuit Tsakoka, on hillsides above stream (Sahanody River); P.K. 14, 18°46′S,
48°25′E, 900–1000 m, bud, fl., 13.XII.2006 (MO!, P!, TAN!). — *Wahlert et al.
65*, Same locality and date, fl. (MO!, P!, TAN!). — *Wahlert et al. 66*, Same
locality and date, fl. (MO!, P!, TAN!). — *Wahlert et al. 67*, Same locality and
date, bud (MO!, P!, TAN!). — *Wahlert et al. 68*, Same locality and date, bud, fl.,
(MO!, P!, TAN!). — *Wahlert et al. 70*, P.N. Mantadia, Circuit Indri 1, Piste Liane
Sacréé, vers Vatofotsy, 18°56′S, 48°26′E, 900–1000 m, fl., imm. fr., 13.XII.2006
(MO!, P!, TAN!). — *Wahlert et al. 71*, Same locality and date, bud, fl., (MO!, P!,
TAN!). — *Wahlert & Rakotonasolo 75*, Ambatovy, Dynatec mining site,
commune Ambohibary, between Dynatec and Berano, 18°49′S, 48°18′E, 1000
m, bud, fl., fr., 14.XII.2006 (MO!, P!, TAN!). — *Wahlert & Rakotonasolo 77*,
Same locality and date, bud, fl., fr (MO!, P!, TAN!). — *Wahlert & Rakotonasolo
79. Same locality and date, bud, fl. (MO!, P!, TAN!). — *Wahlert & Rakotonasolo*

80. Same locality and date, bud, fl. (MO!, TAN!).


**DESCRIPTION.** Shrub ca. 2 m tall; young branches flattened in cross section, glabrous to sparsely pubescent. Leaves opposite, some branch apices with leaves in whorls of 3, anisophyllous; petioles 2.0–11.0 mm long, pubescent; stipules caducous, lanceolate-deltoid, 1.0–1.2 × 0.3–0.5 mm, outer surface glabrous or sparsely pubescent, margin entire to ciliate, apex mucronate; terminal bud scales deltoid-ovate, concave, 1.2–2.8 mm long, pubescent, margin entire to ciliate, apex acute, mucronate; lamina obovate to broadly elliptic, 2.9–9.5 × 2.0–5.0 cm; lamina upper surface glabrous, lower surface sparsely puberulent; primary and secondary veins glabrous on upper leaf surface, puberulent on lower leaf surface; secondary vein pairs 4–5, ascending, tertiary veins reticulate; base attenuate, symmetrical, aequilaterial; margin crenulate to low-serrrate, revolute; apex cuspidate to shortly acuminate. Inflorescence a terminal compound cyme, less than 1.0 cm long, axis sparsely pubescent, peduncle 0.9–1.3 mm long, peduncle subtended by two persistent
bud scales; pedicels 1.0–1.1 mm long, pubescent; pedicel bractlets deltoid-ovate, 0.4–0.7 × 0.5 mm, keeled, pubescent, margin ciliate, apex acute, mucronate. Flowers 2.9–3.2 mm long, flower buds conical. Sepals unequal, ovate, 0.9–1.6 × 0.6–1.1 mm, outer surface glabrous to sparsely pubescent, margin ciliate, apex rounded. Petals unequal, lanceolate to broadly elliptic, 2.9–3.3 × 0.9–1.5 mm, outer surface glabrous, inner surface sparsely pubescent near the middle, margin entire, ciliate towards the base, apex subacute to rounded, erect. Stamens 2.0–2.3 mm long; staminal tube 0.3–0.5 mm tall, outer and inner surfaces glabrous, vestiges of filaments visible in tube, usually swollen; anthers filamented, filaments 0.2–0.4 mm long, anther connectives 0.6–0.9 × 0.3–0.4 mm, base of anthers pubescent; anther ventral connective scales bifid or deeply lobed, 0.1–0.2 × 0.1–0.25 mm; anther dorsal connective scales large and conspicuous, apical, deltoid-ovate, scarious, white, 0.7–0.9 × 0.5–0.6 mm, surface glabrous, margin entire, apex subacute. Pistil 2.2–2.5 mm long; ovary ovoid, 0.7 × 0.5–0.6 mm, glabrous; style 1.6–1.7 mm long, erect, fluted in cross-section, straight, tapered, glabrous. Fruit not seen. — Figure 54.

**ADDITIONAL MATERIAL EXAMINED.** Madagascar. Antsiranana Province: — Boivin 2120, Nossi Mitsiou [Nosy Mitsio], [12°54'S, 48°35'E], bud, fl., 1847–1852 (P[030628]!), syntype.

**DISTRIBUTION AND PHENOLOGY.** *Rinorea verticillata* is only known from Nosy Mitsio Island. Phenology unknown. — Figure 58.
CONSERVATION STATUS. There were insufficient collections for estimation of EOO and AOO. The species is only known from the heavily degraded Nosy Mitsio. Trips to collect the species in 2006 and 2007 were unsuccessful. Perrier (1949) noted that the species may be extinct.

26. Rinorea vohemarensis Wahlert sp. nov.

Frutex vel arbor. Lamina elliptica, obovata, vel lanceolata, 1.9–5.5 cm longa, 1.8–2.3 cm lata, apice rotundato vel subacutato, basi cuneata, adaxialiter et abaxialiter glabra; petiolo 2.0–8.0 mm longo. Inflorescentiae terminale, cymosae, 1.0 cm latae. Calyce 1.0–1.7 mm longo, glabro. Corolla 4.1–4.8 mm longo.


Description. Shrub or small tree, 3–8 m tall; young branches flattened in cross section, puberulent. Leaves opposite, anisophyllous; petioles 2.0–8.0 mm long, glabrous; stipules caducous, free, lanceolate-deltoid, 0.5–0.7 × 0.3–0.4 mm, outer surface glabrous, keeled, margin ciliolate, apex acute, mucronate or horned; terminal bud scales foliaceous, lanceolate-linear, 0.6–1.1 mm long, glabrous, margin entire, apex acute, mucronate; lamina broadly elliptic,
obovate, or lanceolate, 1.9–5.5 × 1.8–2.3 cm; lamina upper and lower surfaces glabrous; primary and secondary veins glabrous; secondary vein pairs 3–6, ascending, tertiary veins reticulate; base attenuate-cuneate, symmetrical, subaequilateral; margin low-serrate to serrulate-crenulate, revolute; apex subacute to rounded. Inflorescence a terminal cyme, less than 1.0 cm long, axis sparsely pubescent, peduncle 1.0–1.5 mm long, peduncle subtended by two persistent bud scales; pedicels 1.0–3.0 mm long, glabrous; pedicel bractlets persistent, broadly ovate to subulate, 0.3–0.8 × 0.4–0.6 mm, glabrous, margin ciliolate, apex acute to rounded, mucronate. Flowers 3.3–3.9 mm long. Sepals unequal, lanceolate-deltoid, 1.0–1.7 × 0.5–1.0 mm, glabrous, usually keeled, margin entire to ciliolate, apex acute, mucronate or horned. Petals subequal, lanceolate, 3.3–3.7 × 0.8–1.1 mm, outer surface glabrous, inner surface sparsely pubescent in the upper half, margin entire to ciliate, apex acute, erect. Stamens 1.9–2.1 mm long; staminal tube 0.5–0.8 mm tall, outer and inner surfaces glabrous, with membranous, dentate margin subtending anthers; anthers filamented, filaments 0.15–0.2 mm long, anther connectives 0.3–0.5 × 0.3–0.5 mm, base of anthers with a few hairs; anther ventral connective scales lanceolate, 0.25–0.4 × 0.15 mm, apex bifid; anther dorsal connective scales large and conspicuous, apical, lanceolate-ovate, scarious, white, 0.6–1.0 × 0.4–0.5 mm, surface glabrous, margin entire, apex rounded. Pistil 2.6–2.8 mm long; ovary ovoid, 0.6–0.7 × 0.5–0.6 mm, glabrous; style 1.9–2.1 mm long, erect, fluted in cross-section, straight, glabrous. Fruit not seen. — Figure 55.
DISTRIBUTION AND PHENOLOGY. *Rinorea vohemarensis* is distributed to the north and south of Vohemar, in littoral and sublittoral forests, at elevations of 0–30 m. The species flowers March through July, with a single fruiting specimen from March.— Figure 57.

CONSERVATION STATUS. The estimated EOO of *Rinorea vohemarensis* was 225 km² and the AOO was 230 km², giving the species an Endangered Status. The species is represented by several recent collections from unprotected areas.

Literature Cited


Figure 30: *Rinorea allorgeae*; from holotype, Allorge & Rakotozafy 2640 (P).
Figure 31: Rinorea ambanizanensis; from holotype, Zjhra & Hutcheon 157 (MO).
Figure 32: Rinorea analavelensis; from lectotype, Humbert 14247 (P).
Figure 33: Rinorea antsalovensis; from holotype, Leandri & Saboureau 3043 (P).
Figure 34: Rinorea auriculata; from Friedmann 484 (TAN).
Figure 35: Rinorea boinensis; from Morat 3777 (TAN).
Figure 36: *Rinorea bullata*; from Descoings 159 (TAN).
Figure 37: Rinorea capuronii; from holotype, SF (Capuron) 27990 (P!).
Figure 38: *Rinorea cornigera*; from isolectotype, *Armand 58* (P).
Figure 39: Rinorea coursii; from holotype, Cours 2006 (P).
Figure 40: Rinorea diversifolia; from isolectotype, Perrier 791 (P).
Figure 41: Rinorea mcphersonii; from holotype, McPherson & Dumetz 14335 (MO).
Figure 42: Rinorea mandrarensis; from isolectotype, Humbert 13840 (P).
Figure 43: Rinorea microphylla; from holotype, Perrier 2230 (P).
Figure 44: Rinorea monticola; from lectotype, Boivin s.n. (P).
Figure 45: Rinorea mutica; from isolectotype, Richard 968 (P).
Figure 46: *Rinorea pauciflora*; from isolectotype, *du Petit Thouars s.n.* (P).
Figure 47: Rinorea pauciflora f. latidentata; from isolectotype, Humbert 13862 (P).
Figure 48: *Rinorea pauciflora* f. *sempervirens*; from lectotype, Humbert 6477 (P).
Figure 49: Rinorea rubra; from isolecotype, Boivin s.n. (P).
Figure 50: Rinorea sahafarensis; from holotype, SF (Capuron) 24529 (P).
Figure 51: Rinorea sambavensis; from holotype, Lowry & Rabenantoandro 5197 (K).
Figure 52: Rinorea ternifolia; from isolecotype, Perrier 14169 (P).
Figure 53: Rinorea urschii; from isolecototype Perrier 5060 (P).
Figure 54: Rinorea verticillata; from isolectotype, Perville 322 (P).
Figure 55: Rinorea vohemarensis; from holotype, SF (Capuron) 27456 (P).
Figure 56: Distribution of *Rinorea mcphersonii*, *R. cornigera*, *R. urschii*, *R. diversifolia*, *R. rubra*, *R. monticola*, and *R. microphylla*.
Figure 57: Distribution of *Rinorea coursii*, *R. vohemarensis*, *R. ambanizanensis*, *R. capuronii*, *R. mutica*, *R. pauciflora f. sempervirens*, *R. sambavensis*, *R. analavelensis*, and *R. antsalovensis*. 

Key: *Rinorea coursii* (■); *R. vohemarensis* (●); *R. ambanizanensis* (◇); *R. capuronii* (■); *R. mutica* (◇); *R. pauciflora f. sempervirens* (▲); *R. sambavensis* (◇); *R. analavelensis* (●); *R. antsalovensis* (◇).
Figure 58: Distribution of Rinorea auriculata, R. allorgeae, R. bullata, R. mandrarensis, R. boinensis, R. pauciflora f. latidentata, R. ternifolia, R. sahafarensis, and R. verticillata.
Chapter 5.

Phylogeny of *Rinorea* (Violaceae) in Madagascar: more evidence that dispersal has been the most important process in the assembly of the Malagasy flora

Introduction.

Madagascar is one of the world’s great biodiversity hotspots, and while the flora is not completely known, it is estimated that there are 10,000–12,000 species of plants in Madagascar, roughly 85% of which are endemic (Koechlin, 1972; Schatz, 1996; Gautier and Goodman, 2003). Of the nearly 4,200 species of trees and shrubs, 96% are endemic (Schatz, 2001). Important factors contributing to the floristic diversity and high rates of endemism include: the tectonic history and relative isolation of Madagascar, a wide variety of geologic substrates, a variable topography, and climatic gradients—including some very steep east-west moisture gradients (Wells, 2003; Jury, 2003; Yoder and Nowak, 2006; Du Puy and Moat, 2003).

The phytogeographic affinities of the Malagasy flora have been studied using comparative taxonomic approaches (Humbert, 1959; Dejardin et al., 1973; Leroy, 1978; Phillipson, 1996). These and other studies have shown that the Malagasy flora has its strongest affinity to the flora of Africa but that it also contains floristic elements in common with Southeast Asia, India, Sri Lanka, Australia, and other source areas (Schatz, 1996). Both vicariance and long-distance dispersal have been invoked to account for the origin of paleoendemic
and neoendemic taxa, respectively, but it is generally agreed that long-distance dispersal of plant propagules to Madagascar has been the more important process in the development of the flora (e.g., Janssen et al., 2008; Gautier and Goodman, 2003; Briggs, 2003; Schatz, 1996).

Yoder and Nowak (2006) and Briggs (2003) have summarized the most recent estimates for the timing of the break up of Madagascar from adjacent landmasses: Madagascar-India-Antarctica drifted east from Africa 158–160 Ma (million years ago), Madagascar (still attached to India) arrived at its current position relative to Africa 130–118 Ma, and India separated from Madagascar 84–96 Ma. Invoking vicariance to explain the African elements in the Malagasy flora (i.e., a shared Gondwanan flora, which was present in situ and later diversified when Madagascar separated from Africa) is inconsistent with the fact that the diversification of modern flowering plant families had not yet taken place (e.g., Gautier and Goodman, 2003). In addition, much of the Malagasy flora present during the mid- to late Cretaceous probably changed drastically as Madagascar drifted north through an arid subtropical zone during the Paleocene and Eocene (Wells, 2003).

Others have advocated biotic exchange between Africa and Madagascar via a continuous land bridge that lasted from ca. 45–25 Ma (e.g., McCall, 1997). Supporters of the African-Malagasy land bridge hypothesis cite evidence from cores taken from the Davie Fracture Zone, which seem to indicate sedimentation from above-water islands into the Mozambique Channel. However, Krause et al. (1997) were skeptical of this interpretation and presented geologic evidence that suggests a generally constant width for the
Channel since the late Cretaceous, with periodic narrowing since the mid-Oligocene. In a simple, but forceful argument against a land bridge, Simpson (1950, cited in Krause et al., 1997) stated that the “existence of such a route would have made dispersal of many [mammal] groups practically certain and determinate, which is contrary to the given biogeographic data.” Other hypotheses of continuous land bridges between Madagascar and South America, Antarctica, and India are even more tenuous (Krause et al., 1997). Finally, fossil-calibrated molecular phylogenetic studies in both animal and plant groups provide numerous examples for the origin of lineages after the separation of Africa and Madagascar (e.g., Janssen et al., 2008 and citations therein).

Long-distance dispersal of plant propagules to Madagascar from Africa and other source areas—including India and Southeast Asia—is a more likely hypothesis to explain the African and Asian floristic affinities of many taxa in the Malagasy flora. At its narrowest point, Madagascar is separated by the Mozambique Channel from Africa by 430 km. Large rivers that frequently flood (e.g., Ruvuma, Zambeze, Save) can raft propagules far out into the Mozambique Channel towards Madagascar. The volcanic islands of the Comoro Islands, Bassas da India, and Europa that emerged ca. 8 Ma could have served as “stepping stones” between Africa and Madagascar (Krause et al. 1997). Also, the submerged Davie Ridge and continental shelves may have been partially exposed as sea levels dropped during climatic oscillations since the Paleocene, thereby narrowing the Channel and facilitating floristic
exchanges between Africa and Madagascar (Krause et al., 1997; McCall, 1997).

Schatz (1996) provided numerous examples of Southeast Asia floristic elements in Madagascar that are best accounted for by long-distance dispersal across the Indian Ocean Basin. By the late Eocene or early Oligocene, the Indian subcontinent had drifted far enough north to allow the Southern Equatorial Current to reach the eastern shores of Madagascar with the potential to raft plant propagules from Southeast Asia, India, and Australia (Wells, 2003; Krause et al., 1997). Trade winds and cyclone tracks moving from east to west across the western Indian Ocean Basin have been active for ca. 8 Ma, also allowing for the rafting of propagules toward Madagascar (Krause et al., 1997).

More recently, molecular phylogenetic analyses have provided new lines of evidence to infer the taxonomic affinities and phytogeographic origins of the Malagasy flora. In a review of 53 molecular phylogenetic studies that included Malagasy plant taxa, Yoder and Nowak (2006) reported that 36% of Malagasy taxa showed a sister relationship to African taxa, and that 15% and 10% showed a sister relationship to Southeast Asian and South Asian taxa, respectively. Patterns of relationships recovered in species-level molecular phylogenies of Malagasy species often show the signature of long-distance dispersal. In many phylogenetic reconstructions, Malagasy species are resolved in clades with other African and/or Asian species, or Malagasy clades are resolved in sister relationships to African and/or Asian clades (e.g., Cyathea (Cyatheaceae), Janssen et al., 2008; Polyscias (Araliaceae), Plunkett et al. 2004; Ormocarpum (Fabaceae), Lavin et al., 2000; various Apocynaceae, Meve
and Liede, 2002; *Bridelia*, *Phyllanthus*, and *Uapaca* (Phyllanthaceae), Li et al., 2009; *Begonia* (Begoniaceae), Plana et al., 2003; *Coffea* (Rubiaceae), Cros et al., 1998; *Acridocarpus* (Malpighiaceae), Davis et al., 2002; *Kalanchoe* (Crassulaceae), Gehrig et al., 2001; *Gaertnera* (Rubiaceae), Malcomber, 2002; etc.). Clearly, the very close relationship of so many Malagasy species to African and/or Asian species suggests many independent and recurring episodes of long-distance dispersal to and from Madagascar, in many different plant groups.

The genus *Rinorea* Aubl. (Violaceae) is a pantropical group of shrubs and small trees and is the second largest genus in the family with an estimated 220–260 species (Ballard and Wahlert, unpubl. data). The diversity of species is mostly well known for the Neotropics (49 species; Hekking, 1988), Asia (ca. 30 species; De Muria and Ballard, unpubl. data), and Madagascar (ca. 45 species, this volume, Chapters 1, 3, and 4). The number of species in Africa is not well known, but it is estimated to be between 110 and 150 species (Achoundong, 1996; Wahlert and Ballard, unpubl. data).

As currently circumscribed, *Rinorea* is not a monophyletic group. Molecular phylogenetic studies in the family have placed *Rinorea uxpanapana* with *Hybanthus* (Feng, 2005). Also, the two species *Rinorea virgata* and *R. heteroclita* are distantly related to the core *Rinorea* clade and are to be transferred back to the earlier generic name *Scyphellandra* (Feng, 2005; Ballard et al., unpublished data). Other molecular phylogenies have shown the genus *Fusispermum* to be basalmost in the Violaceae, with the divergent *Rinorea apiculata* group interior to *Fusispermum*. Then, interior to the *Rinorea apiculata*
group is the “core” *Rinorea* and the remaining Violaceae. Figure 1 summarizes the pattern of relationships that have been recovered in different molecular phylogenetic studies using both chloroplast and nuclear DNA regions (Wurdack and Davis, 2009; Tokuoka, 2007; Feng, 2005). This study focuses on the Old World species in the “core” *Rinorea* group. A Neotropical origin for both *Rinorea* and Violaceae is suggested by the basal phylogenetic position of the Neotropical species of *Rinorea* and the genus *Fusispermum*, as well as the generic diversity of Violaceae in the New World (14 of 23 genera and six of eight lineages of the polyphyletic genus *Hybanthus*) (Tokuoka, 2007; Ballard, 2009; Feng, 2005).

No genus-wide infrageneric classification has been proposed for *Rinorea*. Hekking (1988) grouped the Neotropical species into three informal groups, and preliminary revisionary work in the Asian taxa suggests that there are eight morphological groups possibly deserving infrageneric recognition if supported by further phylogenetic evidence (De Muria and Ballard, unpubl. data). An infrageneric classification for a number of African and Malagasy *Rinorea* was proposed by Engler (1904) and elaborated upon by Brandt (1914) and de Wildeman (1920), but there are some significant problems with these classifications. A proposed infrageneric classification for the African and Malagasy species based on morphometric analysis and phylogenetic reconstruction, supports recognition of 11 infrageneric groups, six of which contain species from Madagascar (this volume, Chapter 2). Table 7 summarizes the infrageneric taxa and informal groups of African and Malagasy *Rinorea* referred to throughout this study. Five sections (see Chapter 2) contain
Malagasy species that are closely related to—or conspecific with—species in
Africa (Rinorea sect. Ilicifoliae, sect. Squamosae, sect. Arboreae, sect. Ellipticae, and sect. Angustifoliae; Chapter 2). A sixth sect. is the Malagasy and Comorian endemic Verticillatae, which contains 26 species (Wahlert and Ballard, 2008; this volume, Chapter 4).

A reliable chromosome count for Rinorea is not yet available (2n = 24, 48?), nor are there any fossils that are referable to the Violaceae (Feng, 2005). Instead, inferences of the biogeographic history of Malagasy Rinorea depend on evidence from taxonomic studies and phylogenetic relationships. A newly revised classification for African and Malagasy species (Chapter 2, this volume) provides for more explicit biogeographic hypotheses to explain the origins of the Malagasy Rinorea. As Leroy (1978) pointed out: “...any judgment concerning floristic affinities...depends greatly upon taxonomic concepts.”

In this study we asked three questions: 1) What are the phylogenetic relationships and biogeographic affinities of Malagasy Rinorea? 2) Do phylogenetic reconstructions in Malagasy Rinorea indicate the directionality of dispersal into or out of Madagascar? and 3) How do the taxonomic and biogeographic affinities of Malagasy Rinorea compare to the flora of Madagascar as a whole?

Materials and Methods.

TAXON SAMPLING. The use of Fusispermum and two species in the Rinorea apiculata group as outgroup taxa was based on Tokuoka (2007) and
Feng (2005). Seventy-five ingroup accessions, representing 48 unique taxa were included in the ingroup. Six Neotropical species were included that represent exemplars from the three informal groups of Hekking (1988). Eight Asian accessions were included in the study, representing five of eight putative morphological groups (De Muria and Ballard, unpubl. data), with geographic sampling from southern China, Thailand, peninsular Malaysia, and Borneo. Heavy taxon sampling of African and Malagasy species included 61 accessions from each of the 11 infrageneric groups identified by Wahlert (unpubl. data). Voucher information and geographic origin are given in Appendix A.

**DNA Extraction, Amplification, and Sequencing.** The extraction of DNA, amplification, and sequencing used the same protocols given in Chapter 2, this volume.

**Phylogenetic Analyses.** Sequences were aligned manually using BioEdit (Hall, 2007). Gaps in the alignment arising from insertions or deletions (indels) were coded using the Simple Indel Coding algorithm of Simmons and Ochoterena (2000), as implemented in FastGap (Borchsenius, 2009). Maximum parsimony (MP) analyses were conducted on each data partition (i.e., trnL intron/trnL-trnF spacer, trnD-trnE spacer, and coded gap matrix) and a combined matrix in PAUP* v4.0b10 (Swofford, 2003) using a heuristic search strategy with TBR branch swapping, 1,000 random addition replicates, saving one tree per replicate, steepest descent off, and MULTREES in effect. All characters were equally weighted and unordered. Internal branch support of
phylogenetic trees from each analysis was estimated with 100 bootstrap (BS) replicates (Felsenstein, 1985) using a full heuristic search with TBR branch swapping, 10 random stepwise addition replicates, and MULTREES in effect. Combinability of the two chloroplast data sets (\textit{trnL} intron/\textit{trnL-trnF} spacer and \textit{trnD-trnE} spacer) was assessed using the Incongruence Length Difference (ILD) test (Farris et al., 1994), implemented in PAUP* v4.0b10 (Swofford, 2003) as the Partition Homogeneity Test. The test was conducted using 1,000 partition replicates, each with 10 random addition replicates, and TBR branch swapping. The best-fit model of nucleotide substitution was estimated using Modeltest (Posada and Crandall, 1998) for each of the two chloroplast partitions and the combined matrix using PAUP* v4.0b10 (Swofford, 2003). Maximum likelihood (ML) analyses were conducted for each data partition and the combined matrix using GARLI v0.951b (Zwickl, 2006), using a model of GTR + \Gamma + I, as recommended by Zwickl (2006), with base frequencies estimated by Modeltest (Posada and Crandall, 1998), and all other options set to default values. Branch support of ML searches was estimated using GARLI v0.951b (Zwickl, 2006), with 100 BS replicates.

**RECONSTRUCTION OF ANCESTRAL AREAS.** Reconstruction of the ancestral areas of common ancestors to clades containing Malagasy species was conducted under a criterion of maximum parsimony. Fitch parsimony optimization was conducted using MacClade v.3 (Maddison and Maddison, 1992) with area occurrences for each taxon appended to the DNA sequence matrix. Characters were unordered and unweighted, and character state
reconstructions were made on a strict consensus parsimony tree. An accelerated transformation (ACCTRAN) optimization was used to explore the most parsimonious ancestral area reconstruction of nodes leading to clades containing both Malagasy and African species (Swofford and Maddison, 1987).

Results.

**PHYLOGENY.** The aligned length of the three data partitions (\(trnL\) intron/\(trnL-trnF\) spacer, \(trnD-trnE\) spacer, and gap matrix), tree scores, and estimated models of molecular substitution are summarized in Table 8.

Maximum parsimony analysis yielded 74 most parsimonious trees of length 747 steps, which are summarized in a strict consensus cladogram (Figure 59). Three basal clades containing Neotropical species correspond to Hekking’s (1988) three informal infrageneric groups ‘Apiculata’, ‘Rinorea’, and ‘Pubiflora’. A clade containing all Paleotropical species sampled in this study was highly supported (100% BS). Twelve large subclades were recovered within the Paleotropical clade, but relationships among clades were weakly supported. Eleven clades correspond to the eleven infrageneric groups of African and Malagasy species recognized in Wahlert (Chapter 2, this volume), most with strong BS support for each subclade (ranging from 83% to 100%; Figure 59).

Five of the 12 Paleotropical clades contain both African and Malagasy species: *Ilicifoliae*, *Squamosae*, *Arboreae*, *Ellipticae*, and *Angustifoliae*. A clade consisting of the Malagasy and Comorian endemic species of *Rinorea* subsect.
Verticillatae was highly supported (100% BS) and showed a moderately supported (82%) sister relationship to a clade containing all eight accessions of Asian taxa (83% BS).

Five clades in the phylogeny contain only Africa species: Cycloglossae, Brachypetalae, Subintegrifoliae, Dentatae, and Crassiflorae, and were all resolved with very strong bootstrap support in both MP and ML analyses (BS 99–100%; Figures 59 and 60). The species composition of each African clade corresponds to the infrageneric groups that have been identified (this volume, Chapter 2). The same African clades contain species occurring in East Africa that either did not disperse to Madagascar (or the Comoro Islands), or did disperse but did not successfully establish reproducing populations or later became extinct. Such biogeographic scenarios highlight the randomness of rare, long-distance dispersals between Madagascar and Africa (or other source areas).

Results from the ILD test did not indicate significant conflict between the two chloroplast data partitions ($p = 0.267$). The GTR + $\Gamma$ + I model was selected as the best-fit model of nucleotide substitution for both chloroplast data partitions and the combined matrix (Table 8). The two data sets were therefore combined and analyzed as a single matrix in a ML analysis. The best ML tree had a -ln likelihood score of 7196.8840 (Figure 60). The resulting ML tree is 100% congruent with the MP tree as far as species composition of each clade, but had slightly better resolution of nodes among Paleotropical subclades and terminal taxa (Figures 59 and 60).
BIOGEOGRAPHIC RECONSTRUCTIONS OF MALAGASY AND COMORIAN SPECIES.

Based on a most parsimonious reconstruction on the MP tree using ACCTRAN optimization in MacClade, the ancestral area of the common ancestor of all Paleotropical taxa sampled in the study was resolved as Africa (Node 1; Figure 61). This complements the Neotropical area of origin hypothesized for *Rinorea* as a whole: the ancestor of the Paleotropical species was likely the result of an ancient dispersal from the Neotropics to Africa. Biogeographic reconstructions of each of the six infrageneric groups that contain Malagasy species are given below.

*Ilicifoliae Clade*. The *Ilicifoliae* clade corresponds to sect. *Ilicifoliae* (Chapter 2). The clade is moderately well supported in both MP and ML analyses (94% MP bootstrap (MPB) and 89% ML bootstrap (MLB), respectively). The five accessions of *R. ilicifolia* from mainland Africa are in different areas within the clade, rendering the species non-monophyletic. The three accessions of *R. spinosa* from Madagascar and the Comoro Islands form a well supported monophyletic group and are resolved as a derived lineage within the *Ilicifoliae* clade. The reconstructed ancestral area for the node leading to the branching of African species and Malagasy/Comorian species was resolved as Africa (Node 2; Figure 61). Further, the three accessions of *Rinorea spinosa* share a 122 bp deletion in the *trnD-trnE* spacer region. Thus, *R. spinosa* cannot be the result of a simultaneous dispersal to both Madagascar and the Comoro Islands from Africa, as this would require a parallel 122 bp
deletion in both colonists. Instead, the colonist arrived in Madagascar from Africa and later dispersed to the Comoro Islands, or vice-versa.

**Squamosae Clade.** The *Squamosae* clade recovered in both analyses was highly supported (99% MPB; 100% MLB). The six accessions resolved in the clade belong to a morphologically distinct infrageneric group not previously recognized in Engler (1904) or Brandt (1914) but now given formal rank as sect. *Squamosae* (Chapter 2). The *R. squamosa* group contains ca. six species with a distribution throughout tropical Africa, Madagascar, and the Comoro Islands. Given the more derived position of the clade containing the Malagasy and Comorian accessions of *R. squamosa*, an African origin is inferred for the group, with subsequent dispersal to Madagascar and the Comoro Islands. There are no synapomorphic substitutions or indels that would indicate the pattern of dispersal (i.e., from Africa to Madagascar and then to the Comoro Islands, or vice-versa, or a simultaneous dispersal to both Madagascar and the Comoro Islands). The area reconstruction for the ancestor to *R. squamosa* suggests an origin in Africa with subsequent dispersal to Madagascar and/or the Comoro Islands (Node 3; Figure 61). The occurrence of *R. squamosa* in the Comoro Islands and several small islands in the Mozambique Channel (Wahlert, pers. obs.), as well as the semi-woody capsules, suggests that the species could have dispersed via ocean currents.

**Arboreae Clade.** The *Arboreae* clade was recovered as a well supported monophyletic group (92% MPB; 91% MLB), and corresponds taxonomically to
the sect. *Arboreae* recognized in Chapter 3. The clade is further divided into two clades: one containing five accessions from Madagascar and the Comoro Islands, and the other containing three accessions from mainland Africa. The taxa in the Malagasy/Comorian clade share three synapomorphic indels, and phylogenetic reconstructions show *Rinorea arborea* to be paraphyletic (Figures 59 and 60). The reconstructed ancestral area for the node leading to the branching of African species and Malagasy/Comorian species was resolved as equivocal (Node 4; Figure 61). Thus, there are two likely scenarios: 1) the group had an origin in Africa and later dispersed to Madagascar and/or the Comoro Islands, or 2) the group had an origin in Madagascar and later dispersed to Africa, perhaps via the Comoro Islands. As with *Rinorea squamosa*, *R. arborea* has a woody capsule and occurs on several islands in the Mozambique Channel, suggesting dispersal via ocean currents.

*Ellipticae Clade*. The *Ellipticae* clade was resolved as a highly supported monophyletic group (97% MPB and MLB). The *R. elliptica* group contains relatively few taxa (ca. six) with a distribution in tropical East Africa, northern and western Madagascar, and the Comoro Islands (this volume, Chapter 2). The clade containing *Rinorea elliptica*, *R. pugionifera*, and *R. greveana* from Madagascar and the Comoro Islands was highly supported (100% MPB; 99% MLB). The derived position of the Malagasy and Comorian clade, the presence of five synapomorphic substitutions, and an inferred ancestral area of Africa for the *Ellipticae* group suggests an origin in Africa with subsequent dispersal to Madagascar and/or the Comoro Islands (Node 5; Figure 61).
Angustifoliae Clade. The *Angustifoliae* clade, containing three accessions of *Rinorea angustifolia* from Madagascar and three closely related accessions from mainland Africa, was highly supported (both MPB and MLB 100%). Taxonomically, *R. angustifolia* and the ca. 20 closely related species are highly distinctive and are placed in sect. *Angustifoliae* (this volume, Chapter 2). The more derived position of the three Malagasy accessions, and an ancestral area of the Angustifoliae ancestor in Africa, suggests an African origin and later dispersal to Madagascar (Node 6; Figure 61). Species in the *Angustifoliae* are conspicuously absent in the Comoro Islands, suggesting a direct dispersal to Madagascar, bypassing the Comoro Islands as a “stepping stone.” However, ancestors may have been present in the Comoro Islands, having gone extinct there.

Verticillatae and Asian Clades. The *Verticillatae* clade was highly supported in both analyses (100% MPB and MLB). The clade is congruent taxonomically with sect. *Verticillatae*, a group endemic to Madagascar and the Comoro Islands (Wahlert and Ballard, 2008). A clade containing all eight accessions of Asian taxa sampled in this study was moderately supported (83% MPB; 89% MLB). Preliminary revisionary work on the Asian species suggests eight morphologically divergent morphological groups, with species distributed across a large area from southern India and Sri Lanka east to Queensland, Australia, Papua New Guinea, and Micronesia (absent in New Caledonia), and from the Philippines and southern China south to Thailand, Malaysia, and
Indonesia (De Muria and Ballard, unpubl. data). More work is needed to understand infrageneric groupings of Asian species and the phylogenetic relationships among groups.

The monophyly of the Asian clade, and the sister relationship to sect. *Verticillatae*, were completely unexpected results. Not only do all Asian species have an alternate leaf arrangement (compared to opposite leaf arrangement in sect. *Verticillatae*), but they also lack any morphological characteristics that would suggest a relationship to any African or Malagasy group (Wahlert and Ballard 2008). Ancestral area reconstruction of the common ancestor to the *Verticillatae*-Asian clade was equivocal in parsimony reconstructions (Node 7; Figure 61). This ambiguity suggests three hypotheses to explain the historical biogeography of the *Verticillatae*-Asian clade: 1) the most recent common ancestor of the two groups dispersed from Africa to Madagascar and then another dispersal event occurred eventually to Asia following diversification on Madagascar, 2) the most recent common ancestor dispersed from Africa to Madagascar and immediately (or well before diversification there) a second dispersal event occurred to Asia, or 3) the most recent common ancestor dispersed first from Africa to Asia (possibly India or peninsular Malaysia) and then back-dispersed to Madagascar. These alternative hypotheses are addressed in greater depth below.

**Dispersal from Africa to Madagascar, and then to Asia.** If, in Hypotheses 1 and 2, the most recent common ancestor of the *Verticillatae*-Asian clade first dispersed to Madagascar from Africa, then the initially dispersed and
successfully established taxon must have remained *in situ* and potentially “evolutionarily quiescent” for a relatively long time in Madagascar in order to accumulate the many substitutions along the branch leading to the *Verticillatae*, much later exploding in a relatively recent species-level radiation (Figure 60). Over the course of diversification in Madagascar, the *Verticillatae* would evolve opposite-leaved phyllotaxy from alternate-leaved phyllotaxy (from the African ancestor). In Hypothesis 1, the Asian species are derived from a *Verticillatae* ancestor dispersed sometime after initial diversification on Madagascar, invoking the evolution of a morphological reversal back to alternate-leaved phyllotaxy, as well as a tremendous amount of divergence away from the typical morphologies presently found in Malagasy taxa. The greater rate of taxonomic diversification of Asian taxa is reflected in the topology of the Asian clade compared to the comb-like topology of the *Verticillatae*, making this hypothesis unlikely (Figure 60). While the *Verticillatae* shows variability among species, the group is uniform in sectional-level characters (e.g., morphology of the androecium and fruit, floral architecture, ovule number, and type of inflorescence). In contrast, the Asian species show great variability in sectional level characters—similar to the level of infrageneric diversity seen among the African and Malagasy groups. This may be the result of differential rates of evolution in the sister lineages. Beyond the differences in morphological evolution, the stepping-stone pattern of Africa to Madagascar to tropical Asia with relatively long diversification time between the latter two regions would be expected to produce a paraphyletic assemblage of Malagasy taxa in which a
monophyletic tropical Asian clade is embedded. This is not found in the results, suggesting that Hypothesis 1 is not currently supported by the data at hand.

In Hypothesis 2, the dispersal event from Madagascar to Asia would have necessarily been almost instantaneous with the Africa-to-Madagascar event or relatively soon after successful establishment of the initial dispersal propagule to Madagascar (at least some time before diversification on that island). These “almost simultaneous” dispersal events would result in descendant sister clades from the most recent common African ancestor, as observed in the phylogenetic structure of the Old World species. If the ancestor did first disperse to Madagascar (particularly before ca. 45 Ma), then the Indian subcontinent could have served as a “stepping stone” for continued dispersal eastwards (Krause et al., 1997). However, as the Indian subcontinent continued to drift north, the east to west ocean currents and trade winds across the Indian Ocean Basin would not favor dispersal eastwards to Asia from Madagascar (Krause et al., 1997).

*Dispersal from Africa to Asia, and then to Madagascar.* Hypothesis 3 explaining the *Verticillatae*-Asian sister-group relationship would involve first a dispersal event to India, peninsular Malaysia or another Asian region from Africa. Subsequent eastward dispersal and diversification across the entire region in Southeast Asia would have been facilitated by reproductive isolation and varied niches for the diversification of the ca. eight morphological groups of Asian *Rinorea*. Perhaps much later, one ancestor from within one of the several Asian groups would have back dispersed westwards to Madagascar to give rise
to the *Verticillatae*. Dispersal to Madagascar in the last ca. 12 million years would have been facilitated as currents and winds would favor dispersal west across the Indian Ocean Basin.

Also, this hypothesis would only incur one change of state from alternate to opposite phyllotaxy, whereas Hypothesis 1 would involve two state changes. While it is possible that phyllotaxy may be under the genetic control of a simple “on-off switch”, opposite-leaved phyllotaxy is a derived condition in the Violaceae seen in only two other Neotropical lineages. Thus, from the standpoint of state changes in phyllotaxy, an Asian origin of the *Verticillatae* is the more parsimonious model. In addition, the taxonomic diversification of the *Verticillatae* at the species level would have been very slow had it been the ancestor of all Asian *Rinorea*, especially given the sectional-level taxonomic diversity found in Asian *Rinorea*. While there are examples of different rates of diversification between phylogenetic sister-pairs, in this case, there has been a highly asymmetrical amount of diversification between Asian *Rinorea* and the *Verticillatae*. Cladistically, however, a long residence time in tropical Asia, with diversification in that region, followed by a dispersal event to Madagascar, would lead theoretically to a paraphyletic assemblage of Asian taxa within which a monophyletic *Verticillatae* would be nested. The support for sister-group status in the two regions, Madagascar and tropical Asia, is relatively strong. Nevertheless, the weak sampling of Asian taxa in the phylogenetic analysis does not allow this hypothesis to be ruled out, as future inclusion of the several taxa found in India and peninsular Malaysia may reveal paraphyly in Asian *Rinorea* relative to Malagasy *Verticillatae*. 
More data are needed to test various competing hypotheses for the origins of the Verticillatae-Asian clade. Added sampling of species in the *R. javanica* and *R. macrantha* groups (which are found in peninsular Malaysia as well as island archipelagoes to the east and south) may resolve the Verticillatae as nested among the Asian clade. Chromosome counts could also provide a valuable data set to test biogeographic hypotheses. In the absence of fossils referable to the Violaceae, biogeographic inferences of the Verticillatae-Asian clade will have to rely on phylogenetic and other data sets to reconstruct the historical biogeography of this enigmatic group.

**Comparison of Taxonomic Affinities to the Malagasy flora.** Another objective of this study was to compare the taxonomic affinities of Malagasy *Rinorea* to the flora as a whole. There are ca. 45 species of *Rinorea* in Madagascar, and they are placed in six infrageneric groups (this volume, Chapters 2, 3, and 4). Taxonomically, at least 90% of the Malagasy *Rinorea* species are endemic—a number very much in agreement with 84% estimated for the flora as a whole (Schatz, 1996; Gautier and Goodman, 2003). Of the ca. 45 Malagasy species of *Rinorea*, 42% show taxonomic affinity—or conspecificity—with African species, also in agreement with the 36% of Malagasy taxa that showed a sister relationship to African taxa in other studies (Yoder and Nowak, 2006). Finally, 55% of Malagasy *Rinorea* (i.e., species in the Verticillatae) show a taxonomic affinity to Asian species, significantly more
than the 25% of Malagasy taxa that showed a sister relationships to Southeast Asian and Asian taxa in Yoder and Nowak (2006).

**Discussion.**

The primary goal of this study was to understand the phylogenetic relationships and biogeographic origins of Malagasy and Comorian *Rinorea*. Phylogenetic reconstructions show that the Paleotropical species form a monophyletic group, which is further divided into 11 clades of African and Malagasy species, and a twelfth clade composed exclusively of Asian taxa (Figures 59 and 60). Five clades are composed of both African and Malagasy species, and five other clades contain only African species. For four of the five clades that contains both African and Malagasy species (*Ilicifoliae*, *Squamosae*, *Ellipticae*, and *Angustifoliae*) reconstruction of the ancestral area of the common ancestor suggests an origin in mainland Africa and subsequent dispersal to Madagascar. In the *Arboreae* group, the ancestral area of the most recent common ancestor was equivocal.

It is well established that the Malagasy flora contains African and Asian floristic elements, as well as affinities to taxa from other source areas, including some very distant ones. Dejardin et al. (1973), Leroy (1978), and Schatz (1996) cite abundant taxonomic evidence for Malagasy taxa with closely related species that are widely distributed throughout the Paleotropics and Indian Ocean Basin. In recent years, many molecular phylogenetic studies at the species level confirm close relationships of taxa disjunctly distributed in
Madagascar, Africa, Asia, India, and other areas. The timing of the break-up of Africa and Madagascar, the drifting of Madagascar through subtropical arid zones in the Paleocene and Eocene, and the lack of geologic evidence for continuous land bridges do not support vicariance as an important process in the assembly of the Malagasy flora. Even the Malagasy tree ferns in the genus *Cyathea*—members of an ancient family dating back to 145 Ma—have been shown to be the result of three separate colonization events and subsequent diversification in Madagascar that occurred in the Miocene (Janssen et al., 2008).

Many phylogenetic studies of Malagasy plants show that long-distance dispersal to Madagascar has been more important than vicariance processes, with new colonists arriving continuously and often diversifying into the neoendemic taxa characteristic of the flora. Since Madagascar drifted away from Africa 158–160 Ma, the tectonic history of the area has had significant impacts on the local climate, causing fluctuations between humid and dry periods (Wells, 2003). As the climate changed, species either became extinct or found a suitable refuge, such as in the arid spiny bush of southwest Madagascar (Koechlin, 1972). Changing climate and floristic composition would provide available niches for newly-arriving colonizers to occupy and perhaps diversify. As for Malagasy *Rinorea*, the evidence presented here indicates at least four independent dispersal events from Africa to Madagascar. The biogeographic history and ancestral areas of the *Arboreae* and *Verticillatae* clades is equivocal.
Molecular phylogenetics will continue to shed light on the relationships and origins of both Malagasy plant species and the flora as a whole. Other fascinating questions, such as the timing of lineage divergence, diversification, and the origin of the Verticillatae clade, await answers from the synthesis of studies using molecules, morphology, cytology, and fossils. More species-level phylogenies of pantropical plant groups containing Malagasy species (accompanied by clear taxonomic concepts) are needed to address questions of relationships and origins of the Malagasy species. However, what has become very clear from many studies is that dispersal has been the most important biogeographic process shaping the Malagasy flora, with many species showing a close affinity to species in Africa, as well as more distant source areas in the Indian Ocean Basin and beyond.
Literature Cited


Appendix A. List of taxa used in this study with voucher specimen information.

*Fusispermum laxiflorum* Hekking: *McPherson 10218* (MO), Panama. 
*Rinorea amplexicaulis* (Grey-Wilson) Wahlert (1): *Abeid et al. 1274* (MO), 
Table 7. Summary of infrageneric taxa and informal groups of African and Malagasy *Rinorea*.
CI = Comoro Islands.

<table>
<thead>
<tr>
<th>Taxon or informal group name</th>
<th>Author</th>
<th>Number of species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Brachypetalae</em></td>
<td>Engler, 1904</td>
<td>ca. 45</td>
<td>Africa</td>
</tr>
<tr>
<td><em>Subintegrifoliae</em></td>
<td>Engler, 1904</td>
<td>ca. 3</td>
<td>Africa</td>
</tr>
<tr>
<td><em>Verticillatae</em></td>
<td>Engler, 1904</td>
<td>26</td>
<td>Madagascar &amp; CI</td>
</tr>
<tr>
<td><em>Illicifoliae</em></td>
<td>Engler, 1904</td>
<td>ca. 20</td>
<td>Africa, Madagascar &amp; CI</td>
</tr>
<tr>
<td><em>Dentatae</em></td>
<td>Engler, 1904</td>
<td>ca. 50</td>
<td>Africa</td>
</tr>
<tr>
<td><em>Crassiflorae</em></td>
<td>M. Brandt, 1914</td>
<td>ca. 6</td>
<td>Africa</td>
</tr>
<tr>
<td><em>Cycloglossae</em></td>
<td>M. Brandt, 1914</td>
<td>ca. 3</td>
<td>Africa</td>
</tr>
<tr>
<td><em>Angustifoliae</em></td>
<td>Wahlert, in prep.</td>
<td>ca. 20</td>
<td>Africa &amp; Madagascar</td>
</tr>
<tr>
<td><em>Ellipticae</em></td>
<td>Wahlert, in prep.</td>
<td>ca. 4</td>
<td>Africa, Madagascar, &amp; CI</td>
</tr>
<tr>
<td><em>Squamosae</em></td>
<td>Wahlert, in prep.</td>
<td>ca. 5</td>
<td>Africa, Madagascar, &amp; CI</td>
</tr>
<tr>
<td><em>Arboreae</em></td>
<td>Wahlert, in prep.</td>
<td>8</td>
<td>Africa, Madagascar, &amp; CI</td>
</tr>
</tbody>
</table>
Table 8. Summary of aligned sequence length, and MP and ML tree scores of the three data partitions analyzed in this study.

PI = parsimony informative; CI = consistency index; RI = retention index; RC = rescaled consistency index; model = model of nucleotide substitution as estimated using Modeltest (Posada and Crandall, 1998); -ln L = -log likelihood score of best ML tree.

<table>
<thead>
<tr>
<th></th>
<th>trnL intron/</th>
<th>trnD-trnE</th>
<th>gap</th>
<th>combined</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>trnL-trnF</td>
<td>spacer</td>
<td>matrix</td>
<td></td>
</tr>
<tr>
<td>spacer</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>aligned length</td>
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<td>693</td>
<td>152</td>
<td>1804</td>
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<tr>
<td>constant</td>
<td>768</td>
<td>540</td>
<td>0</td>
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<td>PI positions</td>
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<td>84</td>
<td>95</td>
<td>291</td>
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<td>CI</td>
<td>0.886</td>
<td>0.806</td>
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<td>0.425</td>
<td>0.608</td>
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<tr>
<td>model</td>
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<td>GTR + Γ + I</td>
<td>n/a</td>
<td>GTR + Γ + I</td>
</tr>
<tr>
<td>-ln L</td>
<td>2863.5096</td>
<td>2302.6546</td>
<td>n/a</td>
<td>7196.8840</td>
</tr>
</tbody>
</table>
Figure 59: Strict consensus cladogram of 74 most parsimonious trees. Bootstrap percentages > 50% are shown above branches; Malagasy groups highlighted in gray.
Figure 60: Maximum likelihood phylogram from combined chloroplast data set. Bootstrap percentages > 50% are shown above branches; Malagasy groups highlighted in gray.
Figure 61: Maximum likelihood phylogram showing nodes leading to branches containing African and Malagasy *Rinorea* lineages. The ancestral states of nodes 1–3, 5, and 6 were resolved as African, whereas nodes 4 and 7 were equivocal.
Chapter 6.

Conclusions

Prior to this study, the most recent revision of *Rinorea* from Madagascar and the Comoro Islands was that of Perrier in 1949, which recognized 32 taxa. This current revision increases the number of taxa to 41. There is reason to expect that the total number of new taxa will increase as new collections from distant or difficult sites are deposited in herbaria. The genus *Rinorea* in Madagascar shows a rate of endemism in excess of 90%, a value very much in line with the flora. Thirty-seven percent of the Malagasy species show a phylogenetic affinity to African species, and the remaining 55% are more closely related to Asian species than they are to African or other Malagasy species. These values are very much in accord with recent phylogenetic studies showing taxonomic affinity of Malagasy taxa to species in other source areas, including some very distant areas (e.g., Borneo).

A revised infrageneric classification based on morphometric and molecular phylogenetic analyses for African and Malagasy *Rinorea* is proposed. The scheme is based on Engler (1904) and Brandt (1914), but has several significant differences. The classification continues to rely on androecial characters, which have been shown to be highly predictive. In summary, 11 infrageneric taxa are recognized: one section is maintained (*Cycloglossae*), five subsections are elevated to the rank of section (*Brachypetalae, Crassiflorae, Dentatae, Ilicifoliae, Subintegrifoliae*, and *Verticillatae*), and four sections are newly erected (*Arboreae, Angustifoliae, Ellipticae*, and *Squamosae*).
Phylogenetic and morphological analyses show that the 41 taxa of \textit{Rinorea} in Madagascar can be classified into six sections. Four sections contain one or a few species: \textit{R.} sects. \textit{Angustifoliae, Ellipticae, Squamosae}, and \textit{llicifoliae}, whereas the other two sections are much more diverse, with sect. \textit{Arboreae} containing eight species and sect. \textit{Verticillatae} with 26 species. \textit{Rinorea} sect. \textit{Verticillatae} is endemic to Madagascar and the Comoro Islands and is the most species rich group of Malagasy \textit{Rinorea}. Given its divergent morphology, its sister relationship to the Asian species was an unexpected result. The other five groups all have obvious affinities to mainland African species, including some shared species among Africa, Madagascar, and the Comoro Islands (e.g., \textit{R. squamosa} and \textit{R. arborea}).

A first estimation of phylogeny for \textit{Rinorea} was reconstructed from chloroplast DNA sequences with extensive sampling across the geographic distribution and morphological breadth of the genus. Results show a basal grade of Neotropical \textit{Rinorea}, consisting of three clades concordant with those morphological groupings identified in Hekking (1988). The Paleotropical species were resolved as a monophyletic group with an ancestral area in Africa. The Paleotropical clade is further resolved into 12 subclades: the 11 groups of African and Malagasy \textit{Rinorea} identified above and an Asian clade. Additional sampling of Asian taxa is needed to better understand infrageneric groupings among Asian species and to test biogeographic hypotheses concerning the origin of sect. \textit{Verticillatae} (and the Asian taxa).

Biogeographic reconstructions of ancestral areas of the common ancestor of each of the six Malagasy clades show that there have been at least
four independent dispersals from Africa to Madagascar. The historical biogeography and taxonomic affinities of sects. *Arboreae* and *Verticillatae* are equivocal and could not be inferred with much confidence. Three hypotheses to account for the *Verticillatae*-Asian clade were examined: 1) dispersal first from Africa to Madagascar, followed by diversification on the island, then a second dispersal event to Asia; 2) nearly “simultaneous” dispersal events from Africa to Madagascar and then to tropical Asia; and 3) dispersal from Africa to Asia, with diversification, then a back-dispersal event to Madagascar. Cladistic expectations of a sister-group relationship between Madagascar and tropical Asia would only be met with the second hypothesis. Paraphyly would be expected in the first and third hypotheses, with the *Verticillatae* paraphyletic to a monophyletic Asian clade in hypothesis 1 and a paraphyletic set of Asian groups with monophyletic *Verticillatae* embedded among them in the third hypothesis. However, caution was advised in rejecting the third hypothesis, given the weak taxon sampling accomplished for the highly diverse Asian species group. Moreover, very different rates of evolution in the two regions and the much greater heterogeneity of morphological evolution in the Asian taxa suggest that the third scenario is still plausible but as yet improperly tested.

Conservation assessments according to IUCN standards show many Malagasy species to be Vulnerable or Critically Endangered. *Rinorea microphylla*, *R. verticillata*, and perhaps a few others are very likely extinct in the wild. Personal observations while conducting field work for this project reveal the enormous challenges facing conservation efforts in Madagascar. The country is among the poorest in Africa, and there has been tremendous impact
on the natural vegetation over the last ca. 1800 years of the human presence on the Island. Threats to the biota include anthropogenic fire, grazing, mining, conversion to plantations, and agriculture. Even some protected areas face heavy impact on their perimeters.

There remains much work to be done on the African species, and the newly proposed infrageneric classification will facilitate these studies. Also, taxonomic studies are needed to understand infrageneric groupings, species diversity, and relationships among the Asian species. More taxon sampling of the Asian species may better resolve their relationship to sect. *Verticillatae*. Continued study of morphology, anatomy, and chromosome numbers across the genus is needed to strengthen the clades recovered in the molecular phylogeny, particularly on deeper branches. Finally, the relationship of the divergent Neotropical *Rinorea apiculata* group, consistently basal to the rest of the genus and anomalous in it, needs more work, as the former may be best accommodated by generic segregation or recognition at the subgeneric level. For now, taxonomic revisions are proceeding on a regional basis, but the present study has made a contribution to the eventual understanding of species diversity, relationships, and biogeography for the whole genus.