KEW BULLETIN (2020) 75: 12
DOI 10.1007/S12225-020-9866-6

ISSN: 0075-5974 (print)
ISSN: 1874-933X (electronic)

Taxonomic revision of *Rinorea ilicifolia* (Violaceae) from Africa and Madagascar

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Summary. The uncertain taxonomic circumscription between *Rinorea ilicifolia* (Welw. ex Oliv.) Kuntze and *R. spinosa* (Boivin ex Tul.) Baill. has led to considerable confusion when attempting to identify the two species. The plants from mainland Africa have typically been determined as *R. ilicifolia* while the plants in Madagascar and the Comoro Islands have been variously assigned to *R. spinosa*, *R. ilicifolia*, or *R. ilicifolia* subsp. *spinosa* (Boivin ex Tul.) Grey-Wilson. A third taxon from east Africa, *R. ilicifolia* var. *amplexicaulis* Grey-Wilson, has auriculate leaf bases and a mostly discrete distribution from *R. ilicifolia*, suggesting a greater degree of divergence than is indicated by its taxonomic rank of variety. To better understand the circumscription among these three taxa, we performed multivariate and discriminant analyses of six quantitative variables measured from herbarium specimens. Based on results from these analyses, we deemed there was insufficient morphological divergence to maintain *R. ilicifolia* and *R. spinosa* as separate species. Instead, we recognise a single species, *R. ilicifolia*, composed of three subspecies: *R. ilicifolia* subsp. *ilicifolia* in mainland Africa, *R. ilicifolia* subsp. *spinosa* in Madagascar and the Comoro Islands, and *R. ilicifolia* subsp. *amplexicaulis* (Grey-Wilson) Wahlert, comb. et stat. nov. from Tanzania and Burundi. Here we provide a taxonomic revision of *R. ilicifolia*, a distribution map and preliminary risk of extinction assessment using IUCN Red List categories and criteria for the three subspecies. We also propose a change of status for *Rinorea* [unranked] *Ilicifoliae* Engl. to the rank of section, an action supported by phylogenetic and morphological evidence. The new section includes *R. ilicifolia* and 13 other taxa from mainland Africa. Lectotypes are designated for the section and for *Alsodeia spinosa* Boivin ex Tul., and a second-step lectotype is selected for *Alsodeia ilicifolia* Welw. ex Oliv.

Key Words. Comoro Islands, conservation, morphometrics, *Rinorea spinosa*, taxonomy.

Introduction

Rinorea Aubl. is the second most species-rich genus in the Violaceae and is composed of c. 250 species of shrubs and small trees occurring in humid and seasonally dry forests across the tropics (Ballard *et al.* 2014). In mainland Africa, there are approximately 150 species, with Cameroon and Gabon being particularly rich in species (Robson 1960; Tennant 1963; Grey-Wilson 1986; Velzen *et al.* 2015). Madagascar is another centre of endemism for the genus with 27 accepted species, 80% of which are endemic (Madagascar Catalogue 2018). The Comoro Islands harbour six species that are shared with either Africa or Madagascar or both (Wahlert 2010).

Alsodeia spinosa Boivin ex Tul. from Madagascar and *A. ilicifolia* Welw. ex Oliv. from Angola were described at nearly the same time (but see below), with Baillon (1886) and Kuntze (1891) making the respective new combinations under *Rinorea*: *R. spinosa* (Boivin ex Tul.) Baill. and *R. ilicifolia* (Welw. ex Oliv.) Kuntze. Since then, the name *R. ilicifolia* has been applied to the African plants, whereas specimens from Madagascar and the Comoro Islands are variously identified or annotated as *R. spinosa* (e.g. Bâthie 1954; Robson 1960; R. Capuron in sched.), *R. ilicifolia* subsp. *ilicifolia* (e.g. Tennant 1963; J.-N. Labat in sched.; Achoundong & Cheek 2005; R. Capuron in sched., C. C. H. Jongkind in sched.), or *R. ilicifolia* subsp. *spinosa* (Boivin ex Tul.) Grey-Wilson (e.g., Grey-Wilson 1981; S. Wohlhauser in sched., L. Gautier & N. Messmer in sched.). The main goal of this study was to re-examine the taxonomic boundaries between *R. ilicifolia* and *R. spinosa* using multivariate and discriminant analyses. We also examined several specimens of *R. ilicifolia* var. *amplexicaulis* Grey-

Accepted for publication 4 February 2020. Published online 29 April 2020

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Wilson from Burundi and Tanzania — an easily recognised taxon with auriculate leaf bases and a mostly non-overlapping geographic distribution from *R. ilicifolia* subsp. *ilicifolia*. These three taxa, along with *R. letouzeyi* Achound., represent the only species with typically spinose leaf margins in *Rinorea* [unranked] *Ilicifoliae* Engl.; the remaining taxa have subentire to serrate margins. Species in *Ilicifoliae* are delimited by various combinations of characters, including: presence or absence of glands on the lower leaf surface, leaf shape, pubescence patterns on young stems and inflorescence axes, morphology of the inflorescence and androecium, and fruit shape.

Results from previous molecular phylogenetic analyses did not resolve species-level relationships among *Rinorea ilicifolia* and other closely related taxa in the informally named Ilicifoliae clade (Wahlert & Ballard 2012; Velzen *et al.* 2015). In both studies, species in the clade were recovered in one of two monophyletic groups that corresponded geographically to a mostly west African subclade and a Madagascar-Comoro Islands-southeastern Africa subclade (Fig. 1). *Rinorea spinosa* and *R. ilicifolia* var. *amplexicaulis* were each resolved in weakly to moderately supported monophyletic groups, while *R. ilicifolia* was polyphyletic, with exemplars of the species recovered in both subclades. Even though results from those studies do not help inform taxonomic circumscription, the pattern of phylogenetic relationships does suggest a peripheral isolates mode of speciation. In the case of *R. spinosa*, a southern or eastern African ancestor of *R. ilicifolia* likely dispersed to Madagascar (or the Comoro Islands) at some time in the last 4.5 million years, giving rise to *R. spinosa* and rendering *R. ilicifolia* as non-monophyletic (Velzen *et al.*, unpubl. data). Alternatively, the plastid and nuclear markers used in those studies may not have been variable enough to resolve species-level relationships.

There is no genus-wide infrageneric classification for *Rinorea*, but Wahlert (2010) has classified the African and Malagasy species into 11 infrageneric groups that correspond in part to groupings proposed by Engler (1904). Among these is *Rinorea* [unranked] *Ilicifoliae*, which was represented by the Ilicifoliae clade in phylogenetic studies and shown to be a well-supported clade based on analyses of plastid and nuclear DNA sequences (Wahlert & Ballard 2012; Velzen *et al.* 2015). In the study of Wahlert & Ballard (2012), branch support for the Ilicifoliae clade was 92% maximum parsimony (MP) bootstrap (BS), 90% maximum likelihood (ML) BS, and 0.99 Bayesian inference (BI) posterior probability (PP), with similarly high support in Velzen *et al.* (2015): 91% ML BS and 1.0 BI PP. Fig. 1 shows a MP consensus cladogram of members of the Ilicifoliae clade based on a combined analysis of taxa and data used in both studies (phylogenetic analysis follows Wahlert & Ballard 2012).

Members of the Ilicifoliae clade are readily circumscribed from other African and Malagasy infrageneric groups by a combination of morphological characters, including: alternately arranged leaves, narrowly cylindrical thyrsoid inflorescences, spherical-ovoid flower buds, a zygomorphic calyx with sepals prominently nerved longitudinally, a weakly zygomorphic corolla, staminal tube with the margin of the tube deeply sinuate between insertion of anthers, six ovules per ovary, and elliptic-ovoid to obovoid capsules containing six yellow-brown seeds. Truly actinomorphic floral symmetry has not been observed for any species in the Violaceae, and magnified observation of flower dissections are needed to reveal the zygomorphy of the calyx and corolla in most species of *Rinorea*, including *R. ilicifolia* (Wahlert *et al.* 2014). There is now ample evidence from molecular phylogenetic studies and morphological characters to recognise Engler's *Rinorea* [unranked] *Ilicifoliae* at the rank of section.

Materials and Methods

A total of 132 herbarium specimens from P and MO (herbarium abbreviations from Thiers, continuously updated) representing *Rinorea ilicifolia*, *R. spinosa*, and *R. ilicifolia* var. *amplexicaulis* were measured for morphometric analyses (Appendix). Six quantitative traits were scored from each specimen: petiole length, lamina length and width, number of secondary vein pairs, inflorescence length, and peduncle length. Examination of flowers and fruits were made from an additional c. 100 herbarium specimens from BM, G, K, PRE, TAN, TEF, and WAG. Study of c. 50 specimens found that floral morphology (shapes and sizes of the sepals, petals, androecium, and gynoecium) was not variable. Likewise, no differences were detected in the morphology of fruit and seed from c. 50 specimens of *R. ilicifolia* and *R. spinosa* (fruiting specimens of var. *amplexicaulis* were not available); flower and fruit characters were therefore excluded from analyses.

For multivariate and linear discriminant analyses, we measured 62 herbarium specimens of *Rinorea ilicifolia*, 64 of *R. spinosa*, and six of var. *amplexicaulis* (in the analyses, the three taxa are referred to as *ilicifolia*, *spinosa*, and *amplexicaulis*, respectively). Differences among the six measured quantitative morphological traits were assessed using parametric analysis of variance (ANOVA) and pairwise comparisons of means using Tukey-Kramer multiple comparisons tests when ANOVA yielded a significant F statistic. All residuals were examined for the assumption of normality using quantile-quantile plots and histograms. Levene's test implemented the "car" package

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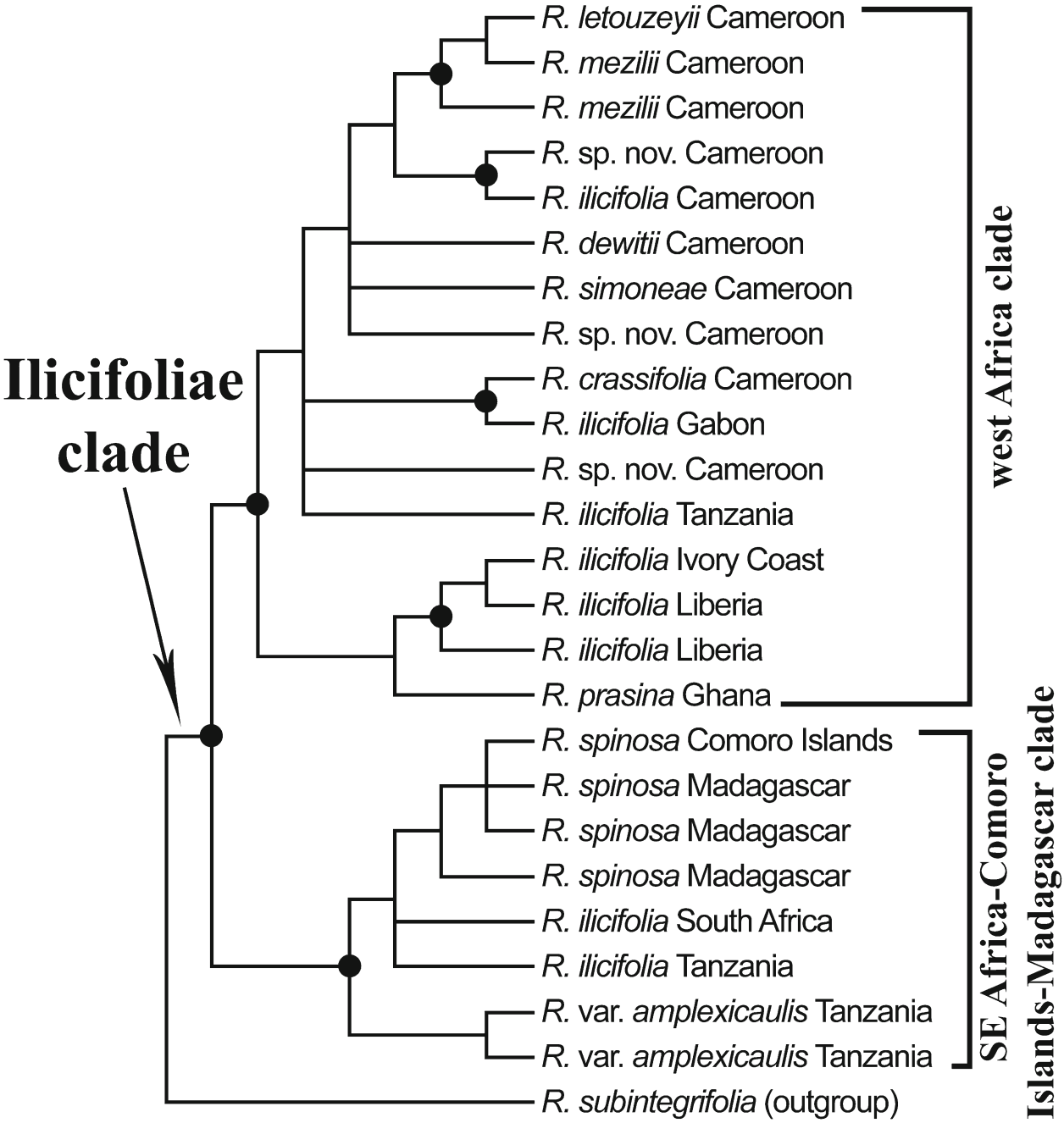

Fig. 1. Consensus cladogram of phylogenetic relationships in *Rinorea* sect. *Ilicifoliae* (Engl.) Wahlert based on Wahlert & Ballard (2012) and van Velzen *et al.* (2015). Black circles indicate combined branch support of ≥ 95% MP bootstrap and ≥ 0.99 BI posterior probability.

(Wuertz 2010) and was used to test for homogeneity of variance.

The ability of combined morphological measurements to distinguish *Rinorea ilicifolia*, *R. spinosa*, and *R. ilicifolia* var. *amplexicaulis* was examined using a linear discriminant analysis (LDA). LDA is a multivariate classification method that generates classification rules by maximising between-species variability in the data (James & McCulloch 1990; Henderson 2006) and was implemented using the MASS package (Venables & Ripley 2002). Taxonomic identification and a priori group assignment for LDA was based on geography for *R. ilicifolia* (Africa) and *R. spinosa* (Madagascar and Comoro Islands), and on leaf morphology for var. *amplexicaulis* (leaf base auriculate vs leaf base cuneate to rounded in *R. ilicifolia* and *R. spinosa*). LDA loadings were examined to understand which traits may be useful for distinguishing species. All analyses were conducted using the R statistical programming environment (R Development Core Team 2013).

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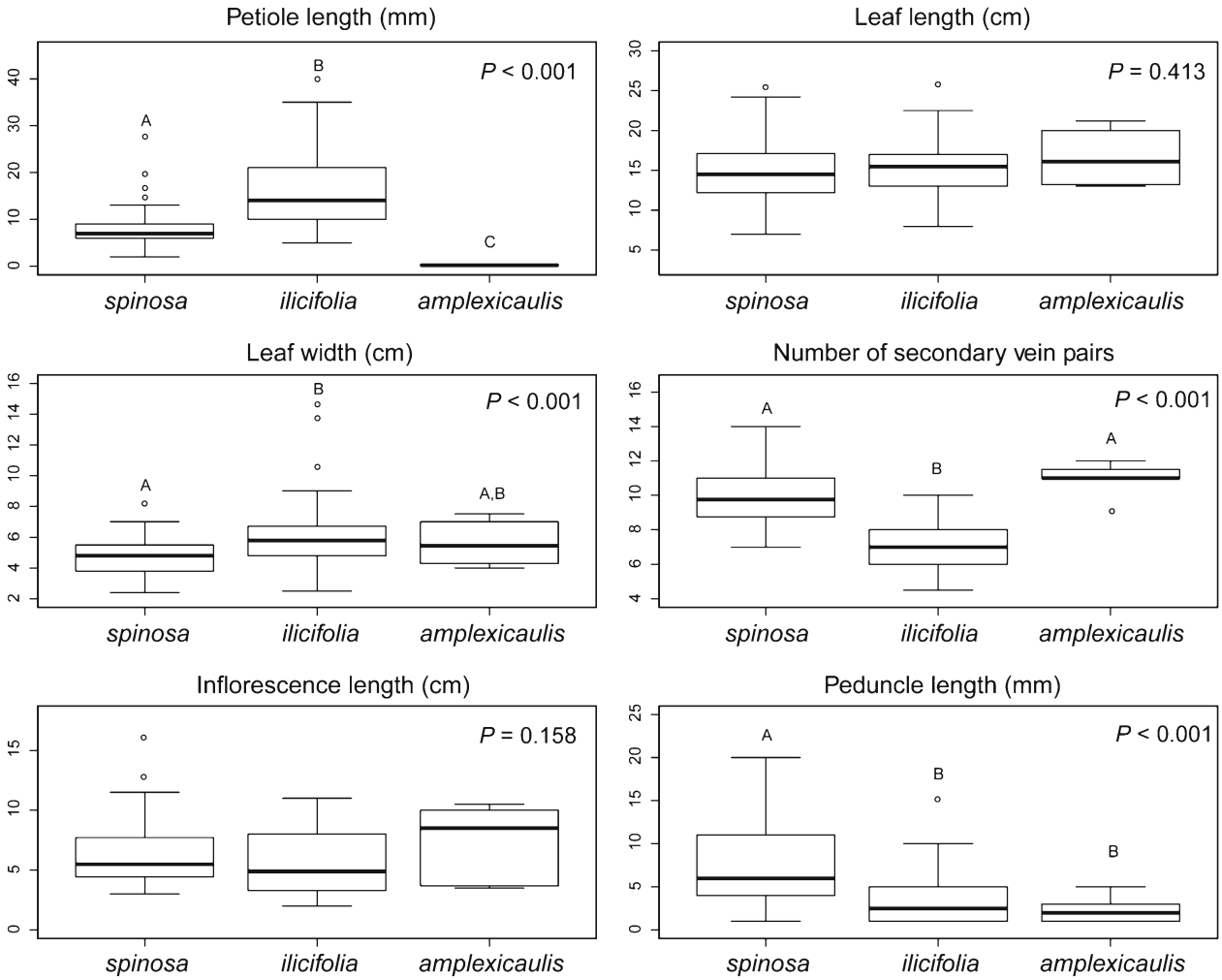

Fig. 2. Box plots showing the results of multivariate analyses of the six characters measured in the analyses.

Assessments of the preliminary risk of extinction were based on the IUCN Red List categories and criteria (IUCN 2012). The extent of occurrence (EOO) and area of occupancy (AOO) were based on 2 km^2 cells and were calculated using the Geospatial Conservation Assessment Tool (GeoCAT, Bachman *et al.* 2011). All specimens cited have been seen by the first author; abbreviations used in the list of specimens examined include: SF (*Service Forestier* [collector series]), RN (*Réserves Naturelles*: collector series or protected area), RS (Réserve Spéciale), PN (Parc National), NP (National Park), and RNI (Réserve Naturelle Intégrale). Our recognition of taxa at the rank of subspecies is based on the concept of Rietz (1930), where "a subspecies is a population of several biotypes forming a more or less distinct regional facies [appearance] of a species (p. 354)."

Results

Results of the multivariate analyses are summarised in Fig. 2. and Table 1. Leaf length ($P = 0.413$) and the length of the inflorescence ($P = 0.158$) did not vary among the three taxa. *Rinorea ilicifolia* had slightly wider leaves than *R. spinosa*, while *R. ilicifolia* var. *amplexicaulis* did not differ from either one ($P < 0.001$). Both *R. spinosa* and var. *amplexicaulis* had a similar number of secondary vein pairs ($P < 0.001$), while *R. ilicifolia* had fewer, and *R. spinosa* had longer peduncles than the other two taxa ($P < 0.001$). The only character that varied among all three taxa was petiole length ($P < 0.001$).

A scatterplot of the best two discriminant functions showed only moderate separation among the three taxa (Fig. 3). The first discriminant function achieved the most separation (92.06%), separating *spinosa* from *ilicifolia* and *ilicifolia* from *amplexicaulis*; the second discriminant function achieves fair separation of *spinosa* from *amplexicaulis*, accounting for 9.94% of the separation observed. The first discriminant function was mainly influenced by number of secondary vein pairs and leaf lamina width (Table 1), while the second discriminant function was mostly influenced by leaf lamina width followed by peduncle length (Table 2). The LDA misclassification rate was 7.5%

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Table 1. Mean values (range) for the six morphological characters measured in this study. Coefficients showing the results of multivariate analyses using morphological variables. LD1 and LD2 give the respective loadings for each variable in each discriminant function.

Character	*spinosa*	*ilicifolia*	*amplexicaulis*	Tukey-Kramer multiple comparison test	Standardised coefficient	
					LD1	LD2
Petiole length (mm)	8.1 (2 – 27)	15.8 (5 – 40)	2	All different	0.104	-0.082
Lamina length (cm)	14.9 (7 – 25.2)	15.5 (8 – 25.6)	16.6 (13 – 21.2)	None different	-0.046	0.106
Lamina width (cm)	4.8 (2.4 – 8.3)	6.2 (2.5 – 14.6)	5.6 (4 – 7.5)	*ilicifolia* differs from *spinosa*; *amplexicaulis* not different from either	0.164	0.183
Secondary vein pairs	9.7 (7 – 14)	7.2 (4.5 – 10)	10.9 (9 – 12)	No difference between *spinosa* and *amplexicaulis*; *ilicifolia* differed from both	-0.482	0.034
Inflorescence length (cm)	6.4 (3 – 16)	5.6 (2 – 11)	7.5 (3.5 – 10.5)	None different	-0.048	0.085
Peduncle length (cm)	0.8 (0.1 –3.2)	0.3 (0.1 – 1.5)	0.2 (0.1 – 0.5)	No difference between *ilicifolia* and *amplexicaulis*; *spinosa* differed from both	-0.094	-0.160

(Table 2) indicating the allocation rule functioned reasonably well.

Discussion

Over the course of this study, examination of herbarium specimens and morphometric analyses have not revealed any single morphological character nor any combination of characters that reliably separate *Rinorea ilicifolia* from *R. spinosa*. Neither have we discovered any characters of flowers, fruits, or seeds that differentiate the three infraspecific taxa examined in this study. The lack of consistent and observable morphological distinctiveness between *R. ilicifolia* and *R. spinosa* becomes evident when they are examined side by side. Indeed, the pattern of variation between *R. ilicifolia* and *R. spinosa* aligns well with observations of a subspecies by Rietz (1930), where "...it is not always possible to tell from an isolated specimen in a collection to which subspecies it belongs, if the locality of the specimen or the range of the subspecies is unknown..." and that "...subspecies are best described by a statistical survey of the forms constituting it." With only slight trends in a few vegetative differences — which are nevertheless correlated with geographic distribution — and lacking any further evidence of reciprocal monophyly or ecological differentiation, we recognise a widely distributed *R. ilicifolia* composed of three subspecies: subsp. *ilicifolia* in Sub-Saharan Africa, subsp. *spinosa* in Madagascar and the Comoro Islands, and subsp. *amplexicaulis* in Tanzania and Burundi.

Taxonomic Treatment

Rinorea sect. **Ilicifoliae** (*Engl.*) *Wahlert*, **comb. & stat. nov.**

http://www.ipni.org/urn:lsid:ipni.org:names:77205198-1

Rinorea [unranked] *Ilicifoliae* Engl., *Bot. Jahrb. Syst.* 33: 133 (Engler 1904). Type: *Rinorea ilicifolia* (Welw. ex Oliv.) Kuntze (lectotype, designated here).

DISTRIBUTION. Sub-Saharan Africa, northern and western Madagascar, Mayotte and Comoros.

NOTES. *Rinorea* sect. *Ilicifoliae* includes 16 taxa: *Rinorea abbreviata* Achound. & Bos, *R. afzelii* Engl. var. *afzelii, R. afzelii* var. *pubescens* Taton, *R. breteleri* Achound., *R. comperei* Taton, *R. crassifolia* (Baker f.) De Wild., *R. dewitii* Achound., *R. ilicifolia* subsp. *ilicifolia, R. ilicifolia* subsp. *spinosa, R. ilicifolia* subsp. *amplexicaulis* (Grey-Wilson) Wahlert [name based on *R. ilicifolia* var. *amplexicaulis*; see below], *R. keayi* Brenan, *R. letouzeyi* Achound., *R. mezilii* Achound., *R. prasina* (Stapf) Chipp, *R. simoneae* Achound. and *R. wagemansii* Taton. Further systematic study within *Rinorea* sect. *Ilicifoliae* is

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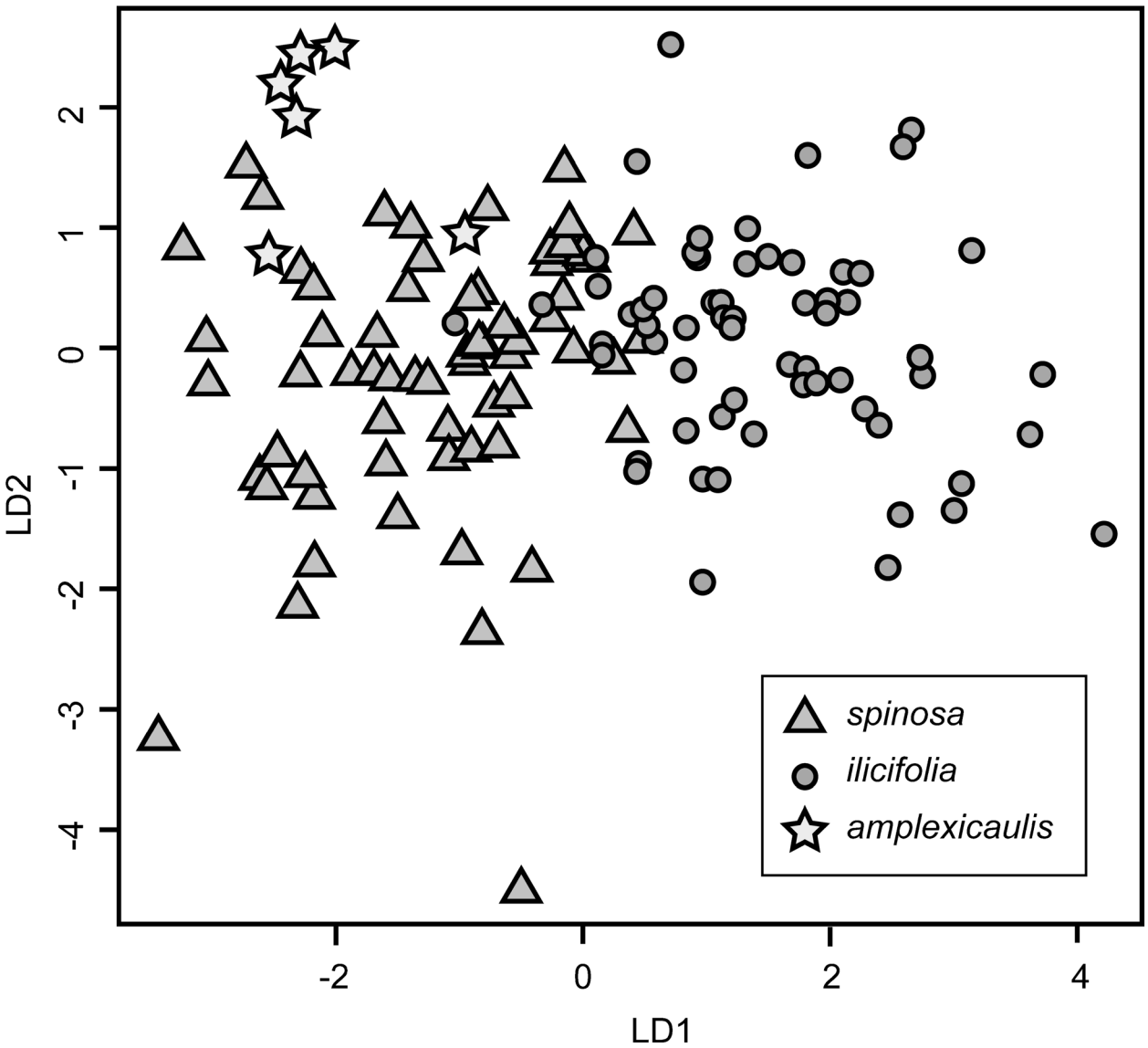

Fig. 3. Taxon assignment of 132 *Rinorea* individuals using linear discriminant analysis (LDA). The analysis is based on six morphological characters. LDA axis 1 accounts for 92.06% group separation; axis 2 accounts for the remaining 9.94% group separation.

needed to better understand relationships and species diversity among the included taxa.

1. Rinorea ilicifolia (*Welw. ex Oliv.*) *Kuntze* (1891: 42).

Shrub to 6 m tall, usually much less, evergreen; young branches glabrous to sparsely puberulent. *Leaves* alternate, subsessile to petiolate; petioles 2 – 40 mm long, glabrous to minutely puberulent or rarely pubescent, canaliculate on adaxial surface; stipules quickly caducous,

Table 2. Classification of discriminant analysis of six characters with three predefined groups and the number of correctly classified cases based on LDA classification rule.

	Classified group			
Predefined group	*spinosa*	*ilicifolia*	*amplexicaulis*	Total
R. ilicifolia	2	60	0	62
R. spinosa	58	5	1	64
R. ilicifolia var. *amplexicaulis*	2	0	4	6

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lanceolate-deltoid, c. 8 – 10 × 1.5 – 2.3 mm, apex acute; lamina elliptic to elliptic-oblong or obovate, 7 – 26 × 2.4 – 9 (– 14.6) cm; glabrous on both surfaces or rarely pubescent on midvein abaxial surface; secondary vein pairs 4 – 14, divergent to ascending; base auriculate or cuneate to rounded; margin spinose, rarely serrate; apex acute to acuminate; domatia absent. *Inflorescence* a terminal, or rarely axillary, narrowly cylindrical panicle-like cyme, 2 – 16 cm long, lateral cymules bearing 2 – 9 flowers, axes glabrous to sparsely puberulent, rarely pubescent; peduncle 0.1 – 3.2 cm long; bracts and bracteoles triangular to ovate-deltoid, 0.8 – 3 × 0.8 – 2.1 mm, often keeled, outer surface glabrous to puberulent, rarely pubescent, margin ciliate, apex acute, often mucronate; pedicels 1 – 2 mm long, articulated at base, glabrous to puberulent, rarely pubescent. *Flowers* fragrant, buds ovoid. *Calyx* zygomorphic, sepals ovate to ovate-elliptic or orbicular, concave, 1.4 – 3.5 × 0.9 – 3.5 mm, carnose, nerved longitudinally, outer surface glabrous to pubescent, margin scarious, entire to ciliate, apex rounded. *Corolla* subzygomorphic, petals oblong-lanceolate to oblanceolate, concave, 2.8 – 4.4 × 0.7 – 2.3 mm, pale yellow, yellow-green, or cream, glabrous, inner surface sometimes puberulent near the middle; margin entire to ciliolate, apex rounded, usually recurved. *Stamens* 2.1 – 3 mm long; filaments connate into a staminal tube, staminal tube 0.2 – 0.4 mm tall, sinuate between insertion of anthers, inner and outer surfaces glabrous; anthers sessile on summit of staminal tube or filamented, filament 0.2 – 0.5 mm long, anther connectives 1.2 – 1.4 × 0.4 – 0.6 mm, glabrous; anther ventral connective scales 1 or 2, ovate, 0.3 – 0.6 × 0.1 – 0.4 mm, scarious, drying brown; anther dorsal connective scales large and conspicuous, ovate-lanceolate, 1.3 – 2 × 0.7 – 1.2 mm, scarious, drying orange-brown, glabrous, margin entire, apex rounded or rarely acute. *Pistil* 2.4 – 3.6 mm long; ovary ovoid, 0.5 – 1 × 0.5 – 1.1 mm, glabrous; ovules 6; style 1.6 – 2.4 mm long, erect, filiform, glabrous. *Fruit* a hard, 3-lobed capsule, dehiscent along 3 sutures, elliptic-ovoid to elliptic-obovoid, 1.2 – 1.9 cm long, 1 – 1.4 cm diam., valve 0.3 – 0.7 cm wide, surface glabrous, verrucose, brown at maturity; calyx persistent at base of mature fruit. *Seeds* 4.5 – 6.5 × 3.6 – 7 mm, irregular-tetrahedral, tan-coloured or yellow with light brown mottling, glabrous.

Key to the subspecies of *Rinorea ilicifolia*

1. Leaves subsessile; petioles ≤ 2(7) mm long; leaf base auriculate . . . . . **1c. R. ilicifolia** subsp. **amplexicaulis**
   Leaves petiolate; petioles 2 – 40 mm long; leaf base cuneate to rounded **2**
2. Petioles 2 – 27 mm long; leaf 2.4 – 8.3 cm wide; secondary vein pairs 7 – 14; peduncle 0.1 – 3.2 cm long; Madagascar and Comoro Islands . . . . . **1b. R. ilicifolia** subsp. **spinosa**
   Petioles 5 – 40 mm long; leaf 2.5 – 14.6 cm wide; secondary vein pairs 4 – 10; peduncle 0.1 – 1.5 cm long; – Sub-Saharan Africa . . . . . **1a. R. ilicifolia** subsp. **ilicifolia**

1a. Rinorea ilicifolia (*Welw. ex Oliv.*) *Kuntze* subsp. **ilicifolia**. *Alsodeia ilicifolia* Welw. ex Oliv. (Oliver 1868: 108). Type: Angola, Pungo Andongo, Barrancos de Catete, Feb. 1857, *Welwitsch* 889 (lectotype LISU, designated by Tennant (1963: 409); second-step lectotype LISU [LISU206098!], designated here; isolectotypes BM [BM000617803!], M [M0109597!], LISU [LISU206100!], PRE0291990-0!).

Rinorea khutuensis Engl. (Engler 1900: 436). *Rinorea ilicifolia* var. *khutuensis* (Engl.) Tennant (1963: 411). Type: Tanzania, Khuta-steppe, Morogoro Distr., 300 m, 1898, *Goetze* 117 (holotype B, destroyed; isotypes BM [BM000617805!], K [K000231036!]).

Rinorea angolensis Exell (1935: 12). Type: Angola, Cuanza Norte, Dondo, near the Cuanza R., 50 m, 15 Sept. 1931, *Gossweiler* 9759 (holotype BM [BM000617969!]; isotypes COI [COI00004969!], K [K000231217!], LISC [LISC000523!], US [US00901726!]).

Leaves petiolate; petioles 5 – 40 mm long; lamina 8 – 26 × 2.5 – 14.6 cm; secondary vein pairs 4 – 10; base cuneate to rounded. *Inflorescence* 2 – 11 cm long; peduncle 0.1 – 1.5 cm long (Fig. 4D).

DISTRIBUTION. *Rinorea ilicifolia* subsp. *ilicifolia* is distributed across Sub-Saharan Africa (Map 1).

SPECIMENS EXAMINED. BURUNDI. Bubanza, Kihanga, ravin Katunguru, 850 m, 6 Nov. 1970, *Lewalle* 4900 (MO); Bubanza, vallée Katunguru, 900 m, 31 Oct. 1974, *Reekmans* 3892 (MO [2 sheets]). **CAMEROON.** Near Nkolbisson, 7 km W of Yaoundé, 750 m, 27 Dec. 1962, *Breteler et al.* (P); N'Kolbisson, c. 8 km W of Yaoundé, 650 m, 27 Dec. 1963, *de Wilde & Duyfjes-de Wilde* 1625 (MO, P, PRE); Nkolbison, 8 km W Yaoundé, au pied la colline de Minlo, Feb – April 1963, *Raynal & Raynal* 9561 (P, 2 sheets). **CENTRAL AFRICAN REPUBLIC.** Sangha Economique Prefecture, Ndakan gorilla study area, 02°22'N, 16°09'E, 350 m, 7 Jan. 1988, *Harris & Fay* 76 (MO); Bamingui-Bangoran, Manovo-Gounda-St. Floris NP, Manovo Creek, 08°13'N, 21°09'E, 590 m, 2 March 1984, *Fay* 6418 (MO, P). **CONGO (BRAZZAVILLE).** Territoire de Mambasa, Ituri Forest, Epulu, Mont Mbia, 01°25'N, 28°35'E, 750 M, 21 Feb. 2001, *Dhego*

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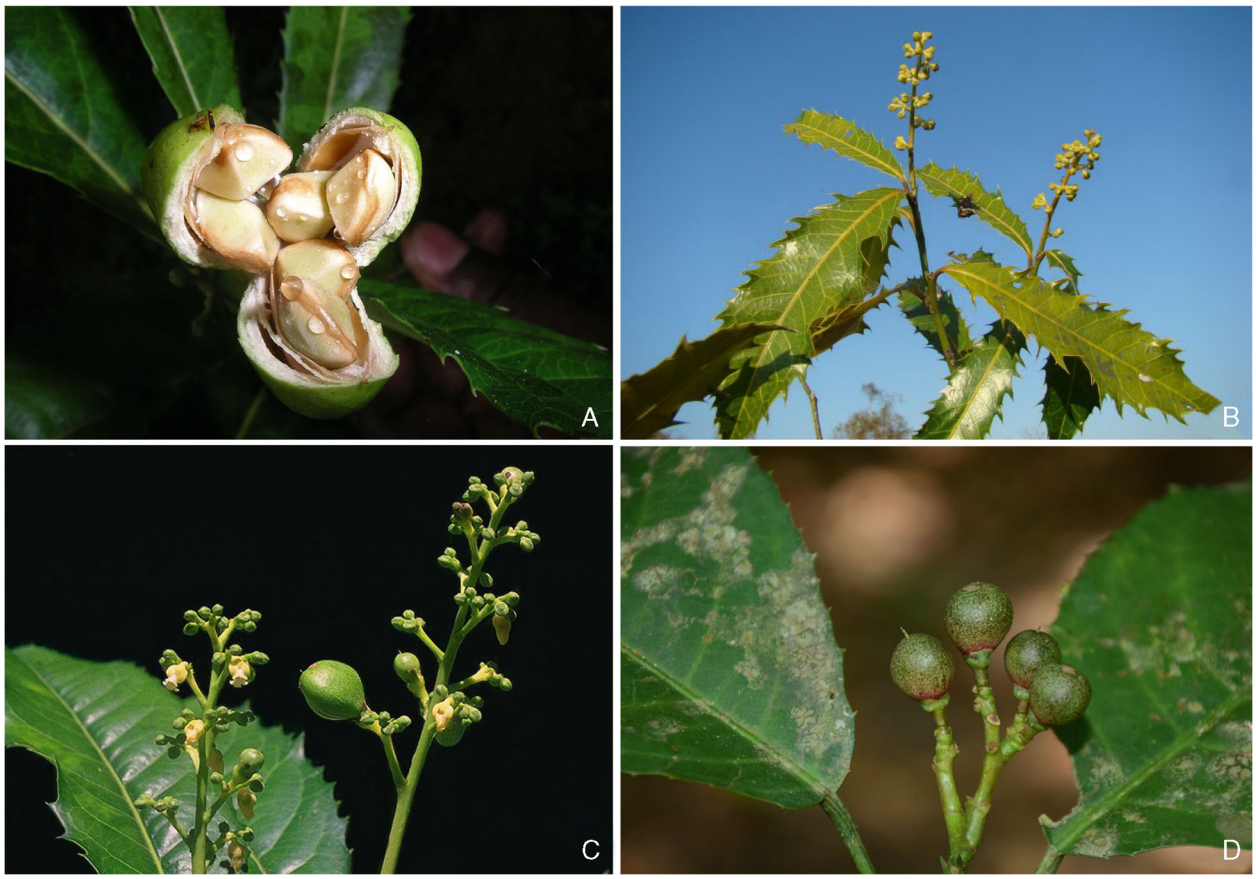

Fig. 4. *Rinorea ilicifolia* subsp. *spinosa* (**A** – **C**). **A** mature fruit (*C. Rakotovao* 4248; Madagascar); **B** inflorescence and habit (*T. H. Andriamihajarivo* 1789; Madagascar); **C** inflorescence with immature fruit and flowers (*G. E. Schatz* 3864; Madagascar); **D** immature fruit of *R. ilicifolia* subsp. *ilicifolia* (*E. Bidault* 2173; Gabon). photos: **A** C. RAKOTOVAO (MO), **B** R. LETSARA (CAS), **C** G. E. SCHATZ (MO), **D** E. BIDAULT (MO).

et al. 592 (MO); Mayama, forêt de Bangou, Dec. 1956, *Koechlin* 3914 or 7262 (P); plateau des cataractes, piste Taba-Mandzakala, région de Kinkala, entre Mandzakala et le pont Voula, 11 Oct. 1968, *Sita* 2656 (P, 4 sheets). **D. R. CONGO.** Forêt de Kinkanga, le long de Inkisi Mbanza-Ngungu, 04°52'S, 15°09'E, 14 June 1978, *Breyne* 3321 (MO); Equateur, Bikoro, Lac Tumba, Île Elua, 17 Sept. 1945, *Léonard* 553 (PRE); Haut-Zaire, at Epulu, along the road between Kisangani and Goma, 750 m, 18 Feb. 1986, *Linder* 3513 (PRE). **ETHIOPIA.** Kefa A. Region, at the Bebeka Coffee Plantation, S of Mezan Tefari, along the track to Gurrafada, about 24 km W of the coffee plantation H. Q., 06°50'N, 35°15'W, 1050 m, 1 Dec. 1984, *Friis et al.* 3919 (MO); Illubabor, about 49 km S of Ganbela, along a track leading to the Gila R., 07°50'N, 34°40'W, 500 m, 25 Feb. 1970, *de Wilde* 6361 (MO). **GABON.** Ogooué-Ivindo, Chantier S. H. M., Layon 'Z, 00°50'N, 12°05'E, 19 Feb. 1988, *Dibata* 418 (P); Région Ogooué-Ivindo, 3 km de la route Koumameyong vers Makokou, c. 00°12'N, 11°55'E, 6 Oct. 1983, *Floret et al.* 1658 (P, 2 sheets); Massif du Chaillu, along road Mimongo-Koulamontou, between Dibandi and Diyanga, 20 – 30 km NE of Mimongo, 01°34'S, 11°44'E, c. 550 m, 27 Nov. 1983, *Louis et al.* 952 (P, PRE); Woleu-ntem, chantier Oveng, 00°47'S, 11°16'E, 2 May 1986, *Louis* 2074 (P); Chantier Oveng, c. 25 km WSW of Mintsie, 00°44'N, 11°22'E, 9 Nov. 1986, *Reitsma et al.* 2584 (MO); Ogooue-Ivindo, Lope Reserve, E of Koumbiane, 00°15'S, 11°40'E, 20 June 1993, *White* 881 (MO); forêt des Abeilles, 40 km SSW of confluence Ogooue-Ivindo, 00°30'S, 12°02'E, 8 Aug. 1993, *Wilks* 2722 (PRE, 2 sheets). **GHANA.** W Afao Hills Reserve, 436 m, 12 Feb. 1952, *Darko* 461 (MO, P); Esen ne Pam Forest Reserve, Oda Road, 26 Nov. 1971, *Enti* 435 (MO); Agriculture Research Station, Kade, 17 March 1972, *Enti* 644 (MO, 2 sheets, PRE); Bia NP and Production Reserve, Game and Wildlife Adufua Camp, S 11 km along main logging road, 06°30'30"N, 03°04'00"W, 150 – 190 m, 29 Feb. 1996, *Merello et al.* 1337 (MO). **GUINEA.** Nzerekore, Mt Nimba, 8 Jan. 1949, *Adam* 3181 (MO, P); Nzérékoré, Koloumba, 24 July 1949, *Adam* 5770 (P); bord à Kourio, 22 Dec. 1905, *Chevalier* 14820 (P); Nzérékoré, E of Nimba Mts, banks of Mien R. on or close to reserve border, 07°40.1'N, 08°19.2'W, 540 m, 14 Dec. 2006, *Jongkind et al.* 7656

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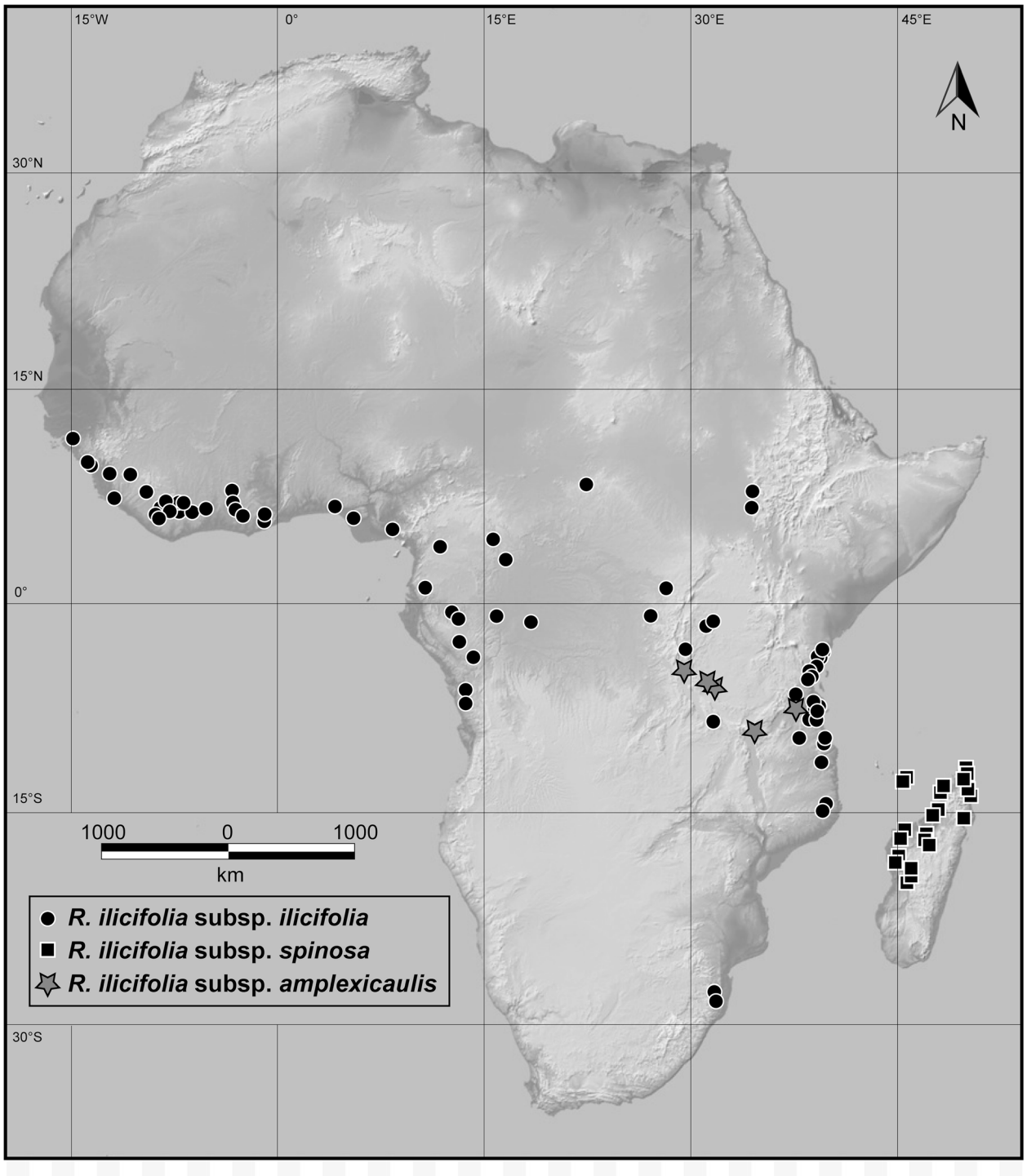

Map 1. Distribution of the three subspecies of *Rinorea ilicifolia* in Africa, Madagascar, and the Comoro Islands.

(P); Nzérékoré, Lola Prefecture, Nimba Mts, inside the WHS, between Bie village and the mountains, 07°40'42"N, 08°20'06"W, 557 m, 29 Oct. 2012, *Jongkind et al.* 11630 (P); Région montagneuse du Nimba, April 1950, *Schnell* 5328 (P). **GUINEA-BISSAU.** Bedanda, 14 Jan. 1962, *Pereira* 2799 (PRE). **IVORY COAST.** 36 km NE of Sassandra, 05°06'N, 05°49'W, 29 Nov. 1968, *Breteler* 6105 (MO, P); bassin de la moyenne Sassandra, 21 – 23 May 1907, *Chevalier* 16421 (P); Bouroukrou, chemin de fer km 92, 20 Dec. 1906 – 20 Jan. 1907, *Chevalier* 16641 (P); sous-préfecture Vavoua, F. C. du Haut-Sassandra, à proximitié de l'ancien chantier de la SIFCI, 07°18'N, 07°01'W, 24 Nov. 1993, *Gautier et al.*

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LG2265 (MO); sous-préfecture Bouaflé, P.N. Marahoué E, forêt-galerie de la Marahoué, 07°05'N, 05°53'W, 9 Jan. 1996, *Gautier et al.* LG2863 (MO). **KENYA.** Utwani Forest, Witu, Dec. 1936, *Abdulla* 3847 (P); Gongoni Forest, Witu, Oct. 1937, *Dale* 3801 (P); Kilifi, Chasimba, 03°44'S, 39°42'E, c. 200 – 220 m, 16 Feb. 1977, *Faden et al.* 77/415 (MO); Kwale Distr., Shimba Hills, Sheldricks's Falls area, 152 m, 2 April 1968, *Magogo & Glover* 632 (PRE); Kwale, Muhaka Forest, 04°20'S, 39°31'E, 40 m, 19 Feb. 1987, *Robertson & Luke* 4544 (MO). **LIBERIA.** Yéképa, route forestière, 1 Feb. 1965, *Adam* 20793 (P, 2 sheets); Yéképa, Mt Bélé road, 3 Oct. 1975, *Adam* 29747 (MO, P); Central Province, near the village Diala, c. 18 km E of Tapeta, 31 March 1962, *de Wilde & Voorhoeve* 3736 (P). **MOZAMBIQUE.** Cabo Delgado, c. 10 km from Nangade on road to Mueda, 11°12'04"S, 39°38'48"E, 359 m, 23 March 2009, *Burrows & Burrows* 11318 (BNRH); Nampula, Mossuril, Serra de Mesa, 250 – 300 m, 19 Feb. 1984, *de Koning et al.* 9747 (MO); Nampula, Eráti, andados 12 km de Namapa para Alua, monte Geovi, 500 m, 8 Jan. 1964, *da Torre & Paiva* 9888 (MO, P, PRE); Cabo Delgado Prov., hunting concession between Pundanhar and Nangade, 10°56'25.5"S, 39°52'46.5"E, 99 m, 18 Nov. 2009, *Goyder et al.* 6088 (P). **NIGERIA.** Benin, Benin, Okomu Forest Reserve, 3.5 miles S of Nikrawa, 12 Dec. 1947, *Brenan* 8491 (P); Calabar, Calabar, Akamkpa Rubber Estate, Calabar River Division, 21 March 1959, *Latilo* 22 (P); Ogun, Omo Forest Reserve, 6 km SE of Etemi, 18 Nov. 1981, *Pilz* 2667 (MO). **SIERRA LEONE.** Kabala, Mt Loma village, Kruto, 6 Feb. 1966, *Adam* 23589 (MO). **SOUTH AFRICA.** Zululand [KwaZulu Natal], Hlatikulu Forest, July 1923, *Boocock* 28 (PRE, 2 sheets]); Zululand [KwaZulu Natal], Ingwavuma, 549 m, s.d., *Dutton & Tinley* 21 (PRE); Natal, Gwaleweni Forest, 610 m, 19 Oct. 1971, *Moll & Nel* 5536 (PRE); KwaZulu Natal, Hlatikulu Forest, N of Jozini, c. 200 m along path from forestry office, 27°20'S, 32°00'E, 500 m, 18 Oct. 2002, *Nowell* 156 (BHO); Zululand [KwaZulu Natal], Ingwavuma Distr., Gwaliweni Forest, 610 m, 10 Aug. 1959, *Tinley* 474 (PRE). **TANZANIA.** Pwani, Rufiji, Kichi Hills, Kungurwe Village, Mkengela Valley, 08°18'S, 38°40'E, 600 m, 22 Sept. 1999, *Abeid & Kibure* 706 (MO); Kigoma Distr., Mt Livandabe [Lubalisi], 05°58'S, 30°02'E, 1100 m, 6 June 1997, *Bidgood et al.* 4325 (K, P); Zanzibar, April – May 1848, *Boivin* s.n. (P); *ibid.*, Sept. 1889, *Sacleux* 862 (P, 6 sheets); Kwale Distr., Mlinga Peak, E Usambaras, 900 m, 7 March 1953, *Drummond & Hemsley* 1452 (K); Lindi, Lindi Rural, Milola, Rutamba Ward, former Rutamba village, Litipo Forest Reserve, c. 8 km from Kinyope, 10°02'47"S, 39°28'20"E, 80 m, 7 Nov. 2005, *Ezrom et al.* 189 (MO); Kagera, Bukoba, Minziro Forest Reserve, Dobero area, N of Nyakabanga, bounded by Kagera R., 01°02'26"S, 31°36'28"E, 1120 m, 16 Oct. 2000, *L. Festo* 817 (MO); Bukoba Distr., Bushenya, 2 April 1948, *J. Ford* 316 (K); Pwani, Rufiji, Mchungu Forest, beside the sea at the mouth of the Rufiji Delta, 07°40'S, 39°17'E, 15 m, 2 Aug – 4 Sept. 1990, *Frontier-Tanzania* 1420B (MO); Tanga, Muheza, Kilulu Hill, 04°46'S, 39°07'E, 200 m, March 1992, *Frontier-Tanzania* 2700 (MO); Rukwa, Sumbawanga Rural, WCS/SHCP Nawinga Camp, Kafukaka Village land, along Nawinga Stream, (tributary of Loasi R.), 08°17'48"S, 31°08'11"E, 1170 m, 12 Nov. 2009, *Gereau et al.* 7100 (MO); Pwani, Mafia Island, Rujifi Distr., Uranzi to Kikuni, 9 m, 13 Aug. 1937, *Greenway* 5081 (PRE); Lindi, Lindi Rural, Mchinga Ward, Kilangala Village, Ruawa Forest Reserve, valley running S from Likonde Ridge, Mpeleganya Valley, 09°43'32"S, 39°32'03"E – 09°44'57"S, 39°33'03"E, 250 – 450 m, 16 Nov. 2003, *C. J. Kayombo et al.* 4678 (MO); Pwani, Rufiji, [Matumbi Hills, Kiwengoma Forest], near WWF Office, 08°18'57"S, 38°57'39"E, 250 m, 19 Sept. 1997, *Kibure* 84 (MO); Pwani, Rufiji, Kichi Hills, Mkengela area, 08°18'S, 38°40'E, 600 m, 22 Sept. 1999, *Kibure* 491 (MO); Pwani, Rufiji, Kichi Hills, near Kungurwe village, 08°17'S, 38°39'E, 600 m, 28 Sept. 1999, *Kibure* 514 (MO); Kele Hill, Mimziro, 1250 m, 20 April 1994, *Longdon* 352 (K); Tanga, Muheza, E Usambara Mts, Kwamtili village, 100 m NW of cocoa factory, 04°55'21"S, 38°43'54"E, 100 m, 20 May 2000, *Mwangoka* 1257 (MO); Pwani, Kisarawe, Kazimzumbwi Forest Reserve, 06°56'41"S, 39°03'14"E, 200 m, 4 June 2001, *Mwangoka & Ali* 2188 (MO); Kilwa, Mbarawala/Uchungwa Forest, N part of forest along ridge, 09°00'35"S, 39°10'51"E, 359 m, 12 July 2008, *Mwangoka et al.* 5843 (MO); Tanga, Muheza, E Usambara Mts, W of Kanyani subvillage of Misozwe, 05°02'44"S, 38°43'44"E, 400 m, 4 April 2009, *Mwangoka & Semng'ombe* 6142 (MO); Tanga, Muheza, Segoma Forest Reserve, S part of forest near Segoma village, 04°59'23"S, 38°46'03"E, 220 m, 29 March 2012, *Mwangoka & Walesi* 7736 (MO); Lindi, Lindi Rural, Litipo Forest Reserve, Lake Lutamba, c. 40 km W of Lindi, 10°03'S, 39°28'E, 240 m, 4 Nov. 1984, *Mwasumbi & Mponda* 12643 (MO); Morogoro, Kanga Mts, 90 km N of Morogoro town, *Mwasumbi & Munyenyembe* 13848 (MO); Pwani, Rufiji, Matumbi Hills, Kiwengoma Forest, 08°19'06"S, 38°56'54"E, 375 m, 10 Oct. 1997, *Phillipson et al.* 4947 (MO); Tanga, Manga Forest Reserve, Frontier Plot no. 29, 05°01'08"S, 38°45'24"E, 165 m, 31 July 1997, *Simon et al.* 9 (MO). **ZIMBABWE.** Imbeya Estates, Garliso Forest, 19 Jan. 1936, *Kleinschmidt* 5 (PRE).

HABITAT. *Rinorea ilicifolia* subsp. *ilicifolia* grows in a wide variety of vegetation types, including primary, second-

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ary and degraded humid and seasonally dry forests, gallery forests, semi-deciduous forests, and thickets; alt. near sea level to 1800 m a.s.l. It has been recorded from different substrates such as sand, limestone, basalt, and clay. Observations of plants in the field and from herbarium specimen labels show that subspecies almost always occurs in the understory of forests or thickets

CONSERVATION STATUS. With an Extent of Occurrence (EOO) of 1.3×10^7 km^2, a minimum Area of Occupancy (AOO) of 292 km^2, and at least 99 recorded localities, *Rinorea ilicifolia* subsp. *ilicifolia* is assigned a preliminary conservation assessment of Least Concern [LC] using the IUCN Red List categories and criteria (IUCN 2012).

PHENOLOGY. This subspecies flowers and fruits between September and April.

VERNACULAR NAMES. The following common names were recorded for subsp. *ilicifolia*: *mtakataka* and *vitakataka* in the Ndengeleko language (*O. A. Kibure* 491 and 514, respectively), *amatodofov*, language unknown (*Dhego et al.* 592), and *umkokomane*, language unknown (*Boocock* 28).

NOTES. In considering the nomenclatural priority between the competing names *Alsodeia ilicifolia* and *Alsodeia spinosa*, Tennant (1963) provided compelling evidence that the effective publication of *A. ilicifolia* antedates *A. spinosa* (ICBN Recommendation 31A; Turland *et al.* 2018). Even though the publications containing the protologues of both names bear the printed date of "1868," Tennant (1963) suggested that the effective publication date of *A. ilicifolia* was shortly before 9 July 1868, while that of *A. spinosa* was possibly as late as June 1869.

In the protologue of *Alsodeia ilicifolia*, Oliver (1868) cited three syntypes: *Welwitsch* s.n. (Angola), *Afzelius* s.n. (Sierra Leone; specimen not seen), and *Brass* s.n. (Cape Coast; specimen not seen). Carrisso (1937) first cited the *Welwitsch* 889 specimens at LISU as type material, followed by Tennant (1963), who identified the same collections as a lectotype, even though he did not examine them. Scrutiny of the nine known specimens of *Welwitsch* 889 revealed that they are composed of three different gatherings: one from Jan. 1857 (in bud or sterile), one from Feb. 1857 (in bud, fruit, or sterile), and one from May 1857 (in bud). Indeed, Welwitsch was known to merge different gatherings under the same collecting number (Albuquerque *et al.* 2009). Because Tennant (1963) did not indicate which of the four specimens at LISU he chose as lectotype, the specimen LISU206098 was chosen as the second-step lectotype because it is the most complete, bearing mature fruits, seeds, and some immature flowers (see Article 9.17 of the ICBN; Turland *et al.* 2018). Three of the isolectotypes were also collected in February 1857, and even though they present different phenologies, they are consistent with the lectotype: M0109597 (bud), LISU206100 (sterile), and PRE0291990-0 (bud). The fourth isolectotype, BM000617803, contains a fruiting branch and a branch in bud, and even though it is not possible to reconstruct which elements on the sheet were collected in Feb. 1857, they are all consistent with the lectotype and are considered here collectively as an isolectotype. Three specimens of *Welwitsch* 889 are excluded as isolectotypes because they were either collected in Jan. 1857 (BM000617804, LISU206099) or in May 1857 (LISU206101). A fourth specimen, M0109598, is sterile and without a date and is not considered an isolectotype.

1b. Rinorea ilicifolia (*Welw. ex Oliv.*) *Kuntze* subsp. **spinosa** (*Boivin ex Tul.*) *Grey-Wilson* (1981: 11). *Alsodeia* [as *Alsodea*] *spinosa* Boivin ex Tul. (Tulasne "1868," publ. 1869: 307). *Rinorea spinosa* (Boivin ex Tul.) Baill. (Baillon 1886: 583). Type: Madagascar, Antsiranana Prov., Nossibé [Nosy Be], aux environs de Hellville, June 1847, *Boivin* 2122bis (lectotype P [P030596!], designated here; isolectotypes K [K000231204!], P [P030597!]).

Leaves petiolate; petioles 2 – 27 mm long; lamina 7 – 26 × 2.4 – 8.3 cm; secondary vein pairs 7 – 14; base cuneate to rounded. *Inflorescence* 3 – 16 cm long; peduncle 0.1 – 3.2 cm long (Fig. 4A – C).

DISTRIBUTION. The subspecies is distributed in the Comoro Islands and in northern and western Madagascar (Map 1).

SPECIMENS EXAMINED. COMOROS. Grande Comore, May 1963, *Bosser* 18012 (P); Grande Comore, 25 May 1975, *Coulon* 88 (MO, P); Mohéli, NE centre of island, 14 Aug. 1987, *D'Arcy* 17615 (MO). **MADAGASCAR.** Antsiranana: Nosy-Be, Lokobe RNI, Lokobe Point, 13°24'29"S, 48°18'48"E, 0 m, 28 Dec. 1996, *Antilahimena* 356 (K, MO); Ampasindava, forêt de Betsitsika, 12°45'44"S, 48°59'49"E, 275 m, 6 Jan. 2009, *Ammann et al.* 221 (G); Ambanja, Bemanevika, Bandrakorony, forêt de basse altitude de Bandrakorony, près du ruisseau de Betsitsiky sur la presqu'île Ampasindava, 13°45'36"S, 47°59'15"E, 135 m, 14 Jan. 2009, *Bernard et al.* 1255 (G); RNI 6, Lokobe, S side of the reserve, study site for the Black Lemur Forest Project, 5 km SE of Hell Ville, Nosy Be, 13°25'S, 48°18'E, 50 m, 18 Sept. 1992, *Birkinshaw* 161 (G, MO, TAN); Port Leven, March – April 1849, *Boivin* 2564 (lectoparatype; P); Montagne d'Ambre, July 1953, *Bosser* 5899 (P); Ambilobe, environs d'Ambatoarana, Dec. 1956, *Descoings* 1902 (TAN [3 sheets]); Manongarivo RS; Besinkara, forêt en aval d'Ambalafary, sur le chemin d'Anabotoaka, 14°04'S, 48°17'E, 200 m, 24 Sept. 1996, *Gautier et al.* LG3134 (G, K,

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P, TAN, TEF, WAG); Andrafiabe, Sahafary, 12°34'49"S, 49°26'55"E, 191 m, 26 July 2004, *Guittou et al.* 46 (MO, TAN); Ankarana, 10 – 250 m, Dec. 1937 – Jan. 1938, *Humbert* 18845 (MO, P); Ampasindava, forêt d'Andohankary, 13°38'21"S, 48°04'39"E, 22 Nov. 2007, 30 m, *Nusbaumer* 2518 (G); Lokobe RNI au SE d'Hell-Ville, Ambanoro, Nossy-Bé, 13°25'S, 48°18'E, 200 m, 20 – 22 May 1998, *Rabenantoandro et al.* 2 (MO, WAG); Ambolobozobe, Ankonahona, à 1 km au NW du village d'Ambolobozobe, 12°31'00"S, 49°31'00"E, 26 Dec. 2007, *Rakotonandrasana et al.* 1224 (MO); Ambanja, Bemanevika, Bandrakorony, versant E de la grande rivière de Bandrakorony sur la Péninsule d'Ampasindava, 13°44'50"S, 47°59'26"E, 122 m, 21 Jan. 2009, *Rakotovao et al.* 4248 (G); Ankarongana, Sahafary, forêt d'Andranomadiro, 12°36'18"S, 49°26'34"E, 258 m, 4 Dec. 2006, *Ranaivojaona et al.* 1646 (MO); Ambanja, village de Benavony, Bekaka, à 6 km au SE d'Ambanja, 13°43'32"S, 48°28'48"E, 80 m, 15 May 1998, *Randrianaivo et al.* 228 (G, MO, P); Île Nossi-bé [Nosy Be], s.d., *Richard* 185 (G, P, 2 sheets); *ibid.*, s.d., *Richard* 210 (lectoparatype; K, P, 2 sheets); *ibid.*, s.d., *Richard* 328 (P, TAN); *ibid.*, s.d., *Richard* 357 (lectoparatype; K, P); without precise locality, s.d., *J. M. C. Richard* 555 (lectoparatype; P, 2 sheets!); RN 4, Tsaratanana, Marovato, Ambanja, April 1951, *RN* 2714 (K, MO, P, TAN); RN 6, Nossi-Be, 19 Oct 1951, *RN* 3011 (P, TAN [2 sheets]); Ambanja, Maromiandra, 6 Oct. 1954, *SF* 11089 (K, MO, P, TEF); Bekaka, Ambanja, 20 March 1950, *SF* 3169 (P, TAN, TEF); Nosy Be, Lokobe RNI, village of Ampasindava, 13°24'42"S, 48°18'32"E, 80 – 230 m, 2 Nov. 2006, *Wahlert & Rakotonasolo* 5 (MO); near the bridge over R. Ramena, on road c. 15 km S of Ambanja, Ambodidmaka, 13°45'S, 48°29'E, 150 m, 8 Nov. 2006, *Wahlert & Rakotonasolo* 20 (MO); on road from Ambanja to Antanambao, 2 km N of the confluence of the Ramena and Sambirano Rs, 13°45'01"S, 48°45'12"E, 76 m, 11 Nov. 2006, *Wahlert & Rakotonasolo* 37 (MO); Sahafary forest, 12°34'S, 49°26'E, 176 m, 24 Nov. 2006, *Wahlert et al.* 58 (MO [2 sheets]); *ibid.*, 12°34'33"S, 49°26'26"E, 157 m, 13 Sept. 2007, *Wahlert & Razafimanantsoa* 96 (MO); Orangea forest, 12°14'21"S, 49°22'00"E, 35 m, 20 Sept. 2007, *Wahlert & Bienaime* 102 (MO); RS Manongarivo, Ambahatra, Plateau d'Anketraka Be, 13°56'S, 48°27'E, 200 m, 23 May 2000, *Wohlhauser & Andriamalaza* 60267 (G, K, MO, P, PRE, WAG); Mahajanga: Besalampy, Marovoay S, Angodoka, Anosibe, 16°55'54"S, 44°43'56"E, 58 m, 11 July 2007, *Andriamihajarivo et al.*1221 (MO); Melaky, Maintirano, Belitsaky, Ankilimanarivo, forêt de Beanka, lieu dit Antsakoan'ny Betrongo, 18°00'07"S, 44°27'43"E, 210 m, 20 Oct. 2009, *Andriamihajarivo et al.* 1789 (MO); Antsalova, RN 9, Oct. 1963, *Bosser* 18111 (P, 2 sheets, TAN); Maromandia, Ankaramy, 19 Dec. 1922, *R. Decary* 1356 (BM, K, P, TAN); environs de Bekodoka, 3 Nov. 1923, *Decary* 2361 (P); Namoroka, Soalala, 17 Sept. 1940, *Decary* 15808 (K, MO, P, WAG); Melaky, Beanka, S de la Kimanambolo, 18°06'57"S, 44°33'43"E, 240 m, 2 Dec. 2012, *Gautier et al.* LG5919 (MO); entre la mer et Besalampy, 13 Oct. 1968, *J.-L. Guillaumet* 2256 (P, TAN); Tsingy de Bemaraha N of the Manambolo R., 19°09'S, 44°49'E, 50 m, 1 Dec. 1996, *Jongkind et al.* 3314 (TAN, WAG, 2 sheets); environs d'Antsalova, 5 km à l'Est de Betivika, RN 9, 18°38'S, 44°43'E, 100 – 200 m, 29 Nov. 1992, *Labat et al.* 2230 (K, MO, P, TAN); Tsingy du Bemaraha, RN 9, 1932 – 1933, *Leandri* s.n. (P); Antsalova, 1932 – 1933, *Leandri* 263 (BM, P, PRE); vers Bevary, E d'Antsalova, lisière E de RN 9, 400 – 500 m, Feb. 1960, *Leandri & Saboureau* 2907 (P); bord du Manambolo, RN 9, Oct. 1964, *Morat* 790 (P, TAN); Berizoka [Bertizoka], Oct. 1897, *Perrier* 355 (P, 3 sheets); Belambo, près de Maevetanana, 1900, *Perrier* 1409 (P, 2 sheets); Manongarivo, Ambongo, Dec. 1903, *Perrier* 12117 (P); Kamakama, sur le causse d'Ankara, Nov. 1901, *Perrier* 12118 (P); Soalala, Andranomavo, Namoroka, bas canyon Ampidiranala, 16°24'46"S, 45°18'23"E, 105 m, 26 Oct. 2016, *Rakotovao & Reeb* 7084 (MO, P, TAN); Bekopaka, 6 July 1970, *Rakotozafy* 1005 (TAN); Angonkely, Mitsinjo, 7 July 1977, *Rakotozafy* 1940A (TAN); *ibid.*, *Rakotozafy* 1940B (TAN); Ankarafantsika, Ambato-Boeni, Tsaramandroso, 17 Oct. 1950, *RN* 2008 (MO, P, 2 sheets, TAN, 2 sheets); *ibid.*, *RN* 2548 (P, TAN, TEF); RN 8, Andranomavo, Soalala, 27 Dec 1952, *RN* 4917 (P, 2 sheets, TAN, WAG); *ibid.*, 13 Nov 1953, *RN* 5664 (MO, P, TAN, TEF); *ibid.*, 14 Oct 1956, *RN* 8153 (P, TEF); Bekopaka, Antsalova, 13 Feb. 1959, *RN* 10331 (P, TEF); Ambato-Boeni, Tsaramandroso, 28 Oct. 1960, *RN* 11418 (P); forêt Lomakia, Maintirano, 21 May 1955, *SF* 14197 (MO, P, TEF); Sahankazo, 16 Dec. 1955, *SF* 15513 (K, MO, P, TEF); Ambararatakely, Maintirano, 10 July 1956, *SF* 16343 (K, MO, P, 2 sheets, TEF); *ibid.*, 17 Nov. 1956, *SF* 16571 (MO, P, TEF); environs d'Andranogidro, 10 July 1957, *SF (Capuron)* 18034 (P, TEF); forêt de Tsimembo, 50 – 100 m, 24 Feb. 1961, *SF* 19835 (TEF); Mijamoa, Bevaho, Bekopaka, 16 Oct. 1966, *SF* 26211 (P, TEF); Ankily, Antsalova, 14 Sept. 1967, *SF* 26398 (MO, P, TEF); PN Ankarafantsika, village of Ankoririka, c. 15 km N of Tsaramandroso, 16°15'15"S, 47°03'10"E, 330 m, 12 Nov. 2007, *Wahlert & Wahlert* 120 (MO); Toamasina: Ambodivato, a hill c. 5 km SW of Maroantsetra along coastline of Bay of Antongil, 15°27'25"S, 49°41'41"E, 0 – 30 m, 29 Jan. 1999, *G. E. Schatz et al.* 3864 (K, MO); à l'Ouest de Nantoraka, au Sud-Ouest de Maroantsetra, 5 Nov. 1963, *SF (Capuron)* 22857 (K, 2 sheets, MO, 2 sheets, P, TEF).

MAYOTTE. À la cascade de Moussa-peré, 1847 – 1850, *Boivin* 3296 (lectoparatype; BM, P); forest of Sohoa, W coast of island, 12°49'S, 45°06'E, 100 – 200 m, 20 Nov. 2002, *Hoffmann et al.* 435 (K, MO, P); Sohoa, 12 July 1999, *Mas* 294 (P); Îlot Bouzi (Chissioua Mbouzi), 12°48'20"S, 45°14'00"E, 26 April 1999, *Pignal* 1293 (K, MO); Achirongou, 12°42'S, 45°04'E, 24 Sept. 2001, *Pignal et al.* 1926 (K, MO, P, WAG); Dzoumogné, s.d., *Pobéguin* 68 (P); Saziley, 12°59'18"S, 45°10'50"E, 10 m, 3 Aug. 2000, *Rouhan & Bernier* 38 (K, MO, P); Parc Préfectoral Saziley, 13 Sept. 2000, *Tarnaud* 150 (P); crête au dessus d'Acoua, Madjabalini, 250 m, s.d., *Tinguy* 804 (P).

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HABITAT. *Rinorea ilicifolia* subsp. *spinosa* grows in the understory of primary, secondary, or degraded humid and seasonally dry forests, semi-deciduous forests, and littoral thickets. It grows in sands and in volcanic and calcareous substrates; alt. 0 – c. 500 m a.s.l.

CONSERVATION STATUS. In Madagascar, *Rinorea ilicifolia* subsp. *spinosa* occurs in a number of sites with protected status: Ampasindava, Ankarafantsika, Ankarana, Bemaraha, Galoko, Lokobe, Manongarivo, and Tsimembo-Manambolomaty. Based on an Extent of Occurrence (EOO) of 1.7×10^5 km^2, a minimum Area of Occupancy (AOO) of 172 km^2, and more than 103 recorded localities, many of which are in protected areas, the subspecies is assigned a preliminary conservation assessment of Least Concern [LC] using the IUCN Red List categories and criteria (IUCN 2012).

PHENOLOGY. The subspecies flowers between September and November and fruits between September and January.

VERNACULAR NAMES. The following common names were recorded for *Rinorea ilicifolia* subsp. *spinosa*: *antsotsy* (in the Sakalava language, *Wahlert & Bienaime* 102); *reampy* (Sakalava, *Labat et al.* 2330, *RN* 4917, *RN* 10331, *SF* 16571, *SF* 26211); *reampilahy* (Sakalava, *RN* 8153); *rehampy* (Sakalava, *SF* 14197); *sibabe* (Sakalava, *Humbert* 18845); *tsibabena* (Sakalava, *Gautier et al.* LG3134, *RN* 2008, *RN* 2548, *RN* 2714, *RN* 3011); *tsibabeny* (Sakalava, *Wahlert & Wahlert* 120; *Wohlhauser & Andriamalaza* 60267), *tsibabini* (in the Shibushi language, *Rouhan & Bernier* 38); and *mouho moudrou* (in the Shimaoré language, *Rouhan & Bernier* 38).

NOTES. In the protologue of *Alsodeia spinosa*, Tulasne (1868) lists six syntypes: *Boivin* 2122bis, 2564, and 3296; *Richard* 210, 357, and 555. The specimen *Boivin* 2122bis was chosen as the lectotype because it was among the most complete and was represented by three duplicates.

1c. **Rinorea ilicifolia** *Welw. ex Oliv.* subsp. **amplexicaulis** (*Grey-Wilson*) *Wahlert*, **comb. et stat. nov.**

http://www.ipni.org/urn:lsid:ipni.org:names:77205199-1

Rinorea ilicifolia var. *amplexicaulis* Grey-Wilson, *Kew Bull.* 36: 118 (1981). Type: Tanzania, Kigoma Distr., Uvinsa [Uvinza], 1128 m, Aug. 1950, *A. A. Bullock* 3245 (holotype K000231035!; isotypes BR0000008718532 [image!], K000231034!).

Leaves subsessile; petioles to 2 (7) mm long; lamina 13 – 21.2 × 4 – 7.5 cm; secondary vein pairs 9 – 12; base auriculate. *Inflorescence* 3.5 – 10.5 cm long; peduncle 0.1 – 0.5 cm long.

DISTRIBUTION. The subspecies is distributed in western Burundi (Bubanza Province), and in Tanzania around the southern margins of Lake Victoria (Kagera and Mwanza Regions), and in Rukwa and Morogoro Regions (Map 1).

SPECIMENS EXAMINED. BURUNDI. Bubanza, Kihanga, Katunguru, 850 m, 8 Feb. 1970, *J. Lewalle* 4432 (MO).

TANZANIA. Rukwa, Mpanda Distr., Issa R., along stream, Kabamba evergreen forest, 05°25'33"S, 30°35'22"E, 1185 m, 17 Dec. 2002, *Abeid et al.* 1274 (MO); Rukwa, Mpanda Distr., T4, Misanga Village, Mnyangwa Hill, Ilumba R., 05°40'47"S, 30°55'13"E, 1140 m, 12 Sept. 2005, *Abeid et al.* 2282 (MO); Kigoma, Kigoma Rural Distr., Gombe Stream NP, Bwavi R., 04°44'10"S, 29°37'23"E, 1100 m, 20 May 1999, *Gobbo* 344 (BRIT, MO); Ulanga and Iringa Distrs, Udzungwa Mountain NP, 07°43'S, 36°54'E, 650 m, 6 Oct. 2001, *Luke et al.* 8185 (MO); Morogoro, Morogoro Rural Distr., Mkungwe Forest Reserve, FTEA region T6, 06°53'S, 37°55'E, 450 m, 7 Aug. 2000, *Mhoro* 33 (MO); Mwanza Distr., Sengerema, Maisome Island, Lake Victoria, 1143 m, Aug. 1958, *Proctor* 980 (PRE); Lake Province, Bukota Distr., Minziro forest, Sept. 1958, *Proctor* 987 (PRE); Morogoro, Kilombero, Mwanihana Forest Reserve above Sanje village, 07°52'S, 36°51'E, 950 – 1000 m, 8 Sept. 1984, *Thomas* 3691 (MO).

HABITAT. *Rinorea ilicifolia* subsp. *amplexicaulis* occurs in a variety of forest types, including submontane, *Euphorbia dawei*-dominated, dry evergreen, and lowland; alt. 450 – 1185 m. a.s.l. One specimen (*Proctor* 987) was recorded from a seasonally inundated forest.

CONSERVATION STATUS. In Tanzania, *Rinorea ilicifolia* subsp. *amplexicaulis* occurs in two sites with protected status: Gombe and Udzungwa Mountains NPs. With an Extent of Occurrence (EOO) of 1.1×10^5 km^2, a minimum Area of Occupancy (AOO) of 24 km^2, and nine recorded localities, *Rinorea ilicifolia* subsp. *amplexicaulis* is assigned a preliminary conservation assessment of Least Concern [LC] using the IUCN Red List categories and criteria (IUCN 2012).

PHENOLOGY. Based on herbarium labels, the subspecies is in bud from August through October and is with immature fruit in December; one specimen was in flower in May.

VERNACULAR NAMES. The common name *mholo-solela* in the Kiha language was recorded for the subspecies (*Gobbo* 344).

NOTES. Based on the character differences of shorter petioles and auriculate leaf bases and a mostly non-overlapping geographic distribution with subsp. *ilicifolia*, we recognise *Rinorea ilicifolia* var. *amplexicaulis* at the rank of subspecies. The amount of morphological divergence and geographic isolation, which is greater than would be expected for a taxon at the rank of variety, is further evidenced by the molecular phylogenetic results in Wahlert & Ballard (2012) and Velzen *et al.* (2015).

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Acknowledgements

We appreciate the many herbarium curators at K, MO, P, PRE, TAN, TEF, and WAG who made specimens available for this study. Two anonymous reviewers generously provided detailed feedback which helped to improve the accuracy of this paper. We also thank Jacek Wajer (BM) for providing high resolution images of herbarium material. Peter Phillipson (MO, P) provided assistance with mapping and protected areas in Madagascar. Financial support was provided by an Ohio University Graduate Student Senate Grant for Original Research and Student Enhancement Award (GAW) and an Ohio University Baker Grant (HEB).

Appendix. List of specimens used in morphometric analysis

Rinorea ilicifolia subsp. **ilicifolia**: *Y. S. Abeid & O. A. Kibure* 706 (MO); *Y. S. Abeid & O. A. Kibure* 735 (MO); *J.-G. Adam* 3181 (MO, P); *J.-G. Adam* 20793 (P); *J.-G. Adam* 23589 (MO); *J.-G. Adam* 29747 (MO); *J.-G. Adam* 30109 (MO); *M. Aubréville* 1801 (P); *L. Bernardi* 8304 (P); *L. Bernardi* 8414 (P); *J. P. M. Brenan* 8491 (P); *F. J. Breteler* 6105 (MO, P); *F. B. Dhego et al.* 592 (MO); *A. Chevalier* 14820 (P); *A. Chevalier* 16641 (P); *A. Chevalier* 16741 (P); *A. Chevalier* 16854 (P); *A. Chevalier* 16921 (P); *A. Chevalier* 22601 (P); *K. O. Darko* 461 (MO, P); *J. de Koning et al.* 9747 (MO); *J. J. F. E. de Wilde* 6361 (MO); *J. J. F. E. de Wilde & A. G. Voorhoeve* 3736 (P); *W. J. J. O. de Wilde & B. E. E. Duyfjes-de Wilde* 1625 (MO); *A. A. Enti* 435 (MO); *A. A. Enti* 644 (MO); *A. A. Enti* 1683 (MO); *P. Ezrom et al.* 189 (MO); *R. B. Faden et al.* 77/415 (MO); *L. Festo* 817 (MO); *I. Friis et al.* 3919 (MO); *Frontier-Tanzania* 1420B (MO); *Frontier-Tanzania* 2700 (MO); *L. Gautier et al.* LG2265 (MO); *L. Gautier et al.* LG2863 (MO); *D. J. Harris & J. M. Fay* 76 (MO); *D. J. Harris & J. M. Fay* 228 (MO); *D. J. Harris & J. M. Fay* 534 (MO); *C. J. Kayombo et al.* 4678 (MO); *O. A. Kibure* 84 (MO); *O. A. Kibure* 491 (MO); *O. A. Kibure* 514 (MO); *J. Koechlin* 3914 (P); *M. G. Latilo* 22 (P); *J. Lewalle* 4900 (MO); *Maclaud* 182 (P); *M. Merello et al.* 1337 (MO); *M. A. Mwangoka* 1257 (MO); *M. A. Mwangoka & S. Ali* 2188 (MO); *L. B. Mwasumbi & P. Mponda* 12643 (MO); *L. B. Mwasumbi & P. Munyenyembe* 13848 (MO); *P. B. Phillipson et al.* 4947 (MO); *G. E. Pilz* 2667 (MO); *M. Reekmans* 3892 (MO [2 sheets]); *S. A. Robertson & W. R. Q. Luke* 4544 (MO); *P. Schnell* 5328 (P); *V. Simon et al.* 9 (MO); *A. R. da Torre & J. Paiva* 9888 (MO); *L. White* 881 (MO).

Rinorea ilicifolia subsp. **spinosa**: *L. H. Boivin* 2122bis (P); *L. H. Boivin* 3296 (P); *J. M. Bosser* 5899 (P); *J. M. Bosser* 18012 (P); *J. M. Bosser* 18111 (P [2 sheets]); *G. Cremers* 2443 (P); *P. Coulon* 88 (MO); *R. Decary* 1356 (BM, P); *R. Decary* 2361 (P); *R. Decary* 15808 (P); *L. Gautier et al.* LG3134 (P); *J.-L. Guillaumet* 2256 (P); *P. Hoffmann et al.* 435 (MO); *H. Humbert* 18845 (P); *L. Humblot* 151 (P); *M. Keraudren-Aymonin & G. G. Aymonin* 25629 (P); *J.-N. Labat et al* 2230 (P); *J. D. Leandri* 263 (P); *J. D. Leandri* 666 (P); *J. D. Leandri* 953 (P); *J. D. Leandri* 1067 (P); *J. D. Leandri & P. Saboureau* 2907 (P); *C. Mas* 294 (P); *H. Perrier* 355 (P); *H. Perrier* 1409 (P); *H. Perrier* 12117 (P); *H. Perrier* 12118 (P); *M. Pignal et al.* 1926 (MO); *C. H. O. Pobéguin* 68 (P); *R. Randrianaivo et al.* 228 (P); *J. M. C. Richard* 185 (P); *J. M. C. Richard* 210 (P); *J. M. C. Richard* 328 (P); *J. M. C. Richard* 555 (P); *RN* 2008 (P); *RN* 2548 (P); *RN* 2714 (P); *RN* 3011 (P); *RN* 4917 (P); *RN* 5664 (P); *RN* 8153 (P); *RN* 10331 (P); *RN* 11418 (P); *G. Rouhan & F. Bernier* 38 (MO); *SF* 3169 (P); *SF* 14197 (P); *SF* 15513 (P); *SF* 16343 (P); *SF* 16571 (P); *SF* 18034 (P); *SF* 26211 (P); *SF* 26398 (P); *L. Tarnaud* 150 (P); *H. Tinguy* 804 (P); *S. Wohlhauser & H. Andriamalaza* 60267 (P).

Rinorea ilicifolia subsp. **amplexicaulis**: *Y. S. Abeid et al.* 1274 (MO); *Y. S. Abeid et al.* 2282 (MO); *G. Gobbo* 344 (MO); *W. R. Q. Luke et al.* 8185 (MO); *B. E. Mhoro* 33 (MO); *D. W. Thomas* 3691 (MO).

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