Two new species of *Coffea* L. (Rubiaceae) from northern Madagascar

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KEY WORDS

Rubiaceae, Coffee, coffee, Madagascar, IUCN Red List Categories.

ABSTRACT

Two new species of *Coffea* are described from northern Madagascar (Antsiranana Province): *C. ankaranensis* and *C. sambavensis*. The two new species are compared with *C. perrieri* and *C. millotii*, respectively. The conservation status of each species is summarized using IUCN Red List Categories.

RÉSUMÉ

MOTS CLÉS
Rubiaceae,
Coffea,
café,
Madagascar,
Catégories de l'UICN,
Listes Rouges.

Deux nouvelles espèces de Coffea L. (Rubiaceae) du Nord de Madagascar.

Deux nouvelles espèces de Coffea sont décrites du Nord de Madagascar (Province d'Antsiranana): C. ankaranensis et C. sambavensis. Ces deux nouvelles espèces sont comparées respectivement au C. perrieri et C. millotii. Le statut de conservation est donné pour chacune d'elles, en utilisant les catégories de l'UICN pour les Listes Rouges.

INTRODUCTION

Of the 45 or so *Coffea* species occurring in Madagascar, 26 were described by LEROY (e.g. 1961, 1962a, 1962b, 1972a, 1972b). He also gave provisional names to several species, as written on specimens held in the herbarium at the Muséum National d'Histoire Naturelle, Paris (P). Many of these names have now been validly pub-

lished (e.g. DAVIS & RAKOTONASOLO 2000, 2001, and DAVIS 2001), although some of the original epithets were not used. In this paper we formally name two more of LEROY's provisional species, namely *C. ankaranensis* and *C. sambavensis*. These two species are not closely related, but are described together here because they both have medium sized leaves and come from the province of Antsiranana.

Coffea comprises three subgenera: subg. Coffea (c. 90 spp.), subg. Psilanthopsis (A. Chev.) J.-F. Leroy (1 sp.) and subg. Baracoffea (J.-F. Leroy) J.-F. Leroy (c. 4 spp.). However, according to BRIDSON (1994) subg. Psilanthopsis is not worthy of recognition; the single species in this taxon, C. kapakata (A. Chev.) Bridson, should be transferred to subg. Coffea. And morphological studies by DAVIS, BRIDSON & RAKOTONASOLO (in prep.) show that subg. Baracoffea is more closely related to the genus Psilanthus than subg. Coffea. Coffea ankararanesis and C. sambavensis are members of subg. Coffea.

Coffea subg. Coffea is exemplified by the type species of the genus, C. arabica. Members of subg. Coffea can be characterized by the combination of the following salient features. The leaves are nearly always evergreen. The inflorescences are axillary and the calyculi have bract-like lobes. The architecture of the shoot is not altered by flowering, because the inflorescences are determinate (not producing relay axes). The calyx is shorter than the disc to slightly longer. The corolla is white or rarely pink, and the corolla tube is usually shorter to slightly longer than the corolla lobes; the stamens and style are exserted. The fruits are drupes and contain two seeds, or sometimes one seed, and each seed has a deep invagination on the adaxial (inner) surface (i.e. a "coffee bean"). Coffea subg. Baracoffea shares many of the features of subg. Coffea but there are several differences between these subgenera. The leaves are deciduous. The inflorescences are either axillary or terminal and the (uppermost) calyculi possess leaf-like lobes. The architecture of the shoot is altered by flowering, because the inflorescences are indeterminate (producing relay axes). The corolla tube is always much longer than the corolla lobes, and the stamens are only partially exserted.

The calyculi are important structures for the identification of *Coffea* species, and Coffeeae genera, and it is necessary to give some information on their structure here. The terms calyculi (pl.) and calyculus (sing.) have been used by several Rubiaceae researchers, including ROBBRECHT (1978), STOFFELEN (1998) and DAVIS 2000). Calyculi are bract-like structures that subtend the flowers, and other parts of the

inflorescence, such as the pedicel(s) and inflorescence branches. There are usually three calyculi per inflorescence unit, but this may vary considerably with as few as two and as many as 25, or possibly more, the number varying between species and sometimes within species. Each calyculus has four lobes, two derived from the stipules, called the stipular lobes, and two derived from leaves, called the foliar lobes. Sometimes the lobes are relatively large and conspicuous, and it is obvious whether they are stipular or foliar in origin, or they may be small and rather insignificant. The calyculus is fused below the lobes, forming a more or less cupular or tubular structure.

There are no recent monographic works covering the genus *Coffea*, the last and most important being those by CHEVALIER (e.g. 1942, 1947), although these works are now very much out of date. There are a number of regional revisions, however, notably those by BRIDSON (1988) for East Africa, and STOFFELEN (1998) for Central and West Africa. A regional treatment of *Coffea* from Madagascar, the Comoros Islands, and the Mascarenes is being prepared by us (DAVIS & RAKOTONASOLO, in prep.).

MATERIALS AND METHODS

Herbarium material of *Coffea* was consulted at the Département de Botanique, Parc de Tsimbazaza, Antananarivo (TAN), the Muséum National d'Histoire Naturelle, Paris (P), Recherches Forestières et Piscicoles, Antananarivo (TEF), and the Royal Botanic Gardens, Kew (K). The measurements, colours and other details given in the descriptions are based mostly on herbarium specimens, but also from living plants, and data derived from field notes. Cultivated material of *C. ankaranensis* and *C. sambavensis* was examined at the Coffee Research Station at Kianjavato (FOFIFA); *C. sambavensis* was studied in the wild by F. RAKOTONASOLO.

The conservation status of each species was assessed by calculating the extent of occurrence using a GIS (J. MOAT pers. comm.), and applying the IUCN Red List Category criteria (IUCN 2001).

THE NEW SPECIES

Coffea ankaranensis J.-F. Leroy ex A.P. Davis & Rakotonas., **sp. nov.**

Coffeae perrieri Drake ex Jum. & H. Perrier affinis sed foliis latioribus plerumque ovalibus vel obovatis vel late ellipticis (nec ellipticis nec elliptici-oblongis nec anguste ellipticis nec elliptici-oblanceolatis), calyculis pubescentibus vel villosis (nec puberulis), floribus majoribus [13.5-17 \times 12-14 mm nec 10-13(-16) \times 6-14(-20) mm] et fructibus majoribus (2.3-2.5 \times 1.1-1.3 cm nec 1.1-1.2 \times 0.9-1 cm) distinguenda.

TYPUS. — *Capuron 23166-SF*, Madagascar, Ouest (Nord): plateau de l'Ankarana, massif d'Antsandoko, au Sud d'Antsandoko, au Sud d'Ambondromifehy, 22 Dec. 1963, fl. (holo-, P!; iso-, K!, TEF!).

Tree or small tree, (3-)4-10 m high, dbh (3.5-) 5-9(-10) cm. Bark dark brown to grey-brown, smooth. Branches terete, 6-10 mm in diam., light grey or light brown, or whitish, smooth. Branchlets ± terete, 2-5 mm in diam., light grey to whitish or light brown, smooth to slightly rough, sometimes splitting when dry, glabrous. Stipules caducous, deltate to triangular, 1.6-2 × 1.8-3 mm, subcoriaceous to ± woody, usually with a pitted texture, glabrous, margin glabrous; apex acute to shortly apiculate, apiculum c. 0.5 mm long.

Leaves: petioles 0.4-0.7 cm long; leaf-blades oval, obovate, or broadly elliptic to very broadly elliptic, rarely elliptic, $(4.7-)5.4-12 \times (2.7-)4.4-$ 6.2 cm, subcoriaceous; base attenuate; margins subrevolute to revolute; apex rounded to obtuse or subacuminate; midrib prominent; abaxial surface: midrib prominent; secondary veins manifest, (6-)8-10 pairs, ascending at an angle of c. 45°, straight to slightly curved, joining to form a hooped intramarginal vein; tertiary venation weak to obscure, reticulate; higher order venation invisible; adaxial surface: venation manifest less clearly than that of the abaxial surface; domatia crypt type, indistinct to prominent, located in the axils of the secondary veins, against or on the edge of the midrib, the orifice round, 0.5-0.7 mm in diam., or oval to slit-like, c. 0.1 \times 0.2 mm, margin often chartaceous or darkened, and slightly swollen, glabrous; invisible to indistinct on the adaxial surface.

Inflorescences 1 per leaf axil, 4-6-flowered, ± umbellate, unbranched or with 1 very short (c. 0.2 mm long) branch, 10-15 mm long, elongating during fruit development, not or hardly covered with exudate; inflorescence axis (bearing calyculi) 5-11 mm long. Calyculi 4, the basal calyculi often falling, ± sessile, subcoriaceous, pubescent to villous, margins with many hairs (0.3-0.6 mm long), colleters sometimes present; basal (1st) calyculus $2.5-3 \times 3.1-3.5$ mm, stipular lobes broadly ovate, $2.5-3 \times 2.3-2.5$ mm, foliar lobes ovate-elliptic, 2-2.3 × 1.1-1.3 mm; middle (2nd) calyculus $2.3-3.5 \times 4-4.3$ mm, stipular lobes broadly elliptic to obovate, 3-3.2 × 2.4-2.6 mm, foliar lobes ± ligulate to elliptic, 1- 1.3×0.4 -0.5 mm; middle calyculus (3rd) 2.5- $3.3 \times 4-4.5$ mm, stipular lobes ± square to transversely oblong, $2.7-2.8 \times 2.6-2.8$ mm, foliar lobes ovate-elliptic, 2.2-2.3 × 1.1-1.3 mm; upper calyculus (4th) cupular to ± tubular, 1.1- 1.7×2.5 -2.8 mm, not lobed; internal surfaces of calyculi densely covered with colleters, particularly at the base, interspersed with fine, whitish to semi-translucent hairs (0.2-0.4 mm long); colleters narrowly ellipsoid to ± conical, 0.2-0.3 mm long, white.

Flowers 5-merous; pedicel 3-7(-8) mm long, with 1 or 2 bractlets; bractlets hemi-ellipsoid to ± square, $0.6-1 \times 0.5-0.9$ mm, bearing colleters; colleters 10-16 in each bractlet, ± cylindrical, 0.4-0.6 mm long, white. Calyx (hypanthium) ± turbinate, $1.4-1.7 \times 2.4-2.7$ mm, texture slightly rough, very sparsely papillate or sparsely covered with very short, minute echinae; calyx limb truncate, much shorter than disc. Corolla 13.5-17 × 12-14 mm, corolla tube ± equal to the corolla lobes or slightly shorter, smooth; corolla tube ± very broadly funnel-shaped, 7-9 mm long; corolla lobes 7-8 × 3.6-4 mm. Stamens: filaments infradorsifixed, 2.5-2.7 mm long; anthers narrowly elliptic to linear, 5.7-6.3 mm long. Ovary: disc prominent, ± discoid-tubular. Style 11.5-14.5 mm long; stigma lobes 2.3-2.6 mm long.

Fruit (immature), ellipsoid to ellipsoid-obovoid, $2.3-2.5 \times 1.1-1.3$ cm, green; fruit wall 1.5-2 mm thick; pedicel 7-9 mm long; calyx limb inconspicuous. Seeds (immature) ellipsoid to ellipsoid-obovoid, c. $15 \times 7-8.7$ mm, c. 9 mm thick, brown (when dry). — Fig. 1.

DISTRIBUTION. — Endemic to northern Madagascar, in the Antsiranana Province; mostly restricted to the Ankarana Massif and in nearby forests, but with two collections from the Forest of Sakaramy (due north east of Montagne d'Ambre, c. 12°26'S, 49°16'E). — Fig. 2.

HABITAT AND ECOLOGY. — Seasonally dry forest: either deciduous forest, or mixed deciduous-evergreen forest. On limestone and basalt lavas. Altitude 200-600 m.

PHENOLOGY. — Flowering in November and December; fruiting January and February. Phenology of cultivated material not included.

CONSERVATION STATUS. — IUCN Red List Category: Endangered (EN B1 a,b). B1 — total extent of occurrence less than 5000 km² (c. 500 km²); a. — severely fragmented, and possibly existing at no more than five locations; b (i-v). — continuing decline, observed and inferred. Fieldwork in the forest of Sakaramy (DAVIS & RAKOTONASOLO, pers. observ. 1988) failed to find C. ankaranensis; this forest is now much reduced and highly degraded. This evidence suggests that it has been either erroneously recorded (herbarium specimen locality data incorrect) or is now extinct at this locality. If C. ankaranensis does not occur at Sakaramy, the extent of occurrence and area of occupancy would be significantly reduced, possibly placing this species in the Critically Endangered Category (CR). Some populations of *C. ankara*nensis are located within a protected area, namely the Réserve Spéciale d'Ankarana.

PARATYPES. — N MADAGASCAR, Antsiranana: Capuron 28723-SF, Ouest (Nord): lapiaz dans les calcaires du Mur de l'Ankarana, 16-28 Jan. 1969, fr. (P); Guillaumet 2318, face Ouest de l'Ankarana de Diego-Suarez, village d'Andrafiabe, 19 Jan. 1969, fr. (P, TAN); Capuron 24554-SF, Ouest (Nord): plateau de l'Ankarana: près d'Ambondromifehy, 5 Feb. 1966, fr. (K, P, TAN, TEF); Humbert 32397, forêt de Marovato, canton d'Anivorano Nord, 30 Jan. 1960, fr. (K, P); Vianney A. 529 (herb. Leroy 3-43), forêt d'Antsandoko, 9 Nov. 1966, ster. (P); Davis & Rakotonasolo 2331 (Kianjavato acc. no. A. 525), Andranofehy, recollected from Coffee Research Station at Kianjavato (FOFIFA), recollected 27 Nov. 1999, fl. (K, P, MO, TAN); coll. ignot. A. 526 (herb. Leroy 3-38), forêt d'Antsandoko, 8 Nov. 1966, ster. (P); Guillaumet 2187, route de Jofferville, km 4.5 (Diego-Suarez) [locality not traced], 200 m, 4 Aug. 1968, ster. (P, TAN); coll. ignot. A. 525 (herb. Leroy 3-36), forêt d'Antsandoko, Ankarana, 8 Nov. 1966, ster. (P, TAN); coll. ignot. A. 518, forêt de Sakaramy, 6 Nov. 1966, ster. (K, P); Davis & Rakotonasolo 2336 (Kianjavato acc. no. A. 518), forêt de Sakaramy, recollected from the Coffee Research Station at Kianjavato (FOFIFA), recollected 28 Nov. 1999, fl., fr. (K, P, MO, TAN); coll. ignot., s.n., forêt de Sakaramy, 13 Nov. 1970, fl. (P).

Coffea ankaranesis is characterized by a combination of characters not present in any other Coffea species. The main characters are as follows. The leaves are oval to obovate, or broadly elliptic, and usually rather broad in relation to their width (usually $5.4-12 \times 4.4-6.2$ cm). The calyculi are pubescent to villous, and the flowers $(13.5-17 \times 12-14 \text{ mm})$ and fruits are rather large $(2.3-2.5 \times 1.1-1.3 \text{ cm})$. Coffea ankaranesis is similar to C. perrieri Drake ex Jum. & H. Perrier but the leaves of this species are elliptic to elliptic-oblong, narrowly elliptic, or elliptic-oblanceolate, and not particularly broad in relation to their width (usually 9.5-13 \times 3-5.5 cm); the calyculi are puberulous, and the flowers (10-13 \times 6-14 mm) and fruits are smaller $(1.1-1.2 \times 0.9-1 \text{ cm})$. The ecology of these two species differs considerably. Coffea ankaranensis is usually found in seasonally dry, deciduous forest on limestone and basalt, whereas C. perrieri is almost always restricted to gallery forest, on riverine sand or quartzites.

Coffea ankaranesis is so named because it comes from Ankarana, a large limestone massif in Antsiranana Province in northern Madagascar.

Coffea sambavensis J.-F. Leroy ex A.P. Davis & Rakotonas., **sp. nov.**

Coffeae millotii J.-F. Leroy affinis sed ramulis apicem versus albidis (nec brunneis), venis lateralibus (venis secundariis) foliorum 6-8-jugis [nec (6-)8-10-jugis], lamina in superficie abaxiali laevi (nec rugosicoriacea), domatiis in superficie abaxiali prominentibus (nec obscuris) etiam in superficie adaxiali manifestis (nec invisibilibus), a costa distantibus 2.5-8 mm (nec juxta costam) positis, distinguenda.

TYPUS. — *Capuron 27706-SF*, Madagascar, Est (Nord): forêt littorale, au Sud de Sambava, 1-10 Apr. 1967, fr. (holo-, P!; iso-, K!, TEF!).

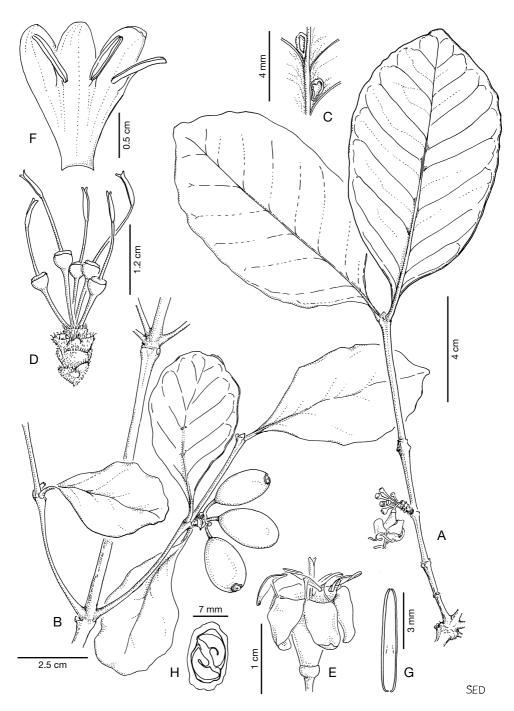


Fig. 1. — *Coffea ankaranensis* J.-F. Leroy ex A.P. Davis & Rakotonas.: **A**, habit (flowering branchlet); **B**, habit (fruiting branchlet); **C**, domatia (adaxial view); **D**, inflorescence, with calyculi (corollas fallen); **E**, flower; **F**, inside of corolla (part removed); **G**, anther; **H**, transverse section of fruit (rehydrated). A, C-G, *Capuron 23166-SF*; B, H, *Capuron 22414-SF*.

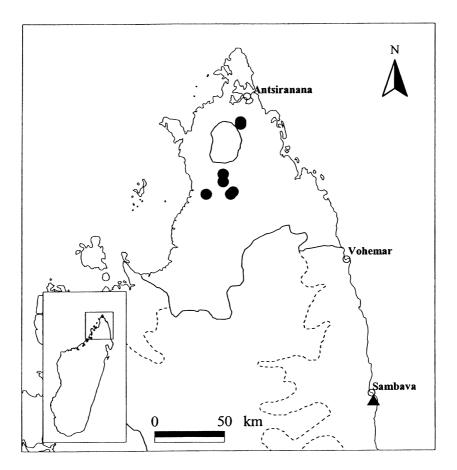


Fig. 2. — Distribution of **Coffea ankaranensis** (●), and **Coffea sambavensis** (▲). Map divided into phytogeographical domains (after Humbert 1955), *C. ankaranensis* occurs in the Western Domain, and *C. sambavensis* in the Eastern Domain.

Small tree, 4-8 m high, dbh 4-16 cm. Bark whitish to grey, slightly rough to rough and peeling in patches c. 7 cm in diam. Branches terete to 4-angled, 5-8 mm in diam., grey to whitish, or brown, smooth, sometimes soft and peeling. Branchlets terete to 4-angled, 2.5-5 mm in diam., white to brown, usually soft and spongy with freely peeling bark, sometimes with many small, black dots (?lenticels or ?asci). Stipules caducous, ovate to broadly ovate or ± deltate, 2.2-3 × 3.5-4.2 mm, subcoriaceous, glabrous, margin glabrous; apex obtuse to acute.

Leaves: petioles 0.9-1.5 cm long; leaf-blades broadly ovate to ovate-orbicular, obovate-orbicular, broadly obovate, or oblong-obovate, $(5.2-)8-9.7(-10.5) \times (2.2-)3.5-7.7$ cm, subcoriaceous;

base attenuate; margins subrevolute to revolute; apex rounded to obtuse, often subacuminate; abaxial surface: midrib prominent; secondary veins prominent, 6-8 pairs, ascending at an angle of 30° to 45°, straight to curved, joining to form a hooped intramarginal vein, with a second intramarginal nearer the margin; tertiary venation manifest to prominent, ± reticulate; higher order venation obscure, ramified; adaxial surface: venation manifest more clearly than that of the abaxial surface; domatia crypt type, few but conspicuous, located 2.5-8 mm from the midrib usually along the secondary veins, orifice 0.1-0.3 mm in diam., or domatia becoming necrotic and orifice 0.4-10 mm in diam., margin slightly raised, or swollen and chartaceous, glabrous;

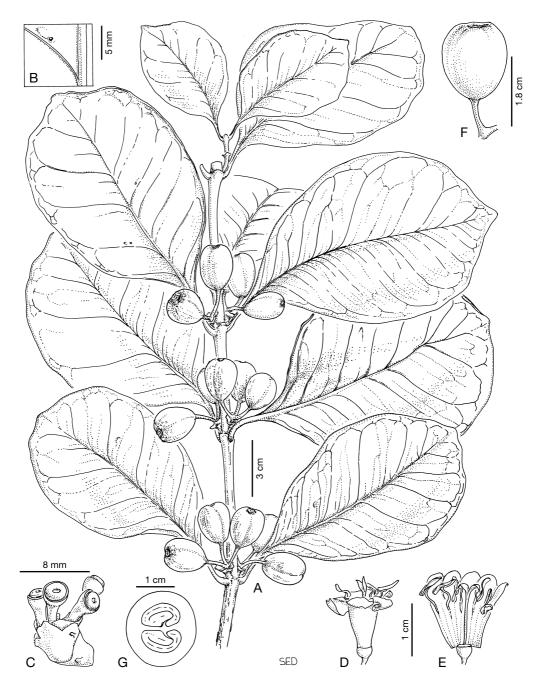


Fig. 3. — *Coffea sambavensis* J.-F. Leroy ex A.P. Davis & Rakotonas.: **A**, habit; **B**, domatia (adaxial view); **C**, inflorescence, with calyculi (corollas and styles fallen); **D**, flower; **E**, flower dissection; **F**, fruit; **G**, transverse section of fruit. A, B, *Capuron 27706-SF*; C-G, *Davis & Rakotonasolo 2323*.

prominent on adaxial surface, manifest as small, elliptic pustules, $1.5-3.5 \times 1-1.2$ mm, these sometimes darker than leaf surface.

Inflorescence 1 per leaf axil, 2-4(-6)-flowered, ± umbellate, very shortly branched, with 1 short branch at base (0.2-0.3 mm long), 5-6 mm long, elongating considerably during fruit development, often slightly covered with exudate; inflorescence axis (bearing calyculi) 4.5-6.5 mm long. Calyculi 3, the basal and lower calyculus often falling or broken, ± sessile, subcoriaceous, glabrous to puberulous, margins glabrous or with few hairs (0.2-0.3 mm long); basal (1st) calyculus $1.8-2.2 \times 2.4-3.6$ mm, stipular lobes $1.7-2 \times 1.6-$ 2.7 mm, foliar lobes not seen; middle and upper $(2^{\text{nd}} \text{ and } 3^{\text{rd}}) \text{ calyculi } (2.5-)4.3-5.5 \times (3.2-)4.9-$ 12 mm, stipular lobes broadly ovate to ± deltate, $(2-)3-5.2 \times 3-5$ mm, foliar lobes elliptic to obovate, distinctly smaller than stipular lobes, $1-1.5 \times 0.3-0.5$ mm; internal surfaces of calyculi and with many colleters, particularly at the base, intermixed with numerous fine hairs (0.2-0.3 mm long); colleters narrowly conical to very narrowly ellipsoid, c. 0.2 mm long, white.

Flowers 5-merous; pedicel 2-5.5 mm long, without bractlets. Calyx (hypanthium) ± obconical to campanulate, 1.8-2.3 × 1.8-2.4 mm, glabrous, smooth; calyx limb very shallowly 5-lobed to truncate, shorter than the disc; disc rather prominent, ± discoid. Corolla 15-17 × 11-14 mm, corolla tube slightly longer than corolla lobes, smooth; corolla tube ± broadly funnel-shaped, 9-11 mm long; corolla lobes 6-8 × 4.7-6 mm. Stamens: filaments infradorsifixed, 4-4.5 mm long; anthers narrowly elliptic to linear, c. 6 mm long. Style 15-16 mm long; stigma lobes 2.5-3 mm long.

Fruit (immature), shortly obovoid to \pm turbinate, $17\text{-}22 \times 14\text{-}18$ mm, slightly bilobed to bilobed (upon drying), shrinking considerably upon drying, green; fruit wall 3.5-4 mm thick; pedicel (6-)9-13 mm long; calyx limb inconspicuous. Seeds (immature) \pm ellipsoid to ellipsoidobovoid, $14\text{-}16 \times 9\text{-}12$ mm, c. 7 mm thick, white (fresh) to light brown (when dry). — Fig. 3.

DISTRIBUTION. — Endemic to north-eastern Madagascar, in the Antsiranana Province; between Sambava and Vohimarina (Vohémar). — Fig. 2.

HABITAT & ECOLOGY. — Lowland humid evergreen forest, including the littoral zone. On loose sands, basement rocks and lavas. Altitude 0-200 m.

PHENOLOGY. — Flowering in November; probably fruiting in April. Phenology of cultivated material not included.

Conservation status. — IUCN Red List Category: Endangered (EN B1 a,b). B1 — total extent of occurrence less than 1000 km² (c. 350 km²); a. — severely fragmented, and possibly existing at no more than five locations; b(i-v). — continuing decline inferred. There are no populations of *C. sambavensis* within the current scheme of protected areas. Fieldwork in areas of remaining primary forest (including degraded primary forest) near Sambava, and along the coast of north-eastern Madagascar, is required for a more confident assessment of extinction risk.

PARATYPES. — NE MADAGASCAR, Antsiranana: Capuron 24928-SF, district Est (Nord): forêt littorale, au Sud de Sambava, 20 Oct. 1966, fl. bud (K, P, TEF); Davis & Rakotonasolo 2346 (Kianjavato acc. no. 955), Sambava, recollected from the Coffee Research Station at Kianjavato (FOFIFA), recollected 28 Nov. 1999, fl. (K, P, TAN); Davis & Rakotonasolo 2323 (Kianjavato acc. no. A. 950), ibid., recollected 27 Nov. 1999, fl., fr. (BR, K, P, MO, TEF); Rakotonasolo RNF 270, Vohémar, Fanambana, 190 m, 24 Nov. 2000, fl. bud. (K, P, MO, TAN, TEF); Rakotonasolo RNF 274, Sambava, Anjangoveratra, Ambodisambalahy, 26 Nov. 2000, fl. (K, TAN, TEF).

Coffea sambavensis is an easily recognized species due to following combination of features. The branches are normally whitish, usually with a soft, peeling bark. The leaves are broad (length to width ration 3:2, or greater), subcoriaceous, and have prominent domatia. The domatia are not located against the midrib but several millimetres away from it, along the secondary veins, and they are often visible on the adaxial surface (see Fig. 3A,B). The fruit is rather large, thickwalled (mostly mesocarp), and born on long pedicels. The pedicels are short in flower but lengthen significantly during fruit development. See description for all measurements.

Coffea sambavensis most closely resembles C. millotii J.-F. Leroy, another species from the

humid forests of eastern Madagascar. Coffea millotii is similar to C. sambavensis in fruit and inflorescence morphology, but is easily separated because the domatia are located against the midrib, and the abaxial surface of each leaf is rough and wrinkled (smooth in C. sambavensis). The colour of the branchlet bark, and the number of pairs of secondary veins are other features that can be used to separate these species, as given in the diagnosis above. The distribution of C. millotii does not overlap with C. sambavensis, as its northern limit of distribution is in the Masoala Peninsula, which is some distance south of Sambava.

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