A review of Madagascan *Uapaca* (Euphorbiaceae *s.l.*)

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KEY WORDS
Euphorbiaceae,
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Uapaca,
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staminodes.

ABSTRACT
Uapaca in Madagascar, formerly considered to comprise 12 species, is here treated as consisting of eight species, all endemic. Staminodes (in the staminate flowers) are reported for the first time in the genus, and a key is proposed, along with descriptions and notes on variation.

MOTS CLÉS
Euphorbiaceae,
Phyllanthaceae,
Uapaca,
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RÉSUMÉ
Une révision du genre Uapaca *de Madagascar (Euphorbiaceae* s.l.*).*
Le genre *Uapaca* à Madagascar, qui était auparavant considéré comme comprenant 12 espèces, est ici considéré comme en comprenant huit. Les staminodes (dans les fleurs staminées) sont décrites pour la première fois au sein de ce genre, et une clé est proposée, ainsi que des descriptions et des notes sur la variabilité.

INTRODUCTION

Published in 1958, Leandri's treatment of Madagascan *Uapaca* was based on only 66 collections. Half a century later, more than 500 are available, and, perhaps not surprisingly, a study of these specimens supports some modification of the early interpretation. Only eight species, all of them endemic and some of them remarkably variable, are recognized here, instead of the 12 in Leandri's treatment. Radcliffe-Smith (2001) states that a further 49 occur on the African mainland, while Govaerts *et al.* (2000) put that number at 40.

The genus is easily separated from other Madagascan Euphorbiaceae because of its involucrate inflorescences (the pistillate uniflorous and the staminate of many flowers in a globose head) and drupaceous fruit. As well, most species exhibit stilt roots, resinous twigs tips, and clustered leaves and are thus easily identified to genus in the field (Fig. 1; additional

images of several of the species treated here can be found on the website of the *Catalogue of the Vascular Plants of Madagascar*, at http://www.tropicos.org/ImageSearch.aspx?projectid=17). The genus is placed in the monogeneric subtribe Uapacinae of tribe Antidesmeae of subfamily Phyllanthoideae by Radcliffe-Smith (2001), a position consistent with recent molecular work (Wurdack *et al*. 2004).

One quite unanticipated finding emerged during this study. Staminate collections, although much less common than pistillate ones and of less use in species delimitation, nevertheless have revealed the existence of a floral feature apparently previously unrecorded in *Uapaca*. Linear, somewhat distally expanded and pubescent structures *c*. 1 mm long often alternate with the five stamens in staminate flowers of Madagascan members of the genus (Fig. 2). These structures, variable in number from none to five, occasionally bear two much-reduced, barren pollen sacs, and are hence here interpreted as staminodes. No similar structures were observed in dissections of a small sample of mainland African species and they are not mentioned in such standard literature as Baillon (1858), Müller Argoviensis (1866), Pax & Hoffmann (1922), Webster (1994), Radcliffe-Smith (2001), and Govaerts *et al*. (2000). They are, however, easily overlooked – in the *Flore de Madagascar* (Leandri 1958), the illustrations of the staminate flowers of *U. bojeri* and *U. thouarsii* do not portray them, although in both species these staminodes are typically present. A careful re-examination of all the African species is therefore in order.

The key below and the brief descriptions and notes following it summarize my interpretation of species diversity within Madagascan *Uapaca*. Specimen identifications beyond those listed as representative after each species entry can be obtained from Tropicos at http://www.tropicos.org/SpecimenSearch.aspx; species distribution maps can be found via their specimen lists also on Tropicos.

Key to *Uapaca* species in Madagascar

1. Leaf blade wide (typically, length < 2 × width); ovary pubescent distally; northwestern Madagascar (a few specimens of *U. ferruginea* Baillon have blades of similar shape, but this form appears to occur only in the Southeast) ..... 2. *U. amplifolia* Denis
— Leaf blade narrower (typically, length > 2 × width); ovary pubescent or glabrous; variously distributed 2

2. Leaf blade relatively narrow (often up to length = 3-4 × width); tertiary venation subscalariform; pistillate calyx in fruit 2-3 mm in height, 6-10 mm in diameter in fruit, glabrous on abaxial surface and on rim, often conspicuously pubescent within; mature fruit 25-30 mm long; northwestern Madagascar ..... 1. *U. ambanjensis* Leandri
— Leaf blade various, but if narrow (length = 3-4 × width), then with tertiary venation non-scalariform; pistillate calyx in fruit 1-3 mm in height, but if more than 2 mm, then tertiary venation obscure and non-scalariform, of various diameters in fruit, pubescent or glabrous; mature fruit 15-30 mm long; variously distributed 3

3. Trees of open dry forests and savannas of the central plateau; stilt roots absent; pistillate calyx up to 5 mm in diameter, pubescent abaxially, 1.5-2 mm in height; petioles short (3-6[-11] mm long); mature fruit obovoid to ellipsoid, 17-25 mm long ..... 3. *U. bojeri* Baillon
— Trees of the humid coastal, montane, and remnant plateau forests; stilt roots rarely absent; pistillate calyx, petioles, and fruit various 4

4. Mature fruit small (12-15 mm long, rarely to 18 mm long and then attenuate at base); tertiary venation non-scalariform; pistillate calyx 3-4.5(-5.5) mm in diameter, often markedly lobed, typically glabrous or merely ciliate; staminate pistillode densely pubescent on flat top; rarely occurring below 500 m ..... 4. *U. densifolia* Baker

— Mature fruit mostly 20-30 mm long (but if less than 20 mm, then tertiary venation scalariform), tertiary venation subscalariform or not; pistillate calyx 3.5-9 mm in diameter, entire to somewhat lobed, glabrous or pubescent; staminate pistillode sparsely to densely pubescent on top; coastal to montane 5

5. Tertiary venation scalariform (often obscure); twigs, leaves, and inflorescences usually coated with glossy exudate; twigs sometimes hollow 6
— Tertiary venation not scalariform, if visible; twigs, leaves and inflorescences typically less glossy; twigs solid 7

6. Leaf blades 3.5-14(-17) cm long; pistillate peduncles up to 20(-23) mm long; calyx glabrous to sparsely pubescent but the hairs usually completely obscured by the glossy exudate ... . 7. *U. louvelii* Denis
— Leaf blades (11-)15-28 cm long; pistillate peduncles, at least the longer ones, 25 mm long or longer; calyx typically densely pubescent (but occasionally glabrous) and the hairs only partly obscured by glossy exudate ..... 5. *U. ferruginea* Baillon

7. Leaf blades, at least the longer ones, with length = 3-4 width; secondary veins typically 8-10 on each side of the midrib, usually slender, not raised abaxially, obscure; pistillate calyx often glabrescent ..... 6. *U. littoralis* Denis
— Leaf blades with length < 2.5 width; secondary veins typically 4-6(-7, but up to 11 if leaves 20 cm long or more), relatively thick, often raised abaxially, evident; pistillate calyx typically persistently pubescent ..... 8. *U. thouarsii* Baillon

SYSTEMATICS

1. ***Uapaca ambanjensis*** Leandri

Mémoires de l'Institut scientifique de Madagascar, Série B, Biologie végétale 8: 256 (1957).

TYPUS. — **Madagascar**. Prov. Antsiranana, Andampy, près d'Ambanja, 100-200 m, 17.IX.1954, fr., *Service forestier 10674* (lecto-, P [sheet P00132895], here designated; isolecto-, MO).

MATERIAL EXAMINED. — **Madagascar**. Prov. Antsiranana, Lokobe RN, 13°24'40"S, 048°19'07"E, 20-200 m, 20.IV.1994, *Antilahimena 86* (MO, P, TAN). — Eod. loc., 5 km SE of Hell Ville, 13°25'S, 048°18'E, 150 m, 28.I.1992, *Birkinshaw 102* (MO, P). — Eod. loc., 200 m, 25.II.1992, *Birkinshaw 119* (MO, P, TAN). — Manongarivo, 14°04'S, 048°17'E, 300 m, 5.IX.1997, *Gautier* et al. *3248* (MO, P). — Ampondrabe, 13°33'S, 048°33'E, 300 m, 3.X.1952, *Service forestier 5839* (P). — Andranomatavy-Ambanja, 13°57'30"S, 047°58'30"E, 668 m, 11.X.1953, *Service forestier 7691* (MO, P). — Andampy, 14°06'10"S, 048°15'30", 100-200 m, 17.IX.1954, *Service forestier 10674* (MO, P).

DESCRIPTION

Tree 8-25 m; stilt roots usually present but occasionally absent; leaf-bearing twigs 2.5-6(-10) mm in diameter, solid. Leaf blades narrowly oblong or narrowly obovate to obovate, (4-)10-20 cm long, (1.5-)2.5-8.5 cm wide, base cuneate to attenuate, apex obtuse, secondary veins 6-8 on each side of the midrib, readily visible, tertiary veins subscalariform, visible; petioles (0.5-)1.0-2.7(-4.0) cm long. Staminate peduncles 2.5-4.5 cm long; petaloid bracts (few seen) 4-10 in number, 10-14 mm long, 6-8 mm wide, the inner ones sometimes short-pubescent; head of flowers 10-12 mm in diameter excluding the exserted stamens; staminodes typically present, pistillode glabrous to sparsely pubescent on the exposed distal surface. Pistillate peduncles 1.1-4.5 cm long; petaloid bracts (few seen) 4-7 in number, 7-10 mm long, *c*. 6 mm wide, calyx *c*. 5.5 mm in diameter in flower, glabrous abaxially, in fruit 2-3 mm high, 6-8(-10) mm in diameter, entire or somewhat lobed and often undulate, often pubescent within at junction with axis; ovary glabrous, fruit 2.5-3.0 cm long, 2.2-2.5 cm in diameter, glabrous, yellow, apex pointed or rounded.

DISTRIBUTION

Northwestern Madagascar at elevations of 20-700 m.

Remarks
Distinguished by its relatively narrow and non-lustrous leaves with subscalariform tertiary venation, its large glabrous pistillate calyx that is often pubescent within at its junction with the floral axis, and its glabrous ovary. The leaves of this species most closely resemble those of *U. littoralis*, but that species does not exhibit subscalariform venation.

2. ***Uapaca amplifolia*** Denis

Archives de Botanique, Bulletin mensuel, Caen 1: 224 (1927).

Uapaca rivularis Denis, *Archives de Botanique, Bulletin mensuel*, Caen 1: 225 (1927). — Type: Madagascar, Domaine de l'Ouest, bord du Mananzovo à Tsaratanana, s.d. ft., *Perrier de la Bâthie 4632* (lecto-, P [sheet P00132898], here designated).

Typus. — **Madagascar**. Prov. Antsiranana, forêts du massif de Manongarivo au-dessous de 500 m alt., sur les grès liasiques exclusivement, VI.1909, fl. ♂, *Perrier de la Bâthie 11590* (lecto-, P [sheet P00132876], here designated).

Representative material examined. — **Madagascar**. Prov. Antsiranana, Anjahana, 13°21'15"S, 049°11'01"E, 118 m, 07.VI.2005, *Hong-Wa 314* (MO, P, TAN). — Tsaratanana RNI, 13°52'33"S, 048°48'44"E, 700 m, 26.III.2000, *Antilahimena 422* (MO, P). — Antsahabe, 13°47'22"S, 048°13'50"E, 516 m, 11.XI.2001, *Antilahimena 779* (MO, P, TAN). — Manongarivo, 14°04'S, 048°17'E, 270 m, 11.VI.1994, *Gautier 2299* (G, MO, P). — Eod. loc., 300 m, 5.IX.1997, *Gautier 3251* (G, MO, P). — Manongarivo, 14°02'S, 048°19'E, 800-1100 m, 7-12.XII.1992, *Malcomber 1958* (MO, P, TAN). — Prov. Mahajanga, Irony-Bealanana (*c.* 14°45'S, 048°22'E), 300-500 m, 21.VI.1953, *Service forestier 7440* (MO, P).

Description
Tree 8-20 m; stilt roots reportedly sometimes absent or reduced; leaf-bearing twigs 3-7(-10) mm in diameter, solid or hollow. Leaf blades obovate, (8-)11-24 cm long, (4.5-)7.0-18 cm wide (blade width at least 0.6 × length for all but the smallest leaves), base broadly cuneate to obtuse, apex obtuse, secondary veins 5-8(-9) on each side of the midrib, sharply raised and readily visible, tertiary venation subscalariform, both it and the higher venation visible abaxially; petiole 2.0-4.0(-5.5) cm long. Staminate peduncles 1-3.3 cm long; petaloid bracts *c.* 10 in number, *c.* 8 mm long, *c.* 5 mm wide; flowering heads 4-5 mm in diameter excluding the exserted stamens; calyx, at least in part, of free or nearly free narrow segments; staminodes apparently infrequent, but present in at least some flowers; pistillode somewhat pubescent on distal surface. Pistillate peduncles 0.5-3 cm long; petaloid bracts 3-10 in number, 5-11 mm long, *c.* 5 mm wide; calyx in flower 2.5-3 mm in diameter, often broadly lobed, glabrous or somewhat pubescent abaxially, pubescent adaxially at the junction with the axis, the hairs often somewhat exserted beyond the sinuses, calyx in immature fruit up to 5.5 mm in diameter, the calyx wall remaining merely *c.* 1 mm high; ovary typically coated with exudate, pubescent at least distally, immature fruit *c.* 2 cm long, pubescent distally or glabrescent.

Distribution
Northwestern Madagascar at elevations of 120-1200 m.

Remarks
Distinguished by its typically broad leaf, its short, abaxially glabrous or nearly glabrous pistillate calyx that is adaxially pubescent at its junction with the floral axis, and its distally pubescent ovary. Resembling *U. ferruginea* but with wider leaves typically, smaller staminate heads and a northwestern distribution.

3. ***Uapaca bojeri*** Baillon

Adansonia 11: 176 (1874).

Uapaca clusiacea Baker, *Journal of the Linnean Society, Botany* 18:278 (1881). — Type: Madagascar, Ankaratra Mountains, s.d., fl. ♂, *Kitching s.n.,* (lecto-, K [sheet K000406452], here designated).

Typus. — **Madagascar**. *Crescit in montibus provinciae madagascariensis* Imamou, s.d., fr., *Bojer s.n.*, (holo-, P [sheet P00298670]).

Representative material examined. — **Madagascar**. Prov. Antananarivo, Itasy, 18°59'S, 047°04'E, 1300-1400 m, 9.I.1985, *Dorr 3438* (MO, P). — Behenjy, 19°13'S, 047°33'E, 1400 m, 16.I.1950, *Service forestier*

665 (K, MO, P). — Ibity, 20°03’47”S, 047°00’02”E, 1650 m, 16.II.1997, *Lowry 4810* (MO, P, TAN). — Prov. Fianarantsoa, Col des Tapia, 20°15’S, 047°09’E, 1400-1500 m, 26.X.1960, *Leandri 3323* (MO, P). — Vozontanin’i Tapia, 20°15’00”S, 047°06’30”E, 1500 m, 3.XII.1954, *Service forestier 11103* (G, K, MO, P, WAG). — Itremo, 20°32’30”S, 046°38’43”E, 1260 m, 24.III.1996, *Rakotomalaza 674* (MO, P, TAN). — Prov. Toliara, Atsimo-Andrefana, 22°17’S, 044°31’E, 30.X.1940, *Decary 16238* (MO, P). — Eod. loc., 23°15’S, 045°09’E, 400-1000 m, 19.X.1924, *Humbert 2805* (MO, P).

Description

Trees (1-)3-10 m tall; stilt roots absent; leaf-bearing twigs 2-4 mm in diameter, solid. Leaf blades obovate, elliptical, or sub-oblong, 3.5-9.5(-12) cm long, 1.3-3.6(-4.5) cm wide, base cuneate and tapering into narrow petiole wing; apex obtuse, secondary veins 6-8 on each side of the midrib, tertiary venation, when visible, non-scalariform; petiole 3-6(-11) mm long, slightly winged. Staminate peduncles 1.8-3.7 cm long; petaloid bracts *c*. 8 in number, 7-11 mm long, 5-7 mm wide, glabrous or the inner ones pubescent abaxially; heads of flowers 4.5-6 mm in diameter excluding the exserted anthers; staminodes present, sometimes bearing two much-reduced, barren pollen sacs, pistillode glabrous or very nearly so on distal surface. Pistillate peduncles 0.7-3.2 cm long; calyx in flower *c*. 3.5 mm in diameter, calyx in fruit 1.5-2 mm high, 4.5-5 mm in diameter, often somewhat lobed, pubescent abaxially but somewhat glabrescent; ovary sparsely pubescent (at least distally), somewhat glossy, mature fruit 17-25 mm long, rounded or pointed at apex; pubescent distally but glabrescent, reported as yellow, red, or brown near maturity.

Distribution

Central Plateau at elevations of 800-1650 m.

Remarks

Distinguished by its lack of stilt roots, short petioles, small pubescent pistillate calyx, and its occurrence in dry forests and savannas of the Central Plateau. Most similar to *U. louvelii*, but not usually as glossy-coated as that species, as well as differing in the features given in the key.

4. ***Uapaca densifolia*** Baker

Journal of the Linnean Society, Botany 20: 252 (1883).

Uapaca myricaefolia Baker, *Journal of the Linnean Society, Botany* 21: 440 (1884). — Type: Madagascar. Central Madagascar, s.d., fr., *Baron 2209* (lecto-, K [sheet K000406450], here designated)

Uapaca perrieri Denis, *Archives de Botanique, Bulletin mensuel*, Caen 1: 228 (1927). — Type: Madagascar, Domaine du Centre, Anosimbohampy au nord d’Andilamena, bois à 900 m alt., XI.1922, fr., *Perrier de la Bâthie s.n.* (holo-, P [sheet P00298678]).

Uapaca angustifolia Denis, *Archives de Botanique, Bulletin mensuel*, Caen 1: 227 (1927). — Type: Madagascar, Domaine de l’Est, Forêt d’Analamazoatra, 800 m alt., s.d., fl. ♂, *Perrier de la Bâthie 9618* (lecto-, P [sheet P00298668], here designated).

Uapaca densifolia var. *humbertii* Leandri, *Mémoires de l’Institut scientifique de Madagascar*, Série B, Biologie végétale 8: 257 (1957). — Type: Madagascar, Prov. Antsirana, Vallée de la Lokoho (Nord-Est), Mont Beondroka au nord de Maroambihy, sylve à lichens sur gneiss et quartzite, 1000-1450 m alt., 17-22.III.1949, fl. ♂, *Humbert 23499* (lecto-, P [sheet P00539632], here designated).

Uapaca sambiranensis Denis, *Archives de Botanique, Bulletin mensuel*, Caen 1: 226 (1927). — Type: Madagascar, Basses montagnes du Haut Sambirano, 500 m alt, XII.1922, fr., *Perrier de la Bâthie 15207* (holo-, P [sheet P00132880]; iso-, MO [sheet 04954787]).

Typus. — **Madagascar**. Central Madagascar, s.d., fl. ♂, *Baron 1917* (holo-, K [sheet K000406451]).

Representative material examined. — **Madagascar**. Prov. Antsiranana, Daraina, forêt d’Antsahabe, 13°13’S, 049°33’E, 1005 m, 19.I.2004, *Nusbaumer 1045* (G, MO, P). — Eod. loc., 910 m, 23.XI.2004, *Gautier 4737* (G, MO, P). — Marojejy RN, Mt. Anjenabe, 14°17’S, 049°46’E, 1100 m, 3-7.XI.1950, *Humbert 24126* (MO, P). — Eod. loc., Andranomilolo, 14°19’02”S, 049°19’04”E, 1222 m, 19.XI.2006, *Razakamalala 2988* (MO, P, TAN). — Eod. loc., Mt. Beondroka, 14°27’S, 049°47’E, 830-1210 m, 26.X.1989, *Miller 4440* (MO, P). — Prov. Toamasina, Ankirindro, 15°17’18”S, 049°32’49”E, 671 m, 22.XI.2002, *Antilahimena 1452* (MO, P). — Zahamena, 17°41’S, 048°49’E, 800-900 m, 24.VII.2003, *Rakotonandrasana 710*, *711* (MO, P). — Mantadia PN, 18°55’S, 048°25’E, 950-1150 m, 7.XI.1994, *McPherson 16528* (MO, P, TAN). — Eod. loc., 900 m, 10.XI.1994, *McPherson 16577* (MO, P, TAN). — Route de Lakato, 19°11’00”S,

048°26'00"E, XII.1972, *Morat 3974* (MO, P). — Prov. Antananarivo, 7 km E of Anjozorobe, 18°22'S, 048°00'E, 1300 m, 11.V.1987, *Schatz 1385* (MO, P).

DESCRIPTION

Tree (2-)5-15 m tall; stilt roots often reported as present; leaf-bearing twigs 3-5 mm in diameter, solid. Leaf blades obovate, (1.6-)3.7-11(-16) cm long, (0.7-)1.2-5(-8.7) cm wide, base cuneate, apex obtuse, secondary veins 6-9 on each side of the midrib, usually not impressed adaxially, higher venation usually not visible, not scalariform when visible; surfaces typically not glossy, drying somewhat reddish brown typically; margin often recurved; petiole (0.1-)0.8-2.0 cm long.

Staminate peduncle 8-15 mm long; flowering heads 3-4(-5) mm in diameter excluding the exserted stamens; staminodes present; pistillode somewhat pubescent on distal surface. Pistillate peduncle 0.8-2.0(-3.8) cm long; calyx 3 mm in diameter in flower, often conspicuously lobed, ciliate or sparsely pubescent on and near distal margin, often glabrate; ovary glabrous; calyx in fruit 1 mm high, 4-4.5(-5.5) mm in diameter, sparsely ciliate or glabrescent; fruit red at maturity, 12-15(-18) mm long, 12-14(-16) mm in diameter, usually pointed, glabrous.

DISTRIBUTION

Found in the forests of the east and north as well as those of the central plateau, at elevations up to 1675 m but rarely below 500 m.

REMARKS

This much-collected species can often be recognized by its small leaves and small fruits. Larger-leaved specimens can be identified by their non-scalariform venation, small, glabrous to sparsely pubescent pistillate calyx, and small fruit. Leaf variation is dismayingly strong in this species. Leaves from mid-elevation trees growing in humid forest are typically 6-11 × 3-5 cm, but leaves from plants apparently growing under similar conditions can be markedly smaller. Intermediates unfortunately connect the various extremes, and I have been unable to split the many specimens into coherent groups based on more than one character. I therefore am forced to recognize a widely delimited *U. densifolia*, much as did Leandri in 1958. The species most easily confused with *U. densifolia* is probably *U. louvelii*; specimens of the latter that lack mature fruits can be separated by their scalariform venation and the fact that all parts tend to be covered in a glossy exudate. *Uapaca bojeri*, also mistakable for *U. densifolia*, can be separated by its more uniformly pubescent pistillate calyx and its glabrous pistillode, as well as by its ecology.

5. ***Uapaca ferruginea*** Baillon
(Figs 1; 2)

Étude générale du groupe des Euphorbiacées: 596 (1858).

Uapaca clusioides Baker, *Journal of the Linnean Society, Botany* 21: 441 (1884). — Type: Madagascar, Central Madagasacar, s.d., fl. ♂, *Baron 2546* (iso-, P [sheet P00298669]).

Uapaca ferruginea var. *carnotiana* Leandri, *Mémoires de l'Institut scientifique de Madagascar*, Série B, Biologie végétale 8: 257 (1957). — Type: Madagascar, Prov. Fianarantsoa, Ambodivanana, près de Fort-Carnot, 800 m alt., 15.VII.1954, fr., *Service forestier 14392* (holo-, P [sheet P00539630]).

TYPUS. — **Madagascar**. Forêt de Ravinatsara, Manambo, Sainte Marie de Madagascar, IX.1850, fr., *Boivin s.n.* (lectotype, P [sheet 00298671], here designated).

REPRESENTATIVE MATERIAL EXAMINED. — **Madagascar**. Prov. Antsiranana, Ambato, 13°26'42"S, 048°33'18"E, 21.XI.1996, *Antilahimena 322* (MO, P). — Manantenina, 14°26'00"S, 049°45'42"E, 750 m, 21.XI.1996, *Messmer 254* (G, MO, P). — Masiaposa, 14°38'S, 049°41'E, 26.IV.1967, *Service forestier 27798* (G, K, MO, P). — Toamasina, Anjiahely, 15°25'01"S, 049°30'39"E, 420 m, 23.XII.2002, *Antilahimena 1578* (MO, P). — Entre Sahamalaza et Vohilava, 15°37'S, 049°30'E, 500 m, 9.III.1954, *Service forestier 9120* (K, MO, P). — Antanambao-Ambodimanga, 16°46'06"S, 049°42'22"E, 16.VI.2003, *Razakamalala 489* (MO, P, TEF). — Ambohidena forest, 16°51'11"S, 049°57'10"E, 10 m, 14.V.2003, *Rabenantoandro 1461* (MO, P, TEF). — Zahamena, 17°38'S, 049°29'E, 0-100 m, 23.I.1986, *Dorr 4618* (MO, P). — Eod. loc., 17°39'07"S, 048°58'14"E, 550-600 m, 21.X.2002, *Andrianjafy 294* (MO, P, TEF). — Mantadia, 18°55'S, 048°25'E, 950-1150 m, 7.XI.1994, *McPherson 16532* (MO, P, TEF).

Fig. 1. — Staminate specimen of *Uapaca ferruginea* Baill. showing capitate inflorescences (*McPherson 14844*).

DESCRIPTION
Trees 5-15 m tall; dbh 13-45 cm; stilt roots present; leaf-bearing twigs 7-15 mm in diameter, solid or hollow, coated with glossy exudate. Leaf blades obovate, elliptic, or suboblong, (12-)15-25(-28) cm long, (5.5-)9-14(-16) cm wide; base cuneate to obtuse, attenuate into petiole, apex obtuse; secondary veins 6-8(-9) on each side of the midrib; tertiary venation scalariform or nearly so, evident to somewhat obscure or nearly invisible, petiole (2.0-)2.5-6(-8) cm. Staminate peduncles 1.5-7.5 cm long; petaloid bracts *c*. 8 in number, 7-13 mm × 5-8 mm, ciliate, flowering head 7-8 mm in diameter excluding the exserted stamens; staminodes present; pistillode densely pubescent on distal surface. Pistillate peduncles (1.0-)2-4(-4.5) cm long, typically coated with exudate; calyx in flower *c*. 4 mm in diameter, coated with glossy exudate, pubescent or apparently sometimes glabrous; calyx in fruit 1-2 mm high, (3.5-)4.5-8(-9) mm in diameter, undulate or slightly lobed, glossy coating usually persistent, indument typically persistent and visible at fruiting time; fruit 15-20(-25) mm long, rounded or pointed at tip, sometimes drying with marked ridges while immature, usually coated with glossy exudate, yellowish or reddish at maturity.

DISTRIBUTION
Eastern and northern forests at lower and middle elevations (5-950 m).

REMARKS
Two forms of fruit seem to exist in this species. Most fruiting specimens bear essentially unridged (although immature) fruit, but a few exhibit a strongly ridged (also immature) fruit. All but two of the latter sort are also unusual in sharing an apparently glabrous calyx and all were collected in the general region of the Bay of Antongil. However, *Boivin s.n.* (type of the species) and *Service forestier 28805*, both from Île Sainte Marie, combine a ridged fruit with a calyx bearing the indument usual in the species. Leandri (1958) recognized *U. ferruginea* var. *carnotiana* as the name for the sort with the unridged fruit.

Typical specimens are marked by their stout leafy branches, large leaves with scalariform venation, and long peduncles. The species can be confused with *U. louvelii* if no large leaves or long peduncles are present; however, the copious indument typically persistent and evident on fruiting calyces will often make identification possible. Alternatively, the form with partly collapsed, and therefore conspicuously ridged, fruit is easily recognized. Also similar is *U. amplifolia*, but that species has smaller staminate heads and broader leaf blades and is restricted to the NW. Further collecting and study may, nevertheless, lead to the inclusion of *U. amplifolia* as a subspecies of *U. ferruginea*.

Two specimens (*Schatz 2312* and *2950*) from Nosy Mangabe in the Bay of Antongil are tentatively placed here, although their short petioles and the pistillate specimen's large fruit (28 mm long) make them somewhat unusual.

6. ***Uapaca littoralis*** Denis

Archives de Botanique, Bulletin mensuel, Caen 1: 228 (1927).

Uapaca betamponensis Leandri, *Mémoires de l'Institut scientifique de Madagascar*, Série B, Biologie végétale 8: 256 (1957). — Type: Madagascar, Prov. Toamasina, Betampona, Vohimarangitra, 1200 m. alt., 22.I.1945, fr., *Cours 2541* (lecto-, P [sheet P00132892], here designated).

Uapaca mangorensis Leandri, loc. cit.: 258 (1957). — Type: Madagascar, Prov. Toamasino, Mangorokely, vers Anosibe, district de Moramanga, 19.V.1954, fr., *Service forestier 10340* (holo-, P [sheet P00132903]).

Uapaca silvestris Leandri, loc. cit.: 259 (1957). — Type: Madagascar, Prov. Toamasina, massif forestier de Farankaraina, près de Maroantsetra, 20-25 m alt., 24.IX.1954, fr., *Service forestier 10838* (not "10858", as mistakenly published) (lecto-, P [sheet P00539625], here designated).

TYPUS. — **Madagascar**. Domaine de l'Est, Bas Matitana, sur la dune littorale, VII.1911, fr., *Perrier de la Bâthie 2379* (holo-, P [sheet P00132883]).

REPRESENTATIVE MATERIAL EXAMINED. — **Madagascar**. Prov. Toamasina, 5-12 km SW of Maroantsetra, 15°30'S, 049°39'E, 10 m, 28.XI.1987, *Schatz 1805* (MO, P). — Andrangazaha, 16°52'02"S, 049°40'52"E, 29.I.2004, *Rabevohitra 4870* (MO, P, TEF). — Île Sainte Marie, Ampanihy, 16°53'S, 049°55'E, 17.V.1969, *Service forestier 28852* (K, MO, P). — Soanierana Ivongo-Ampasimbola, 16°57'23"S, 049°34'04"E, 60 m, 4.VII.1996, *Birkinshaw*

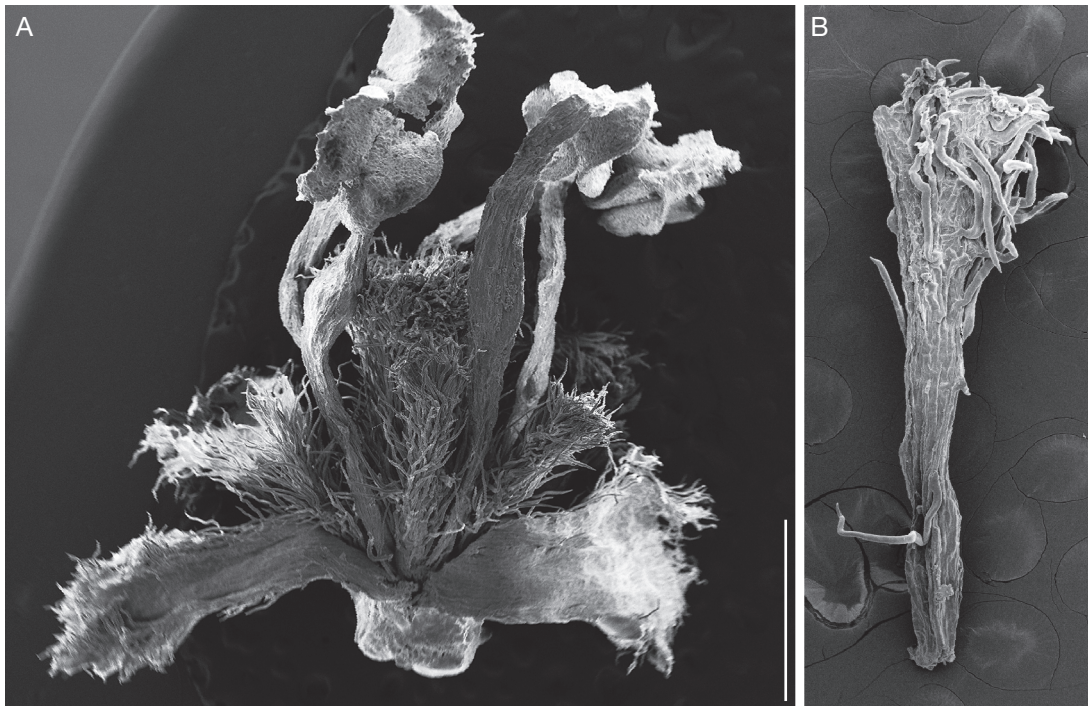

FIG. 2. — **A**, staminate flower of *Uapaca ferruginea* (SEM photo), side view with calyx dissected open, showing stamens and staminodes (2 of each in central foreground) and pistillode (in background) (*McPherson 14844*); **B**, individual staminode of *Uapaca louvelii* Denis (SEM photo) (*Koopman 131*). Scale bars: A, 1 mm; B, 0.5 mm.

340 (MO, P). — Tampolo, 17°16'52"S, 049°24'44"E, 10 m, 25.XI.1994, *Schatz 3607* (MO, P). — Eod. loc., 17°17'05"S, 049°24'34"E, 0 m, 4.VII.2001, *Rabenantoandro 561* (MO, P, TEF). — Zahamena, 17°44'S, 049°00'E, 500-750 m, 15-20.IX.1993, *Malcomber 2525* (MO, P). — Prov. Fianarantsoa, Ambahy, 20°47'53"S, 048°28'57"E, 22 m, 16.II.2004, *Ludovic 609* (MO, P). — Mahabo, 23°11'13"S, 047°42'27"E, 22 m, 26.VIII.2003, *Razakamalala 726* (MO, P, TEF).

DESCRIPTION

Trees 5-20 m tall, stilt roots present; leaf-bearing twigs 2-6 mm in diameter, solid, matte to somewhat glossy. Leaf blades elliptical, obovate or oblong, (4-)8-16 cm long, (1.4-)3-6.5 cm wide, base cuneate, often attenuate into the extended pulvinus, apex obtuse, secondary veins (8-)9-12(-18) on each side of the midrib, evident or obscure, tertiary venation non-scalariform, obscure, intersecondaries often visible, margin flat or recurved; petiole 1-5 cm long. Staminate peduncles 5-15(-40) mm long; the flower head 4-6 mm in diameter excluding the exserted stamens; stamens 5-6; staminodes present; pistillode sparsely pubescent on distal surface. Pistillate peduncles (0.6-)1.0-4.8 cm long; calyx 1.5-3 mm high, in fruit 4-8(-11) mm in diameter, pubescent (often glabrescent) or glabrous, usually undulate; fruit 23-27(-30) mm long and red at maturity, rounded apically or pointed, smooth or roughened by lenticel-like eruptions, pubescent at least distally or glabrous.

DISTRIBUTION

Eastern forests from near sea level up to 1200 m.

REMARKS

Distinguished by its relatively narrow leaf blades, numerous secondary veins, non-scalariform tertiary venation, often glabrescent pistillate calyx, and large fruit. Most readily mistakable for *U. thouarsii*, which, however, has leaf blades clearly less than three times as long as wide.

7. ***Uapaca louvelii*** Denis
(Fig. 2B)

Archives de Botanique, Bulletin mensuel, Caen 1: 230 (1927).

Uapaca louvelii var. *paralia* Leandri, *Mémoires de l'Institut scientifique de Madagascar*, Série B, Biologie végétale 8: 258 (1957). — Type: Madagascar. Prov. Fianarantsoa, région de Mananjary, Marohita, 0-50 m alt., 6.I.1952, fl. ♂, *Service forestier 5616* (holo-, P [sheet P00132889]).

TYPUS. — **Madagascar**. Prov. Toamasina, Tampina, au Sud de Tamatave, forêt littorale, s.d., fr., *Perrier de la Bâthie 14909* (lecto-, P [sheet P00132885], here designated).

REPRESENTATIVE MATERIAL EXAMINED. — **Madagascar**. Prov. Antsiranana, Mont Beondroka, 14°24'S, 049°46'E, 1000-1450 m, 17-22.III.1949, *Humbert 23458* (K, MO, P). — Eod. loc., 14°27'S, 049°47'E, 830-1210 m, 26.X .1989, *Miller 4446* (MO, P). — Prov. Toamasina, Tanambao, 16°46'07"S, 049°42'39"E, 30.I.2004, *Rabevohitra 4887* (MO, P, TEF). — Île Sainte Marie, 16°51'11"S, 049°57'10"E, 10 m, 13.V.2003, *McPherson 18911* (MO, P, TEF). — Eod. loc., 16°51'11"S, 049°57'18"E, 18.II.2004, *Rabevohitra 5064* (MO, P, TEF). — Ambila-Lemaitso, 18°49'S, 049°08'E, 0 m, 2.X.1993, *Lewis 715* (MO, P). — Eod. loc., 18°51'S, 049°08'E, 0-50 m, 29.VIII.1987, *Schatz 1467* (MO, P). — Antaimby, 20°22'21"S, 048°33'15"E, 13 m, 11.VI.2004, *Razakamalala 1368* (MO, P, TEF).

DESCRIPTION
Trees 4-15(-25) m; dbh 15-70 cm; stilt roots present; leaf-bearing twigs 4-5(-6) mm in diameter, typically coated with glossy exudate, solid; leaf blades obovate, (3.5-)7.5-15(-17) cm long, (1.5-)2.5-6(-7.5) cm wide, base cuneate and attenuate into petiole or occasionally obtuse; apex obtuse; secondary veins (4-)6-8(-9), impressed adaxially, slightly raised abaxially, the tertiaries often obscure but scalariform; petiole (0.1-)2-4.5(-5.5) cm long. Staminate peduncles 8-20(-23) mm long; the flower head 5-6 mm in diameter excluding the exserted stamens; stamens 5; staminodes present, pistillode pubescent on distal surface, sometimes densely so. Pistillate peduncles (2-)6-15(-23) mm long; calyx in flower *c*. 4 mm in diameter, coated with glossy exudate typically and appearing glabrous, but when without this coating usually somewhat pubescent, as is the cushion-like receptacle, in fruit 1-1.5 mm high, 4.5-5.5 mm in diameter, undulate or lobed; mature fruit 15-20 mm long, ovoid, rounded or somewhat pointed apically, often slightly ridged on drying, usually coated with glossy exudate.

DISTRIBUTION
Eastern forests from near sea level up to at least 1000 m.

REMARKS
Typical specimens are coated with a glossy exudate over both the vegetative and reproductive structures, but a more sparingly coated form exists that cannot be convincingly separated from this species on any additional basis. Larger-leaved specimens may be mistaken for *U. ferruginea*, but the latter's more evident scalariform venation, typically longer peduncles, and typically more densely pubescent pistillate calyx will usually serve to distinguish the two species, as will the latter's larger staminate flowering heads. Smaller-leaved specimens might be mistaken for *U. densifolia*, but that species' lack of scalariform venation should permit discrimination. Higher elevation forms tend to have shorter petioles.

8. ***Uapaca thouarsii*** Baillon

Étude générale du groupe des Euphorbiacées: 596 (1858).

TYPUS. — **Madagascar**. Prov. Toamasina, Sainte Marie, 1834, fr., *Bernier 252* (lecto-, P [sheet P00298675], here designated).

REPRESENTATIVE MATERIAL EXAMINED. — **Madagascar**. Prov. Antsiranana, Ambondrobe, 13°42'49"S, 050°05'13"E, 5 m, 1.III.2003, *Rabenantoandro 1399* (MO, P, TEF). — Marojejy, 14°27'15"S, 049°47'05"E, 757 m, 3-4.IV.1995, *Rasoavimbahoaka 614* (MO, P, TAN). — Mangerivola, 18°12'S, 048°53'E, 540 m, 10-15.IV.1999, *Ratovoson 67* (MO, P, TAN). — Prov. Toamasina, Ambodivato, 15°19'13"S, 049°33'29"E, 150 m, 20.XI.2002, *Schatz 4001* (MO, P). — Farakaraina, 15°25'S, 049°52'E, 20-25 m, 11.II.1955, *Service forestier 12913* (G, K, MO, P). — Tampolo, 17°17'00"S, 049°23'30"E, 10 m, 5.III.1957, *Service forestier 16624* (K, MO, P). — Prov. Fianarantsoa, Nosy Varika, 21°13'30"S, 048°21'00"E, 14.II.2004, *Ludovic 594* (MO, P, TEF). — Prov. Toliara, Andohahela, 250-500 m, 17-20.X.1992, *Malcomber 1672* (MO, P).

DESCRIPTION

Trees 5-30 m high; stilt roots usually present; leaf-bearing twigs 3-5(-10) mm in diameter, solid, glossy only at tip, matte below. Leaf blades obovate to subelliptic, 6.5-17(-26.5) cm long, 2.5-8(-16) cm wide, base cuneate, attenuate into extended pulvinus, apex obtuse, secondary veins 4-6(-7, but up to 11 if leaves over 20 cm long) on each side of the midrib, evident, tertiary venation very obscure to invisible, non-scalariform; petiole 1.2-4.5(-7) cm long. Staminate peduncles 15-25(-35) mm long, petaloid bracts *c*. 8 mm long, *c*. 7 mm wide; flowering heads 5-6 mm in diameter excluding exserted stamens; staminodes present; pistillode pubescent on distal surface. Pistillate peduncles 15-47 mm long, petaloid bracts *c*. 6-8 mm long, 4-5 mm wide; calyx in flower 5-6 mm in diameter, irregularly lobed or erose, densely pubescent, not coated in exudate; ovary densely pubescent; calyx in fruit 1-3 mm high, 5-9 mm in diameter, usually persistently pubescent but occasionally nearly glabrate, not glossy, entire or somewhat lobed; fruit 2.2-3.0(-3.3) cm long, rounded or broadly attenuate at base, pointed or rounded at the top, occasionally smooth but more usually roughened by lenticel-like eruptions, pubescent but to varying degrees glabrescent.

DISTRIBUTION

Eastern forests from near sea level up to 1600 m.

REMARKS

Distinguished by its relatively broad leaves with few and evident secondary veins, obscure and non-scalariform tertiary venation, and by its typically densely pubescent, coarsely lenticellate fruit. Specimens from near the southern end of the eastern forest tend to have smaller leaves and a less pubescent, smoother fruit, but intergrade with specimens from more northerly populations. Narrow-leaved forms can be distinguished from *U. littoralis* by the latter's more numerous secondary veins.

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