

# The threatened edible yams of the *Dioscorea sambiranensis* R.Knuth species complex (Dioscoreaceae): a new species and subspecies

**Paul WILKIN**

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB (United Kingdom)  
p.wilkin@kew.org

**Annette HLADIK**

CNRS, UMR 5145 et USM 104, Éco-Anthropologie et Ethnobiologie,  
and Muséum national d'Histoire naturelle,  
4 avenue du Petit Château, F-91800 Brunoy (France)  
hladik@mnhn.fr

**Vololoniaina JEANNODA**

Université d'Antananarivo, Faculté des Sciences,  
Département de Biologie et Écologie végétales,  
BP 906, Antananarivo 101 (Madagascar)  
vololoniaina.jeannoda@gmail.com

**Odile WEBER**

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB (United Kingdom)  
o.weber@kew.org

---

Wilkin P., Hladik A., Jeannoda V. & Weber O. 2009. — The threatened edible yams of the *Dioscorea sambiranensis* R.Knuth species complex (Dioscoreaceae): a new species and subspecies. *Adansonia*, sér. 3, 31 (2): 249-266.

## ABSTRACT

The *Dioscorea sambiranensis* species complex is endemic to Northern and North-Western Madagascar. Its taxa have broad, cordate leaves with petioles roughly equal in length to the blade, lax male inflorescences with flowers on long pedicels arranged in cymes of usually five or more flowers and flat discoid floral tori. Following study of its morphological variation, two new taxa in the complex are described and illustrated. *Dioscorea buckleyana* Wilkin was part of a mixed taxonomic concept under the invalid name *D. sambiranensis* R.Knuth subsp. *ambrensis* H.Perrier. It is glabrous like *D. pteropoda* H.Perrier, but differs in petiole and leaf blade morphology (especially blade texture), pedicel length and capsule morphology. Clarification of the limits of *D. sambiranensis* R.Knuth revealed an undescribed subspecies, subsp. *bardotiae* Wilkin, which differs in leaf blade and petiole dimensions, and lacks the surface ornamentation of the ovary and capsule found in subsp. *sambiranensis*. The relationship of *D. sambiranensis* with *D. namorokensis* Wilkin is revealed. Keys, descriptions and a distribution map are provided for all the taxa covered, and conservation status assessments given. The latter show that all of the taxa of the complex are, or are likely to be, threatened.

## KEY WORDS

Dioscoreaceae,  
*Dioscorea*,  
yams,  
Madagascar,  
endemic,  
edible,  
conservation,  
new species,  
new subspecies.

## RÉSUMÉ

*Les ignames comestibles menacés du complexe* *Dioscorea sambiranensis* R.Knuth (*Dioscoreaceae*): *une nouvelle espèce et une nouvelle sous-espèce.*

Le complexe de l'espèce *Dioscorea sambiranensis* est endémique de la région nord-nord-ouest de Madagascar. Les taxons qui le composent présentent de larges feuilles cordées dont la longueur du pétiole est sensiblement égale à celle du limbe, des inflorescences mâles lâches dont les fleurs sont arrangées en cymules comportant habituellement cinq fleurs ou plus dont le torus est de forme aplatie et discoïde. Suite à l'étude des variations morphologiques que présente le complexe, deux nouveaux taxons sont décrits et illustrés. *Dioscorea buckleyana* Wilkin faisait partie du concept hétérogène du nom *D. sambiranensis* R.Knuth subsp. *ambrensis* H.Perrier qui n'est pas validement publié. La plante est glabre comme *D. pteropoda* H.Perrier, mais présente des différences au niveau de la morphologie du pétiole et du limbe (en particulier la texture du limbe), la longueur du pédoncule floral et la morphologie de la capsule. Les clarifications relatives aux limites de l'espèce *D. sambiranensis* R.Knuth ont permis de mettre en évidence l'existence d'une sous-espèce non encore décrite, subsp. *bardotiae* Wilkin, qui diffère par les dimensions du limbe foliaire et du pétiole et par l'absence d'ornementation à la surface de l'ovaire et de la capsule, ornementation que l'on trouve dans la subsp. *ambiranensis*. Les relations entre *D. namorokensis* Wilkin et *D. sambiranensis* sont mises en évidence. Une clé, la description et la carte de distribution ainsi que le statut en matière de conservation sont fournies pour chacun des taxons abordés dans cette étude. L'analyse du statut de conservation montre que tous les taxons sont menacés ou en voie de l'être.

## MOTS CLÉS

Dioscoreaceae,  
*Dioscorea*,  
ignames,  
Madagascar,  
endémique,  
comestible,  
conservation,  
espèce nouvelle,  
sous-espèce nouvelle.

## INTRODUCTION

The first species of the *Dioscorea sambiranensis* R.Knuth species complex to be encountered by Northern Hemisphere science was found in the North of Madagascar on limestone at Lanivato by Boivin on his pioneering travels in the mid 19th century. However, it was not described until the 20th century (Perrier de la Bâthie 1928). This was *D. pteropoda* Boivin ex H.Perrier, a very distinctive taxon with winged petioles, a capsule with a marginal projection and seeds which possessed a small wing on all sides but which was fully developed on the basal side. Four years earlier, a much larger species, *D. sambiranensis* R.Knuth, had been described in the *Pflanzenreich* monograph (Knuth 1924) with extraordinary fleshy projections on the capsule. It was believed to be endemic to the Sambirano region and had the vernacular name *Angona*. Perrier

de la Bâthie (1928) attempted to remedy his earlier confusion of this species with another possessing campanulate floral tori (Jumelle & Perrier de la Bâthie 1910) by placing the name *D. fimbriata* Jum. & H.Perrier in synonymy with both *D. sambiranensis* and *D. tsaratananensis* H.Perrier. “*pro parte*”, because the name *D. fimbriata* was based on a mixed collection. This taxonomy was retained by Burkill & Perrier de la Bâthie (1950). *Dioscorea sambiranensis* has a flat, discoid floral torus and does not appear to be a close relative of any of the species with campanulate tori revised in Wilkin *et al.* (2008) where this nomenclatural problem is resolved. However, Perrier de la Bâthie (1928) also stated that *D. sambiranensis* had a close relative in the region of Diego Suarez (now Antsiranana) and cited his own collections *Perrier de la Bâthie 17511* from the Montagne des Français and *17551* from the Montagne d'Ambre. He indicated that these

specimens were in part glabrous and appeared to lack fleshy projections on the capsules, but that they were insufficient to understand the patterns of variation.

Nearly two decades later, having studied the collections of Prof. Humbert from Northern Madagascar, Perrier de la Bâthie (1946) felt able to link *Perrier de la Bâthie 17511* and *17551* with *Humbert 3956*, *19119* and *17070bis* as syntypes of *D. sambiranensis* subsp. *ambrensis* H.Perrier. This taxon was said to be less pubescent than the type subspecies and lacked its capsular projections. It was retained in the flora treatment four years later (Burkill & Perrier de la Bâthie 1950). Thus during a SYNTHESYS-funded visit to the herbarium of Muséum national d'Histoire naturelle, Paris (P) in 2006 specimens including those cited above were discovered by the first author laid away under *D. sambiranensis* subsp. *ambrensis*. All of the specimens of *D. sambiranensis* subsp. *ambrensis* cited above except *Perrier de la Bâthie 17551* and *Humbert 17070bis* were completely glabrous, with long, flattened and winged petioles and stems which had dried coppery red-brown. In contrast, *Perrier de la Bâthie 17551* and *Humbert 17070bis* were clearly pubescent, had a terete petiole (channeled above) and stems which had dried olive-brown. They appeared in every respect to belong to *D. sambiranensis* s.s.; even the three longitudinal ridges on the ovary margins were undulate in *Perrier de la Bâthie 17551*, suggesting that they would have developed into fleshy projections. Thus the concept of subsp. *ambrensis* of Perrier de la Bâthie (1946) was a combination of two distinct taxa. Furthermore, the protologue lacks a Latin description or diagnosis and thus *D. sambiranensis* subsp. *ambrensis* is an invalid name under article 36.1 of the Vienna code (MacNeill *et al.* 2006; <http://ibot.sav.sk/icbn/main.htm>) having been published in 1946. It has no nomenclatural standing.

The striking stem colour and petiolar morphology of the specimens other than *Perrier de la Bâthie 17551* and *Humbert 17070bis* suggested an affinity with *D. pteropoda*, but in that species the petiole is shorter than in the material under consideration. One of the specimens collected since the era of Perrier de la Bâthie possessed capsules with an unusual morphology, with differentiated layers in the fruit

wall visible at maturity. The outer layer appeared to extend beyond the inner on wing margins. There were other morphological characters in common with *D. sambiranensis*, such as male inflorescences to c. 20 cm long with many small flowers on long pedicels arranged in cymules.

*Dioscorea namorokensis* Wilkin was described by Wilkin *et al.* (2002) with reference to the widespread *D. soso* Jum. & H.Perrier. Its relationship with *D. sambiranensis* did not become clear until comparative study of specimens at P in 2003. Recent research has also uncovered specimens from Ambanja, Ankarana and Analamera with morphological similarities to both *D. namorokensis* and *D. sambiranensis*. Thus it became apparent that the species above formed a complex distributed across Northern Madagascar, with an outlying population or group of populations at Namoroka in the North West. A comparative morphological study of specimens of *D. sambiranensis* subsp. *sambiranensis* and subsp. *ambrensis*, *D. namorokensis* and *D. pteropoda* was undertaken in order to clarify the patterns of variation within and between its taxa. All of them share broad, cordate leaves with petioles roughly similar in length to the blade, lax male inflorescences with flowers on long pedicels arranged in cymules, with usually five or more flowers per male inflorescence node (at least towards the inflorescence base) and flat discoid floral tori.

## MATERIALS AND METHODS

The yams of Madagascar project has involved comparative morphological study and databasing of 1059 specimens from the following herbaria: B, BM, G, K, MO, P, TAN, TCD, TEF, WAG, UPS and the Département de Biologie et Écologie végétales, University of Antananarivo, Madagascar (abbreviated as DBEV below). The specimens used in the study of the *D. namorokensis* complex are cited below. Citations are ordered geographically within provinces and districts from North to South. Floral dissections were carried out where appropriate and measurements made using a Leica MZ95 or Carl Zeiss microscope with a measuring eyepiece. Vegetative and inflorescence characters were measured with a

TABLE 1. — Morphological differences between *Dioscorea pteropoda* H.Perrier and *D. buckleyana* Wilkin. Abbreviations: L, length; W, width. All measurements in millimetres.

Character	<i>D. pteropoda</i>	<i>D. buckleyana</i>
Leaf blade L × W	22-67 × 15-52	(30-)41-77 × 23-82
Leaf blade shape	Ovate to broadly so to ovate-deltoid, broadly so or orbicular-deltoid, never broader than long	Broadly or very broadly ovate to orbicular, sometimes broader than long
Leaf blade texture	Coriaceous	Chartaceous to thickly so and firm when dry
Number of main veins reaching leaf apex	(3 or) 5	(5 or) 7
Petiole L	9-26	24-76
Pedicle length in first flower of cymules in male inflorescence	0.5-2.9	4.8-9
Male flower tepal L × W	0.7-1.6 × 0.4-1.1	1.0-2.0 × 0.6-1.6
Male flower tepal shape	Ovate to broadly so, elliptic or elliptic-oblong	Elliptic to ovate or broadly so or rarely orbicular
Number of capsule per infructescence	1-5	(1-)3-9
Capsule L × W	27-46 × 17-27	23-37 × 13-18
Capsule shape	Elliptic to obovate or broadly so in outline, rounded at base and apex	Oblong-elliptic to obovate in outline, base rounded to cuneate (immature), apex bluntly acute to truncate or shallowly retuse
Capsule morphology	2-layered, exocarp developing to c. 1.5 mm beyond endocarp on margins giving an appearance like a submarginal vein	3-layered, exocarp extending beyond endocarp on margins as a 1.5-3 mm wide wing, tending to curl up when dry giving the whole capsule a more oblong appearance, mesocarp thin and pithy when dry, only present around axis
Seed L × W	c. 6.2 × 4.2	7.0-8.5 × 5.0-6.5
Seed wing L × W	c. 10 × 5.5	13-15 × 5.5-6.5

dial caliper. The distribution map and conservation status assessments were prepared using ArcView 3.3 (see Willis *et al.* 2003 for methods) as part of a larger study of the conservation status and systematics of *Dioscorea* in Madagascar (Wilkin *et al.* unpubl. data).

## RESULTS

Comparative morphological study recovered five entities in the complex. Two are entirely glabrous, with flattened, winged petioles and stems which usually dry red-brown to coppery red-brown. There are discrete morphological differences between them (see Table 1). One of these is *D. pteropoda*, with shorter petioles (usually), shorter pedicels in

the first flower of the cymules at each node of the male inflorescence and a distinct fruit shape and structure. The other corresponds to part of the mixed concept of *D. sambiranensis* subsp. *ambrensis* introduced above. This is described below as a new species, *D. buckleyana* Wilkin.

The remaining three taxa are pubescent on both vegetative and reproductive organs, although pubescence density is variable and fruiting plants are glabrescent, so hairs may need to be searched for on the veins near the leaf blade base or on young growth, for example. Their stems usually dry dull olive brown to dark brown. They also have terete petioles with a narrow channel on the upper surface. Their key morphological characters are summarised in Table 2. This shows that the spatially isolated *D. namorokensis* from the Réserve

TABLE 2. — Summary of the morphological characters of the pubescent taxa of the *Dioscorea sambiranensis* R.Knuth complex with terete petioles. Abbreviations: **L**, length; **W**, width. All measurements in millimetres. \* Only three seeds measured from vegetatively heterogeneous *De Block, Rakotonasolo & Randriamboavonjy 1079* (see taxonomic treatment below).

Character	<i>D. sambiranensis</i> s.s.	<i>D. namorokensis</i> Wilkin	<i>D. sambiranensis</i> subsp. <i>bardotiae</i> Wilkin
Lateral nodal organs	Present	Absent	Present
Leaf blade L × W	67-152 × 64-173	26-85 × 15-75	25-86 × 21-88
Leaf blade shape	Broadly ovate to orbicular, sometimes broader than long	Narrowly to very broadly ovate, never broader than long	Ovate to orbicular, sometimes broader than long
Leaf primary vein number reaching apex	7 or 9	3 (or 5)	5 (or 7) (3 in <i>De Block, Rakotonasolo &amp; Randriamboavonjy 1079</i> )
Leaf lower surface venation	Prominent, primary veins flattened and thus deeper than wide; oblong in cross-section	Prominent, primary veins terete in cross-section, depth and width more or less equal	Prominent, primary veins flattened and thus deeper than wide; oblong in cross-section
Leaf lower surface indumentum	Tomentose when immature; when fully expanded present on veins only, usually dense on primary veins, more lax on secondary and tertiary, glabrescent	Tomentose when immature, when fully expanded present on veins and on blade between them	Tomentose when immature; when fully expanded present on veins only, usually dense on primary veins, more lax on secondary and tertiary, glabrescent
Petiole L	48-143	6-74	13-55
Length of primary branch of cymule of male inflorescence when flowers open	0-1.7(-3.8)	5-11	0-1.1
Length of internal branches of cymule of male inflorescence when flowers open	0-2.4	3.5-6.1	0-1.1
Pedicel length in first flower of cymules in male inflorescence	5.6-8.3(-13)	3.0-7.0	2.3-7.3
Male flower tepal L × W	0.8-1.5 × 0.5 -1	0.5-1.2 × 0.6 -1.3	0.6-1.1 × 0.6-0.9
Male flower torus diameter	0.6-1.0	0.7-1.1	0.6-1.0
Capsule L × W	28 -35 × 14 -18	Capsule unknown	22-30 × 13-18
Capsule shape	Oblong-oblancheolate to oblong in outline, base cuneate, apex acute to rounded	Capsule unknown	Oblong to elliptic or oblong-obovate in outline, base obtuse to cuneate, apex truncate to broadly acute
Capsule morphology	2-layered, axis and margin with dense to lax fleshy, rounded, sinuate exocarpic projections (membranous when dry), endocarp thicker and firmer	Capsule unknown (but ovary longitudinal ridges not undulate)	Appearing 1-layered, no projections present
Seed L × W	8-9.4 × 5.0-5.9	Seeds unknown	6.2-7.1 × 3.7-4.2*
Seed wing L × W	13.2-14 × 5.8-6	Seeds unknown	8.8-9.2 × 5.1-6.1*

naturelle intégrale de Tsingy de Namoroka west of Majunga is discrete in its vegetative morphology. Its floral morphology does not appear to have diverged appreciably, but the primary branch of

the cymules in the male inflorescences are usually longer than in other taxa, contributing to a more lax and gracile appearance of the male inflorescence as a whole.

All other pubescent specimens are from the Manongarivo or Daraina areas or further North. Most have female plants with longer capsules in which fleshy projections develop on the axis and margins of the ovary (Table 2). These correspond to *D. sambiranensis* s.s. A few have shorter capsules which lack fleshy projections (see Table 2). These plants have smaller leaves and shorter male floral pedicels, although the ranges overlap slightly in both characters. Many of the specimens seen were from areas with limestone substrates. *Dioscorea sambiranensis* s.s. has not been collected on limestone to date. However, this raises the possibility that the smaller leaves represent an ecotypic rather than genotypic response. Since they can only be completely reliably distinguished in female plants by means of the ovary or capsule, and because the two entities are allopatric, they are best treated at subspecific rank (cf. Wilkin 2001) and a new sub-

species, *D. sambiranensis* subsp. *bardotiae* Wilkin is described below. There is heterogeneity between the specimens from Ankarana and those from Ambanja and Analamera which requires further study when more material is available. The taxon which lacks capsular projections and is undescribed has only been collected to date on the Ankarana massif, in Ambanja district and as a problematic specimen from Analamera (see below), while specimens of *D. sambiranensis* have been collected from Manongarivo, on Montagne d'Ambre and near Daraina.

New descriptions are also provided below for *D. sambiranensis* subsp. *sambiranensis* and *D. pteropoda*, in which substantial numbers of new specimens have been collected since Burkill & Perrier de la Bâthie (1950) to give the systematic context. Keys to male and female plants are provided for the species complex.

#### KEY TO MALE FLOWERING PLANTS OF THE *DIOSCOREA SAMBIRANENSIS* R.KNUTH SPECIES COMPLEX

1. Indumentum absent on all parts. Petiole flattened, with a broad channel on the upper surface, and winged ..... 2
- Indumentum present on vegetative and reproductive organs. Petiole ± terete, with a narrow channel on the upper surface, not winged ..... 3
2. Petiole 24-76 mm long. Leaf blade chartaceous to thickly so, usually with 7 main veins reaching the apex. First pedicel of cymules in inflorescence not less than 4.8 mm long ..... 1. *D. buckleyana*
- Petiole 9-26 mm long. Leaf blade coriaceous, usually with 5 main veins reaching the apex. No pedicel more than 2.9 mm long ..... 3. *D. pteropoda*
3. Lateral nodal organs present as a semicircular to crescent-shaped amplexicaul flange on either side of node, node and flanges to 8 mm in diam.; leaf lower surface veins prominent and flattened so that they are deeper than wide and they are oblong in cross-section; pubescent only on vein; when fully developed (i.e. with flowers open) first branch of cymule in inflorescence not more than 3.8 mm long, internal cymule branches not more than 2.4 mm long ..... 4
- Lateral nodal organs absent, nodes not exceeding the maximum stem diam. (2 mm); leaf lower surface veins prominent and terete in cross-section so that depth and width are subequal, pubescent on leaf lower surface veins and blade; fully developed first branch of cymule 5-11 mm long, internal branches of cymule 3.5-6.1 mm long ..... 2. *D. namorokensis*
4. Petiole 48-143 mm long; leaf blade 67-152 mm long; not on limestone substrates ..... 4a. *D. sambiranensis* subsp. *sambiranensis*
- Petiole 13-55 mm long; leaf blade 25-86 mm long; on limestone substrates ..... 4b. *D. sambiranensis* subsp. *bardotiae*

KEY TO FEMALE FRUITING PLANTS OF THE *DIOSCOREA SAMBIRANENSIS* R.KNUTH SPECIES COMPLEX

1. Capsule (and ovary after anthesis) with dense to lax fleshy (membranous when dry), rounded, sinuate projections on axis and margins ..... 4a. *D. sambiranensis* subsp. *sambiranensis*  
— Capsule (and ovary) surface smooth, lacking projections ..... 2
2. Capsule with exocarp clearly differentiated and developing beyond thickened margin of endocarp giving an appearance like a submarginal vein when immature. Petiole flattened with a broad channel on the upper surface and winged ..... 3  
— Capsule with exocarp not clearly differentiated from endocarp and not developing beyond thickened margin. Petiole ± terete with a narrow channel on the upper surface, not winged ..... 4
3. Capsule 3-layered, with a thin and pithy mesocarp around axis, exocarp developing 1.5–3 mm beyond thickened margin of endocarp, apex bluntly acute to truncate or shallowly retuse. Leaves chartaceous to thickly so ..... 1. *D. buckleyana*  
— Capsule 2-layered, lacking a mesocarp, exocarp developing to c. 1.5 mm beyond thickened margin of endocarp; apex rounded. Leaves coriaceous ..... 3. *D. pteropoda*
4. Lateral nodal organs absent; leaf blade lower surface primary veins prominent and terete in cross-section so that depth and width are subequal, pubescent on leaf lower surface veins and blade ..... 2. *D. namorokensis*  
— Lateral nodal organs present as 2 c. 1–3 mm broad, flat, semicircular to crescent-shaped projections on either side of node and petiole base; leaf blade lower surface primary veins prominent and flattened so that they are deeper than wide and they are oblong in cross-section; pubescent only on veins ..... 4b. *D. sambiranensis* subsp. *bardotiae*

## SYSTEMATICS

1. *Dioscorea buckleyana* Wilkin, sp. nov.  
(Fig. 1)

*Dioscorea pteropoda affinis sed petiolo 24–76 mm (nec 9–26 mm) longo, lamina folii chartacea vel crasse chartacea (nec coriacea), pedicello primo cymularum in inflorescentia masculina ut minimum 4.8 mm longo (nec ut maximum 2.9 mm tantum longo), capsula ad apicem obtuse acuta vel truncata vel non profunde retusa (nec rotundata) tristrata (nec bistrata) mesocarpio tenui medullosoque circumcirca axem proviso (nec mesocarpio carentia), exocarpio evoluto 1.5–3 mm (nec c. 1.5 mm tantum) ultra marginem incrassatam endocarpi extenso differt.*

TYPUS. — **Madagascar.** Antsiranana (Diégo Suarez) Province, Antsiranana II District, Montagne des Français, 13.IV.1970, ♀ fr., Veyret 1301 (holo-, P! [P00496391]).

PARATYPES. — **Madagascar.** Antsiranana (Diégo Suarez) Province, Antsiranana II District, bord de la route vers Ramena, 30.I.2004, ♀ immat. fr., Hladik 6820 (P!). — Bord de la route vers Ramena, 30.I.2004, ♂ fl., Hladik 6821 (P!). — Environs de Antsiranana (Diégo Suarez), Montagne des Français, end XII.1924, ♂ fl., Humbert

3956 (P!). — Montagne des Français près d'Antsiranana (Diégo Suarez), I.1926, ♂ fl., Perrier de la Bâthie 17511 (P!). — Mahavanona, Mahagaga, Ambohimarina, à 3 km au nord-est du village Mahagaga, 12°24'35"S, 49°22'19"E, 10.II.2005, ♀ immat. fr., Rakotondrifara, Randrianasolo, Be, Benjara & Jaovoavy 286 (MO!). — Collines et plateaux calcaires de l'Analamera, I.1938, ♂ fl., Humbert 19119 (P!). — Ambilobe District, Anivorano, Maraotoalana, Réserve spéciale d'Ankarana, forêt du Mahoro entrée est, traversée en direction du nord-ouest, 12°49'S, 49°15'E, 7.XI.1997, ♂ fl., Bardot-Vaucoulon 934 (K!, MO, P!).

## DESCRIPTION

A twining vine to c. 6 m, stems annual from a fleshy tuber. Tubers (only apical part seen) two, probably one per rainy season, to c. 3 cm in diam., vertically oriented, divergent, epidermis brown with irregularly distributed flat, orbicular to elliptic, cream to brown pustules c. 5 mm in diam., crown not clearly differentiated. Indumentum wholly absent, even from young buds. Stems left-twining, to c. 6 mm in diameter, terete and unarmed, white to pink below ground, above pale green to purplish, drying coppery red-brown.

Leaves alternate, blade (30-)41-77 × 23-82 mm, broadly or very broadly ovate to orbicular, sometimes broader than long, chartaceous to thickly so and firm when dry, especially in fruiting specimens, dull green when fresh, drying olive-brown above, paler below, veins (5 or) 7 to the apex, with a bifid vein to each basal lobe, margins entire, base cordate, with a broad, open, shallow sinus 2-13 mm deep, apex rounded and abruptly narrowed into a 6.5-14 mm long acumen bearing a 2.5-3.5 mm long, deltoid to narrowly so forerunner tip, drying concolorous to brown, margins sometimes curling upwards when dry; primary and secondary venation prominent on lower leaf blade surface; petiole (Fig. 1B) 24-76 mm long, 1.7-2.5 mm wide when dry and flat, colour as stem, flattened, channeled on upper surface, margins winged (often folded in herbarium specimens), wing undulate towards base and apex (only clearly visible in living material); cataphylls to 8 mm long, ovate, acuminate, thickly chartaceous, colour as stem, with lateral nodal flanges on either side at base; lateral nodal flanges ("stipules" of Burkill 1960) amplexicaul around node, semicircular, to *c.* 6 mm in diameter together, continuous with petiole base and undulate in fresh material; bulbils absent. Inflorescences 1 per axil, simple, pendent, lax, axes ridged and angled. Male inflorescences 28-205 mm long (including 6-20 mm long peduncle), axis 0.5-2.1 mm wide, colour as stem, sometimes present on stems bearing only cataphylls, (not true leaves) in November and December, leaves developing later in the rainy season; flowers in cymules at nodes or solitary or in pairs in early stages of development or towards inflorescence apex, nodes fairly regularly spaced *c.* 5-8 mm apart, cymules either solitary or appearing to be one cymule above the other (Fig. 1D); cymule bracts (1.0-)1.2-2.1 × 0.7-1.3 mm, ovate, membranous, short-acuminate; bracteoles similar but smaller and inserted at 90° to cymule bract; cymule primary branch to 1.8 mm long, only visible in later stages of cymule development. Female inflorescences only known from infructescences, 50-94 × 1.2-2 mm, peduncle 17-27 mm long, spicate, colour as stem, axis bearing (1-)3-9 capsules. Male flowers rotate at anthesis but tepals ascending to erect before and after anthesis, on (2.5-)4-9 mm

long pedicels (first pedicel of cymule 4.8-9 mm long), angled, thickened only immediately under flower, subtending 0.5-1.3 × 0.2-0.7 mm long, ovate to elliptic or lanceolate, acute to short-acuminate floral bracts; tepal whorls undifferentiated to weakly differentiated (outer narrower), inserted on a flat, discoid to weakly concave, thin torus 0.6-1.1 mm in diam., translucent except in centre where pistillodes are inserted; tepals 6, 0.8-2.0 × 0.6-1.6 mm, free, elliptic to ovate or broadly so or rarely orbicular, pale green, turning brown after anthesis, apex obtuse to acute, thinly chartaceous; stamens erect, filaments 0.1-0.25 mm long, stout, anthers 0.15-0.4 × 0.15-0.5 mm, broadly orbicular-oblongoid, dorsifixed, making a T-shape with filament, pale yellow; pistillodes *c.* 1 mm long, 3 conical, erect fleshy structures in centre of torus, inner margins contingent. Female flowers unknown. Capsules 23-37 × 13-18 mm, ascending at *c.* 30-5° to axis at dehiscence on a 1.5-4.2 × *c.* 1.5-2 mm, (weakly) clavate, angled capsular stipe, oblong-elliptic to obovate in outline, base rounded to cuneate (immature), apex bluntly acute to truncate or shallowly retuse, tepals persistent in immature capsules but lost by dehiscence; wall divided into three layers (only visible at maturity) exocarp externally pale brown with dense red-brown mottling, extending beyond endocarp on wing margins giving an appearance like a submarginal vein, though the 1.5-3 mm wide exocarp wing tends to curl up at maturity giving the whole capsule a more oblong appearance, mesocarp thin and pithy when dry, only present around axis, endocarp tough, smooth and pale tan inside. Seeds winged primarily at base, but with a *c.* 1 mm wide, undulate extension to the wing on the outer side and apex of the seed (thus the side of the seed adjacent to the axis is the only unwinged part), seed 7.0-8.5 × 5.0-6.5 mm excluding wing, flattened ovoid to flattened ovoid-reniform, dark brown, wing 13-15 × 5.5-6.5 mm, oblong, apex obtuse to rounded, membranous, golden-brown.

#### REMARKS

*Bardot-Vaucoulon 934* has 1-1.3 mm long floral bracts, 1.5-2 × 1.1-1.6 mm tepals and 0.3-0.4 × 0.3-0.5 mm anthers. Thus it falls in the high end of the range for all these characters. This variation



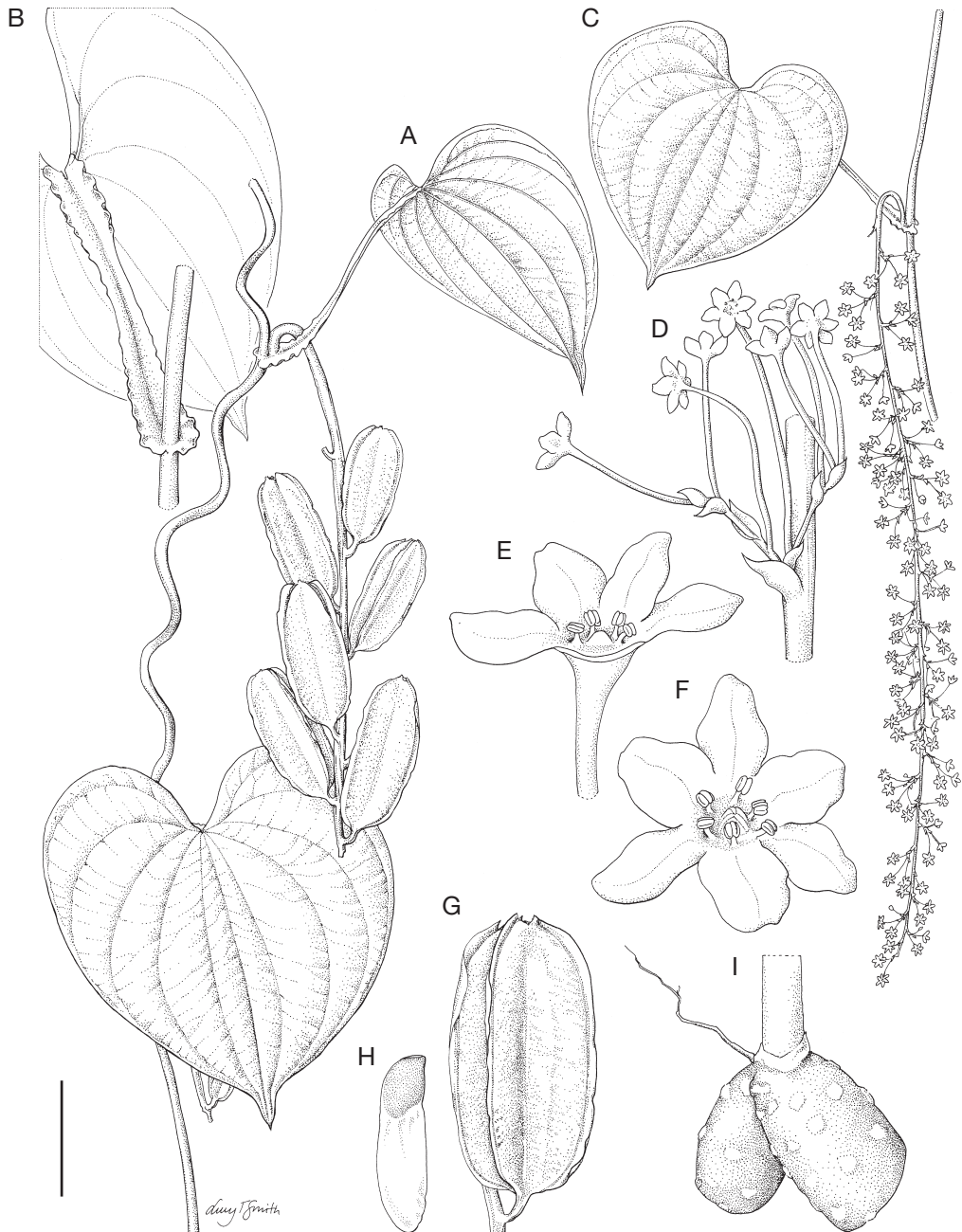


FIG. 1. — Vegetative and reproductive (excluding female floral) morphology in *Dioscorea buckleyana* Wilkin: **A**, habit, showing a node, the petiole, upper and lower leaf surfaces and an infructescence; **B**, detail of a node and petiole, showing the undulate petiole wing and lateral nodal flange; **C**, a node with an axillary male inflorescence; **D**, a cymule (appearing to be one cymule above another due to very short cymule branches) showing the cymule bract, floral bracts and pedicels; **E**, male flower with two tepals and two stamens removed showing the torus, remaining stamens and pistillode; **F**, intact male flower viewed from above; **G**, seed and seed wing; **H**, capsule showing exocarp extending beyond thickened endocarp margin on each wing giving an appearance like a submarginal vein; **I**, apical region of current and previous growing season tuber and stem base. Drawn from Veyret 1301 (A, C, D), Humbert 19119 (E-H) and photographs of Hladik 6820 and 6821 (B, I) by Lucy Smith. Scale bar: A-C, 2.5 cm; D, 3.3 mm; E, F, 1.2 mm; G, H, 1.5 cm; I, 4 cm.

needs review when more material is available. Male plants of *D. buckleyana* can flower before their leaves develop, e.g., *Bardot Vaucoulon 934, Humbert 3956*.

#### DISTRIBUTION AND ECOLOGY

As Figure 3 shows, *D. buckleyana* has been encountered at the Réserve spéciale d'Ankarana, Analamera and in and near the Montagne des Français. It appears to be restricted to limestone substrates, with at least six of the nine specimens seen by the authors being from areas of calcareous rock. It is found in deciduous forest at altitudes from 50 to 300 m.

#### ETYMOLOGY

*Dioscorea buckleyana* is named for Dr George Buckley to recognise his lifetime of dedication to helping children with disabilities, in particular in the United Kingdom and Romania.

#### VERNACULAR NAME

*Dioscorea buckleyana* is known as *Taravy* or *Oviala* in the Antsiranana region, or *Ovy* at Analamera.

#### USES

Tuber edible.

#### CONSERVATION STATUS

The extent of occupancy (EOO) of *D. buckleyana* is 916 km<sup>2</sup>, and its area of occurrence (AOO) is 181 km<sup>2</sup> using a cell width of 6.01 km; it occupies five cells (see Willis *et al.* 2003 and Callmender *et al.* 2007 for discussion of the importance of cell size). Both of these measures suggest that the appropriate IUCN red list assessment is EN (IUCN 2001). Rapoport Analysis (Rapoport 1982) gives an area of 2023 km<sup>2</sup> and three subpopulations. AOO also indicates that there are three subpopulations, as does Figure 3. The exploitation of wild yams in Northern Madagascar is extensive, based on the authors' field experience there, so decline in numbers of mature plants is likely. As Figure 3 shows, the known populations of this species are in or near protected areas. A provisional IUCN red list assessment of EN B1ab(v); B2ab(v) is proposed.

## 2. *Dioscorea namorokensis* Wilkin

*Kew Bulletin* 57: 902 (2002). — Type: **Madagascar**. Mahajunga, Soalala Subprefecture, Commune d'Andranomavo, Réserve naturelle intégrale Tsingy de Namoroka, NE side, 16°27'27"S, 45°23'26"E, 4.II.2000, ♂ fl., Wilkin, Rakotonasolo & Davis 1126 (holo-, TAN!; iso-, K! [K000098740-3]).

#### REMARK

For description, illustration, specimen citations and supporting information see Wilkin *et al.* (2002). We have not seen any specimens collected since that paper was published.

#### CONSERVATION STATUS

*Dioscorea namorokensis* appears to be endemic to the Réserve naturelle intégrale Tsingy de Namoroka. The EOO and AOO of *D. namorokensis* are unknown because there are insufficient collections to calculate them (four specimens from two localities in the NE part of Namoroka). Thus its provisional IUCN red list assessment (IUCN 2001) must be DD. However, even if it was found over the whole of Namoroka (c. 95 km<sup>2</sup>) its EOO and AOO would be small enough to place it in a threatened category, probably EN or CR. Based on the specimens available, its AOO would be c. 2 km<sup>2</sup>, with a cell width of 2 km and one locality. It is unlikely to occur outside Namoroka given the different soils and lack of dense woody vegetation in the surrounding area.

## 3. *Dioscorea pteropoda* Boivin ex H.Perrier

*Mémoires de la Société linnéenne de Normandie*, Nouvelle Série, Section Botanique 1 (2): 17 (1928); Burkill & Perrier de la Bathie in Humbert, *Flore de Madagascar et des Comores*, 44<sup>e</sup> famille: 51 (1950). — Type: **Madagascar**. Antsiranana Province, Antsiranana II District, Lanivato (Liny Vatou), 1835, ♂ fl. & ♀ immat. fr., *Bernier 265* (2<sup>e</sup> envoi), (lecto-, P! [P00442458], selected here; isolecto-, P! [P00442459 & P00442460]). Remaining former syntypes: **Madagascar**. Antsiranana Province, Antsiranana II District, Lanivato (Liny Vatou), *Boivin 2343*, 1846, ♂ fl. & ♀ immat. fr. (P! [P00442461-3]). — Lanivato (Liny Vatou), 1840, ♂ fl., *Bernier s.n.* (K! [K000099031])

OTHER MATERIAL EXAMINED. — **Madagascar**. Antsiranana Province, Antsiranana II District, 5 km from Andranom-ena, on the road towards Sahafary forest, 12°35'10.6"S,

49°27'38.1"E, 26.IV.2008, ♀ fr., *Andriamahay & Rakotoarisoa 2000* (K!, SNGF). — Collines et plateaux calcaires de l'Analamera, I.1938, ♂ fl., ♀ fl. & immat. fr., *Humbert 19163* (K!, P!). — Analamera, along Ambatabe River, 12°40'25"S, 49°32'40"E, 7.I.2002, ♂ fl., *De Block, Rakotonasolo & Randriamboavonjy 1104* (BR, K!, MO, TAN). — Ambilobe District, collines et plateaux calcaires de l'Ankarana du Nord, 29.II.1960, ♂ fl., ♀ fl. & immat. fr., *Humbert & Cours 32769* (P!). — Collines et plateaux calcaires de l'Ankarana du Nord, 29.II.1960, ♀ immat. fr. *Humbert & Cours 32780* (BR, P!). — Mont Ambohipiraka au nord-est d'Ambilobe (Vallée du Mananjeba), 3.II.1960, ♀ immat. fr. *Humbert & Cours 32877* (P!). — Mont Ambohipiraka au nord-est d'Ambilobe (Vallée du Mananjeba), 3.II.1960, ♂ fl., *Humbert & Cours 32878* (K!, P!). — Ankatoto, Mont Ambohipiraka, 5.II.1960, ♂ fl., *Cours & Humbert 5658* (P!). — Ambilomagadro, km 114, Montagne Ambohibe, 8.II.1960, ♂ fl. & ♀ fl. & immat. fr., *Cours & Humbert 5699* (P!). — Collines et plateaux calcaires de l'Ankarana, forêt près d'Ambodimagadro, XII.1937-I.1938, ♀ fl. & immat. fr., *Humbert 19038* (K!, P!). — Massif de l'Ankarana, Ambilomagadro, partie ouest, 13°00'46"S, 49°07'51"E, 31.I.2003, ♀ fl., *Bardot-Vaucoulon, Andriananantoanina & Manesy 1384* (MO, P!, TAN). — Massif de l'Ankarana, Ambilomagadro, partie ouest, 13°00'46"S, 49°07'51"E, 31.I.2003, ♂ fl., *Bardot-Vaucoulon, Andriananantoanina & Manesy 1384bis* (MO, P!, TAN). — Vohemar District, commune rurale de Daraina, Daraina, forêt de Solaniampilana-Maroadabo à 580 m du point cote 214, au 90°, 10.III.2004, ♀ fr., *Gautier, Wohlhauser, Nusbaumer & Ranirison LG4539* (G, K!).

#### DESCRIPTION

A twining vine to about 2 m in height, stems annual from a fleshy tuber. Tuber 1.2-1.5 m long and 5-7.5 cm in diameter according to label of *Bernier 265* (2<sup>e</sup> envoi) collected in 1835, apparently not investigated since. Indumentum wholly absent. Stems left-twining, to *c.* 2 mm in diameter, terete, unarmed, drying smooth and dull brown to red-brown, lower stem and cataphylls not seen. Bulbils not present. Leaves alternate, blade 2.2-6.7 × 1.5-5.2 cm, ovate to broadly so to ovate-deltoid, broadly so or orbicular-deltoid, coriaceous, dark green and sometimes glossy above, paler green to glaucous-green or grey-green below, drying olive-green to brown above, grey-green below, sometimes with a reddish hue, margins entire, base cordate to shallowly so or rarely truncate, sinus 2-12 mm deep, smaller in leaves towards vegetative shoot tips and in fertile shoots, apex 4-13 mm long, acute

to acuminate with a 0.8-3.6 mm long, deltoid to narrowly deltoid, thickened, concolorous to dark brown forerunner tip, veins (3 or) 5 to the apex, with a bifid vein or pair of veins to both sides of the base, both primary and secondary veins prominent on both leaf blade surfaces; petiole 9-26 mm long, to 2.5 mm in width (including wings), flattened, channeled above and strongly winged on both sides, usually reddish-brown, blotched on wings, darker at base and apex, wings sometimes excurrent at apex onto basal vein for a few mm; lateral nodal spines ("stipules" of Burkill 1960) not present but petiole base also winged and partially to wholly amplexicaul, resulting on an ovate or elliptic winged petiole base, and sometimes the whole node, to 6 mm in diameter. Inflorescences one per axil, simple, pendent. Male inflorescences racemose, primary axis 1.5-11.8 cm long (including 4-16 mm long sterile basal region), flattened and possessing narrow wings, with up to 25 nodes *c.* 2-6 mm apart, each with a lax cymule of 3-5(-8) flowers, reduced to 2 flowers per cymule or rarely solitary flowers towards the apex, cymule bract 0.8-2.0 mm long, narrowly elliptic to very narrowly ovate, thickly membranous with a thicker midrib, apex long-acuminate, bracteoles not present, cymule primary branch 0.4-2.3 mm long. Female inflorescences to 4 cm long, racemose, axes flattened and angled to more or less terete, sometimes winged, bearing 1 to 5 solitary flowers on the apical part, 5-7 mm apart on the axis. Male flowers scent not recorded, pedicels 0.5-2.9 mm long, weakly clavate, 0.2-0.55 mm in diameter at apex, ridged, one floral bract at each pedicel base, 0.35-1.5 × 0.15-0.6 mm, size diminishing towards cymule apex, narrowly elliptic to narrowly lanceolate, basal bracts of cymule sometimes narrowly ovate or lanceolate, apical bracts sometimes sublinear, apex always long-acuminate; tepal whorls not differentiated, free or slightly fused at base, erect in most flowers (presumably post/pre anthesis) but fully open and rotate in one or two flowers per inflorescence, inserted on a discoid torus 0.6-1.2 mm in diameter, only thickened around the pistillode and area of filament insertion, marginal texture as tepals, tepals 6, 0.7-1.6 × 0.4-1.1 mm, ovate to broadly so, elliptic or elliptic-oblong, thickly membranous, apex acute to obtuse; stamens erect,

filaments 0.1–0.3 mm long, filiform, inserted in two triangular whorls around pistillode towards torus centre, anthers 0.15–0.3 × 0.15–0.3 mm, ovoid-oblongoid, dorsifixed and therefore making a T-shape with filament, pale yellow; pistillode a 3-lobed, subconical central projection to *c.* 0.3 mm long, drying dark brown. Female flowers scent not recorded, each on a long stalk comprising a (0.6–)1.3–2.6 mm long primary branch (from basal bract to floral bracteole) and a 1.1–1.9 mm long pedicel (from floral bract to ovary base), both flattened and ridged, basal bract (equivalent to cymule bract in male inflorescence) 1.1–1.6 × 0.3–0.4 mm, lanceolate to narrowly so, apex acuminate, thickly membranous, midrib thicker, floral bract like basal bract but smaller; ovary *c.* 5.3–7.5 mm long, 3-angled, narrowly elliptic to narrowly lanceolate in outline; tepals not differentiated into 2 whorls, 6, 1.3–1.9 × 0.9–1.3 mm, ovate to oblong ovate, acute to obtuse, inserted on a flat, discoid torus 1.3–1.6 mm in diameter; staminodia 6, 0.2–0.4 mm long, erect to ascending, clearly staminiform to scarcely differentiated, filamentodes inserted around style bases; styles/stigmas 3, 0.4–0.5 mm long, fused at base to form a broad column, free and reflexed above with the bifid stigmas at the tips of its horizontal branches, diameter *c.* 1.2 mm. Capsule 2.7–4.6 × 1.7–2.7 cm, on a 5–10 mm long stipe, ascending at *c.* 70–45° to axis at dehiscence, elliptic to obovate or broadly so in outline, rounded at base and apex, capsules collected before dehiscence drying pale tan and “double wing” (where thin exocarp develops beyond endocarp giving an appearance like a sub-marginal vein; Fig. 1H) often only weakly developed; mesocarp absent even at maturity. Seeds (immature only) *c.* 6.2 × 4.2 mm, chestnut-brown, flattened-ovoid, winged at base only, wing *c.* 10 × 5.5 mm, membranous, translucent golden-brown.

#### REMARKS

The lectotype above was selected because it is the most representative specimen of those sheets and did not comprise mixed male and female material. One specimen of *D. pteropoda*, *d'Alleizette 1407* was collected near Toamasina in eastern Madagascar according to the label. This locality is undoubtedly erroneous.

#### DISTRIBUTION AND ECOLOGY

*Dioscorea pteropoda* has been collected near Daraina and Ambilobe, in the Réserve spéciale d'Ankarana and at Lanivato and Analamera in Northern Madagascar (see Fig. 3). It is found in dry, semideciduous to deciduous forest with a low canopy, occurring in dense forest but sometimes persisting in regularly burnt or degraded areas with mixed grassland and shrubs, at altitudes from 40 to 400 m. *Dioscorea pteropoda* is often associated with limestone, or more rarely with sandstone, and has been found on red sand and sandy clay soils. It can be associated with, for example baobabs, *Pachypodium* Lindl. and *Adenia* Forssk. as at Analamera.

#### VERNACULAR NAME

*Totongana* (Analamera), *Ovifotsy* (Lanivato). The name *Totongana* is applied to an *Aristolochia* species at Antrema near Mahajanga.

#### USES

Tuber edible cooked.

#### CONSERVATION STATUS

The EOO of *D. pteropoda* is 2335 km<sup>2</sup>, and its AOO is 789 km<sup>2</sup> using a cell width of 9.36 km; it occupies nine cells. The former suggests that the appropriate IUCN red list assessment is EN, and the latter VU (IUCN 2001). Rapoport Analysis (Rapoport 1982) gives an area of 1657 km<sup>2</sup> and four subpopulations. AOO also indicates that there are four subpopulations. Unfortunately many of the known localities are outside the protected area of the Réserve spéciale d'Ankarana (Fig. 3) and thus under greater threat of habitat loss. Levels of exploitation of wild yams in Northern Madagascar are high as stated above. Thus we suggest a provisional IUCN red list assessment of VU B1ab(iii,v); B2ab(iii,v).

#### 4. *Dioscorea sambiranensis* R.Knuth

In Engler (ed.), *Das Pflanzenreich* 87 (4. 43): 353 (1924); Perrier de la Bâthie, *Mémoires de la Société linnéenne de Normandie, Nouvelle Série*, Section Botanique 1 (2): 20 (1928); Burkill & Perrier de la Bâthie in Humbert, *Flore de Madagascar et des Comores*, 44<sup>e</sup> famille: 52 (1950). — Type: Madagascar. Antsiranana Province, Ambanja

District, Vallée du Sambirano, Beangona, XII.1922, ♂ fl., *Perrier de la Bâthie* 15684 (holo-, B, not seen; iso-, K! [K000098957], P! [P00442455-7]).

*Dioscorea fimbriata* Jum. & H.Perrier, *Annales du Musée colonial de Marseille*, série 2, 8: 425 (1910). — Types: Madagascar. Antsiranana Province, Ambanja District, Sambirano, VIII.1908, ♀ fr., *Perrier de la Bâthie* 8201 (syn-, P! [P00496536], K!) (mixed collection, see remarks below). — Sambirano, X.1912, *Perrier de la Bâthie* 8244 (syn-, P! [P00496538]).

#### DESCRIPTION

A twining vine to at least 10 m, sometimes very vigorous in humid forest habits, stems annual from a fleshy tuber. Tubers (according to Burkill & Perrier de la Bâthie 1950) one per rainy season, vertically oriented, divergent, to 2 m × 10–20 cm, cylindrical or sometimes forming a spiral, epidermis thin, off-white, parenchyma white, subtended by a crown buried at least 15 cm below the soil surface. Indumentum of 0.05–0.7 mm long, straight hairs, erect to appressed, slightly swollen and straw-yellow at the base, otherwise acuminate in outline, colourless, hairs appearing grey when dense and tomentose (for example on young growth and inflorescence apices and ovaries), usually present on veins only of leaf lower surface (though usually increasingly lax on secondary and tertiary veins), pedicels and tepal dorsal surfaces, less dense on stems, inflorescence axes and developing capsules, occasionally a few on leaf upper surface, all older parts glabrescent. Stem base not seen. Upper stems left-twining, terete or drying with a longitudinal groove, to 6 mm in diameter, sometimes drying with a deep longitudinal groove, unarmed, dull light brown, olive-brown to black-brown or russet brown when dry, when fresh green above, paler below. Leaves alternate, blade 35–152 × 25–173 mm when fully expanded, usually broadly ovate so to orbicular or broader than long, rarely ovate, chartaceous to thinly so, often thickly so in fruiting material, shiny bright green above, paler below, drying dull mid to dark olive-green to grey-green, sometimes brown with age, margins entire; base cordate, sinus 5–44 mm deep, usually narrow, sometimes weakly hippocrepiform; apex rounded and acuminate to broadly deltoid, 12–17 × 7–18 mm, with a *c.* 3–8 × 1 mm long, narrowly deltoid, darker forerunner tip at the apex,

one seen with inrolled margins; veins (5 or) 7 or 9 to the apex, with a smaller, often bifid, vein to each basal lobe, primary venation prominent on lower leaf blade surface, sides flattened and thus deeper than wide and oblong in cross-section; petiole 18–143 mm long, colour as stem, basal and apical pulvini darker, terete but deeply channeled on upper surface, wings absent; lateral nodal organs (“stipules” of Burkill 1960) *c.* 1–3 mm broad, (projections plus node to *c.* 8 mm in diam.), flat, semicircular to crescent-shaped, thick and firm, on node and petiole base; cataphylls unknown (stem base not seen); bulbils not present. Inflorescences usually simple, pendent, axes and flowers green or yellow-green, usually with some red or purple pigmentation except towards the margins, scent not recorded. Male inflorescences 1 or 2 per axil, racemose, rarely compound, peduncle 3–42 mm long, axis 32–332 × 0.4–2.2 mm, flattened, ridged and angled colour as stem; nodes 3–8 mm apart, irregularly spaced; cymules 1 or sometimes apparently 2 per node (probably due to very short basal cymule branches), bearing up to 12 green flowers, sometimes with a reddish or purplish hue, where 2 cymules one inserted above the other, cymule primary branch absent or to 1.7(–3.8) mm long and stout in some older cymules; cymule bracts 0.9–2.7 × 0.3–1.1 mm, ovate to elliptic, narrowly so or lanceolate, membranous with a thick opaque midrib, apex acute to acuminate; female inflorescences 19–137 mm long, on a 9–58 mm long peduncle, simple, spicate, axis colour as stem. Male flowers on pedicels 1.2–8.3(–13) × 0.2–0.4 mm, very slender in appearance, filiform, angled, only broadened immediately under flower; floral bracts at pedicel bases, 0.6–1.3 × 0.2–0.6 mm, narrowly ovate to lanceolate, like cymule bracts but smaller, decreasing in size towards cymule apex; tepal whorls undifferentiated to weakly differentiated (outer narrower and more acute), inserted on a 0.6–1.1 mm in diameter, ± flat, discoid torus, tepals 6, 0.6–1.5 × 0.5–1.0 mm, free, spreading to ascending, ovate or elliptic to narrowly to broadly so or ovate-oblong, thickly membranous, apex acute to obtuse, rarely short-acuminate; stamens in 2 whorls of 3, filaments erect, 0.05–0.25 mm long, anthers 0.15–0.3 × 0.1–0.25 mm, oblong to elliptic-oblong in outline,

dorsifixed, yellow; pistillode 3-lobed, *c.* 0.1 mm long, in a depression surrounded by a raised annulus in torus centre or with lacunae between pistillode lobes. Female flowers sessile, floral bracts 1.1-3.3 × 0.3-1.4 mm, linear to ovate, apex acuminate, bracteole if present like bract but smaller, inserted at 90° to it, *c.* 1 mm apart in immature fruit; ovary *c.* 3.3-5.9 mm long, 3-angled, narrowly oblong to elliptic in outline, sometimes with a few flat, fleshy, rounded projections (membranous when dry) on the margins even when barely expanded; tepal whorls undifferentiated, inserted on a flat, discoid torus 0.5-1.0 mm in diameter, tepals 6, 0.9-1.6 × 0.7-1.0 mm, ovate to broadly so or ovate-oblong, chartaceous, apex acute to obtuse; staminodia 6, 0.1-0.15 mm long, substaminiform, 0.2-0.3 mm wide at antheriform apex; styles 3, 0.25-0.35 mm long, centrally fused at base, free part stout, spreading, stigmatic region bifid, lobes *c.* 0.2 mm long, spreading at *c.* 90° to each other (i.e. Y-shaped). Capsule 22-35 × 13-18 mm, patent to axis to ascending at *c.* 90°-30° to axis at dehiscence on a 2.3-7.7 × 1.2-1.7 mm, weakly clavate stipe, oblong-oblancheolate or oblong-obovate to oblong or elliptic in outline, green or yellow-green to purple or brown-hued, base obtuse to cuneate, apex truncate to broadly acute or rounded, bearing floral remains, axis and margin with dense to lax fleshy, rounded, sinuate projections (membranous when dry) present at maturity, in immature capsules small sinuate lobes on margins, axis undulate; tepals persistent at capsule apex until capsule fully expanded; capsule dehiscing almost to base to expose seed, operculum breaking away still bearing sinuate lobes, capsule dark to pale brown, lobes rigid, 2-layered (sinuate lobes part of thin outer layer), inner layer thicker and firmer, smooth inside. Seed winged at base only, 6.2-9.4 × 3.7-5.9 mm excluding wing, flattened lenticular-reniform, dull matt brown, wing 8.8-14 × 5.1-7.1 mm, oblong to weakly deltoid-oblong, apex truncate to obtuse, membranous, translucent golden-brown.

4a. *Dioscorea sambiranensis* R.Knuth  
subsp. *sambiranensis*

MATERIAL EXAMINED. — Madagascar. Antsiranana Province, Antsiranana II District, autour du Camp

d'Ambre, Montagne d'Ambre, I.1926, ♂ fl., ♀ fl., immat. fr., *Perrier de la Bâthie 17551* (K!, P!). — Montagne d'Ambre National Park, de la Voie des Mille Arbres à la Grande Cascade, 21.I.2002, ♀ immat. fr., *De Block, Rakotonasolo & Randriamboavonjy 1332* (BR, K!, MO, P, TAN). — Montagne d'Ambre National Park, de la Voie des Mille Arbres à la Grande Cascade, 21.I.2002, ♂ fl., *De Block, Rakotonasolo & Randriamboavonjy 1331* (BR, G, K!, MO, P, TAN). — Antsiranana, à la limite Nord de l'Ankarana, forêt d'Analamahitso, au S d'Anivorano-Nord, I.1938, ster., *Humbert 17070bis* (P!). — Vohehar District, commune rurale de Daraina, Daraina, forêt d'Antsahabe à 980 m du point cote 1088, à 122°, 13°13.19'S, 49°33.15'E, 3.XII.2004, ♀ fl., *Nusbaumer & Ranirison LN1344* (G, K!). — Commune rurale de Daraina, Daraina, forêt d'Antsahabe à 1150 m du point cote 1088, à 81 degrés, 13°12.81'S, 49°33.32'E, 13.I.2004, ♂ fl., *Nusbaumer LN946* (G, K!). — Ambanja District, River Antsaharatsy, Réserve naturelle intégrale de Tsaratanana, 13°48'49"S, 48°47'29"E, 16.IV.2000, ♀ immat. fr., *Birkinshaw, Alamaitsy, Razafindrazaka & Rabenantoandro 694* (MO, P). — Besaratribe (locality?), 6.XII.1963, ♂ fl., ♀ fl., immat. fr., *Rakotozafy 293* (P!, TAN!). — Antsiranana, Sambirano, IV.1922, ♀ fr., *Perrier de la Bâthie 16285* (P!). — Antsiranana, Bassin moyen du Sambirano au sud de Marovato, ♀ fr., II.1951, *Humbert & Capuron 25450* (BR!, K!, P!). — Antsiranana, bassin supérieur du Sambirano, berges du Sambirano, XII.1937, ♂ fl., *Humbert 18566* (P!). — Antsiranana, Réserve spéciale de Manongarivo, bassin-versant de rano Biromba, bas Ambahatra: cours inférieur du bassin-versant rano Ambahatra, 13°55.336'S, 48°27.905'E, 2.VI.1999, ♀ fr., *Wohlhauser & Andriamalaza SW60140* (G, K!). — Antsiranana, Réserve spéciale de Manongarivo, bassin-versant de rano Bemahalegny, moyen Ambahatra: cours moyen du bassin-versant rano Ambahatra, 13°57.87'S, 48°26.837'E, 15.III.1998, ♂ fl., ♀ fl., immat. fr., *Wohlhauser SW60043* (G, K!, MO).

DESCRIPTION

Leaf blade 67-152 mm long; petiole 48-143 mm long. Pedicel in first flower of male cymule 5.6-8.3(-13) mm long. Capsule 28-35 mm long, oblong-oblancheolate to oblong in outline, base cuneate, apex acute to rounded; appearing 2-layered, axis and margin with dense to lax fleshy, rounded, sinuate exocarpic projections (membranous when dry), endocarp thicker and firmer.

REMARKS

In the protologue of *D. sambiranensis*, Knuth (1924) specifically refers to a specimen of a male plant, although Perrier de la Bâthie also collected



FIG. 2. — Vegetative and reproductive (excluding female floral) morphology in *Dioscorea sambiranensis* R.Knuth subsp. *bardotiae* Wilkin: **A**, habit, showing two nodes, the petiole, upper and lower leaf surfaces and a male inflorescence; **B**, habit, showing a node, upper leaf surface, an infructescence and its capsules; **C**, a node, side view, showing the lateral nodal organs; **D**, the horizontally oriented pubescence on the veins of the leaf lower surface; **E**, a cymule of a male inflorescence; **F**, a male half flower showing three tepals, three stamens and the shape of the torus; **G**, the torus of the male flower viewed from above, tepals removed, showing the insertion of the anther and the lacunae between the lobes of the pistillode (dark areas); **H**, male flower viewed from the side, three tepals removed showing the anthers and pistillode; **I**, the capsule of *D. sambiranensis* subsp. *sambiranensis* for comparison with **B**. Drawn from *Bardot Vaucoulon* 274 (**A**, **C**-**H**), *Lewis et al.* 1134 (**B**) and *Humbert* 25450 (**I**) by Lucy Smith. Scale bar: **A**, **B**, **I**, 2 cm; **C**, **D**, 5 mm; **E**, 3 mm; **F**-**H**, 0.8 mm.

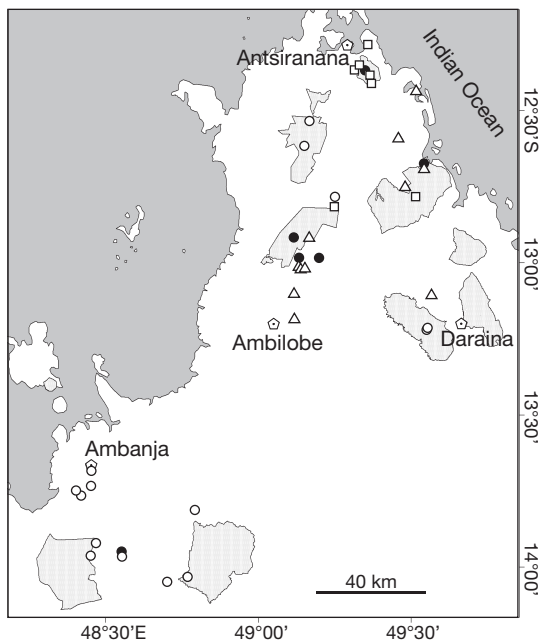


FIG. 3. — Map showing the localities in Northern Madagascar where *D. buckleyana* Wilkin (□), *D. pteropoda* Boivin ex H. Perrier (△), *D. sambiranensis* R. Knuth subsp. *sambiranensis* (○) and *D. sambiranensis* subsp. *bardotiae* Wilkin (●) have been collected. The main settlements are shown to help orientation. The shaded areas are protected zones. From the North they are: Montagne des Français, Montagne d'Ambre National Park, Analamera, Réserve spéciale d'Ankarana, Daraina (3 areas), Réserve naturelle intégrale de Tsaratanana and Réserve spéciale de Manongarivo.

female plants under 15684. One of the three specimens under this number at P comprises female material and seedlings and one at K has female flowers. Thus they cannot be isotypes because they came from a different plant. The single type sheet at B has further locality data: Manongarivo, Ankaizina. The protologue of *D. fimbriata* does not cite any specimens but the description can only have been based on Perrier de la Bâthie 8201 and 8244 because all of the other specimens cited in Perrier de la Bâthie (1928) were collected after 1910. Thus both are syntypes, but not that element of 8201 which became 8201bis after the protologue was published (see Wilkin et al. 2008).

The capsule of *D. sambiranensis* subsp. *sambiranensis* can be as little as 23 mm long when it is insect damaged (e.g., Perrier de la Bâthie 8201).

#### DISTRIBUTION AND ECOLOGY

*Dioscorea sambiranensis* subsp. *sambiranensis* has been collected in the Sambirano area, including the Réserve spéciale de Manongarivo, on Tsaratanana, near Ambanja and Daraina, on the Northern edge of the Ankarana massif and at the Montagne d'Ambre (Fig. 3). It occurs in light gaps, near watercourses or on rocky slopes in shady humid evergreen to deciduous forest at altitudes from 250 to 1100 m, sometimes persisting in areas of shifting cultivation. It is found on cineritic, sandy, siliceous or granitic substrates. Burkill & Perrier de la Bâthie (1950) report that it is found on metamorphic rocks and syenites. There is no record of it being associated with limestone.

#### VERNACULAR NAME

*Angona* (Ambanja, Sambirano) or *Oviala* (Anivorano/Ankarana from Humbert 17070bis).

#### USES

Tuber edible cooked. Burkill & Perrier de la Bâthie (1950) also suggest that tuber sections are sun-dried and sold.

#### CONSERVATION STATUS

The EOO of *D. sambiranensis* subsp. *sambiranensis* is 9604 km<sup>2</sup>, and its AOO is 3115 km<sup>2</sup> using a cell width of 17.6 km; it occupies ten cells. EOO suggests that the appropriate IUCN red list assessment is VU, and AOO NT (IUCN 2001). Rapoport Analysis (Rapoport 1982) gives an area of 5890 km<sup>2</sup> and three subpopulations. AOO also indicates that there are three subpopulations. Thus a provisional IUCN red list assessment of NT is proposed, given that we believe over-extraction to be likely.

#### 4b. *Dioscorea sambiranensis* R. Knuth subsp. *bardotiae* Wilkin, subsp. nov. (Fig. 2)

*Subsp. sambiranensis affinis sed petiolo 13-55 mm (nec 48-143 mm) longo, lamina folii 25-86 mm (nec 67-152 mm) longa, capsula 22-30 mm (nec 28-35 mm) longa, projecturis e margine atque axe carentibus (nec capsula nec ovario ad marginem axemque projecturis rotundatis sinuatis dense nec laxe ornato) differt.*



**TYPUS.** — Madagascar. Antsiranana Province, Ambilobe District, Réserve spéciale d'Ankarana, Camp des Anglais, Massif de l'Ankarana, ♂ fl., 10.XI.1990, *Bardot-Vaucoulon 274* (holo-, P! P00496533).

**PARATYPES.** — Madagascar. Antsiranana Province, Antsiranana II District, Sakaramy, Montagne des Français, ♂ fl., 8.XI.1944, *Homolle 372* (P!). — Analamera, bank of Irodo River, near Irodo camp, 12°40'25"S, 49°32'40"E, 6.I.2002, ♀ fr., *De Block, Rakotonasolo & Randriamboavonjy 1079* (BR, K!, MO, P, TAN). — Antsiranana, Réserve spéciale d'Ankarana, forest on outcropping close to Camp des Anglais, ♀ immat fr., 18.II.1994, *Lewis, McDonagh, Andrianarisata, Randriamabolona, Andiratsiferama & Bled 1134* (K!, MO!, P!). — Antsiranana, District d'Ambilobe, forêt d'Andranonakoho, km 103 de la route de Diégo à Ambilobe, calcaires de l'Ankarana, 29.I.1960, ♀ immat. fr., *Humbert & Cours 32831* (P!). — Antsiranana, District d'Ambilobe, forêt d'Andranonakoho, km 103 de la route de Diégo à Ambilobe, calcaires de l'Ankarana, 29.I.1960, ♀ immat fr., *Cours & Humbert 5540* (P!). — Ambanja District, RN 4, Marovato, 12.XII.1952, ♂ fl., *Sajy in RN 4752* (P!, TAN!).

#### DESCRIPTION

Leaf blade 25–86 mm long; petiole 13–55 mm long. Pedicel in first flower of male cymule 2.3–7.3 mm long. Capsule 22–30 mm long, oblong to elliptic or oblong-obovate in outline, base obtuse to cuneate, apex truncate to broadly acute; appearing 1-layered, no projections present on margins or axis.

#### REMARKS

The specimen *De Block, Rakotonasolo & Randriamboavonjy 1079* is atypical in a number of vegetative morphological characters; its leaves are very thin, and oblong cystoliths are visible in the upper surface. They are pubescent above and below, with the lower surface being tomentose at maturity and appearing to have hairs both on the veins and the areas of blade between them (like *D. namorokensis*). The primary veins are prominent below and terete rather than oblong in cross-section, as in *D. namorokensis*, and just 3 reach the apex. In terms of leaf blade shape, *De Block, Rakotonasolo & Randriamboavonjy 1079* has very shallow basal sinuses. However, it possesses lateral nodal organs and its capsule is typical of *D. sambiranensis* subsp. *bardotiae* (although the capsule of *D. namorokensis* is unknown). It is unfortunate that it is only represented by a single female specimen; further

material, especially male plants, should be sought at Analamera.

#### DISTRIBUTION AND ECOLOGY

The distribution of *D. sambiranensis* subsp. *bardotiae* is scattered, occurring in dry, (semi-) deciduous forest from 40 to 300 m in altitude at Ambanja, Ankarana, the Montagne des Français and Analamera (Fig. 3). At the latter three localities it is on limestone. It is possible that the smaller leaves of subsp. *bardotiae* as opposed to subsp. *sambiranensis* represent an ecological response to lower water and nutrient levels on limestone, rather than genotypic difference. However, the capsules of the two subspecies are substantially different (see Fig. 2B, J).

#### VERNACULAR NAME

*Marika, Oviaala* (Marovato, Ambanja)

#### USES

Unknown but tuber probably edible.

#### CONSERVATION STATUS

The EOO of *D. sambiranensis* subsp. *bardotiae* is 3335 km<sup>2</sup>, and its AOO is 1910 km<sup>2</sup> using a cell width of 19.5 km; it occupies five cells. EOO suggests that the appropriate IUCN red list assessment is EN, and AOO VU (IUCN 2001). Rapoport Analysis (Rapoport 1982) gives an area of 16422 km<sup>2</sup> and two subpopulations, while AOO indicates that there are four subpopulations. Three of the five known localities are in protected areas. The provisional IUCN red list assessment is VU B1ab(iii); B2ab(iii).

#### Acknowledgements

The COLPARSYST programme provided financial support for a visit by the first author to the Muséum national d'Histoire naturelle in Paris in October 2003, and the SYNTHESYS programme a further visit in October 2006; he would like to thank Leandro Leoz and all the staff of the Herbarium for their help, especially Jean-Noël Labat and Thierry Deroin. Lucy Smith produced the excellent Figures 1 and 2. Dave Simpson's constructive comments improved an earlier version of this manuscript.

Thanks also go to Jean-Noël Labat and Oswaldo Tellez Valdez for their reviews which led to significant clarification of this paper, and to the editors of *Adansonia* for their input.

## REFERENCES

- BURKILL I. H. 1960. — The organography and the evolution of the Dioscoreaceae, the family of the yams. *Journal of the Linnean Society (Botany)* 56: 319-412.
- BURKILL I. H. & PERRIER DE LA BÂTHIE H. 1950. — Dioscoréacées, in HUMBERT H. (ed.), *Flore de Madagascar et des Comores*. Muséum national d'Histoire naturelle, Paris, 78 p.
- CALLMANDER M. W., SCHATZ G. E., LOWRY II P. P., LAIVAO M. O., RAHARIMAMPIONONA J., ANDRIAMBOLOLONERA S., RAMINOSOA T. & CONSIGLIO T.K. 2007. — Identification of priority areas for plant conservation in Madagascar using Red List criteria: rare and threatened Pandanaceae indicate sites in need of protection. *Oryx* 41: 168-176.
- IUCN. 2001. — *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission, Gland, Switzerland; Cambridge, UK, ii + 30 p.
- JUMELLE H. L. & PERRIER DE LA BÂTHIE H. 1910. — Fragments biologiques de la Flore de Madagascar IV. Les ignames du nord-ouest. *Annales du Musée colonial de Marseille*, série 2, 8: 388-428.
- KNUTH R. 1924. — Dioscoreaceae, in ENGLER H. G. A. (ed.), *Das Pflanzenreich*, 87 (4. 43). H. R. Engelmann (J. Cramer), Leipzig: 1-387.
- PERRIER DE LA BÂTHIE H. 1928. — Les Dioscoréacées de Madagascar. *Mémoires de la Société linnéenne de Normandie*, Nouvelle Série, Section Botanique 1 (2): 1-48.
- PERRIER DE LA BÂTHIE H. 1946. — Révision des Dioscoréacées de Madagascar et des Comores. *Notulae Systematicae* (Paris) 12: 197-206.
- RAPOPORT E. H. 1982. — *Areography: Geographical Strategies of Species*. Pergamon Press, New York, 269 p.
- WILKIN P. 2001. — Yams of South-Central Africa. *Kew Bulletin* 56: 361-404.
- WILKIN P., RAKOTONASOLO F., SCHOLS P. & FURNESS C. A. 2002. — A new species of *Dioscorea* (Dioscoreaceae) from Western Madagascar and its pollen morphology. *Kew Bulletin* 57: 901-909.
- WILKIN P., ANDRIANTENAINA W. P., JEANNODA V. & HLADIK A. 2008. — The species of *Dioscorea* L. (Dioscoreaceae) from Madagascar with campanulate tori, including a new species from Eastern Madagascar. *Kew Bulletin* 63: 583-600.
- WILLIS F., MOAT J. & PATON A. 2003. — Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern Africa. *Biodiversity and Conservation* 12: 1537-1552.

Submitted on 20 October 2008;  
accepted on 3 July 2009.