Taxonomic revision of the Malagasy endemic and enigmatic *Euphorbia* section *Pachysanthae* (Euphorbiaceae)

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Abstract

Among the more than 170 species of *Euphorbia* (Euphorbiaceae, Malpighiales) that occur in Madagascar, some remain poorly known and dramatically under-collected, and are based on vague and incomplete descriptions. As part of an ongoing study of the genus in Madagascar, a revision is presented of *E* section *Pachysanthae*, which comprises six species endemic to this island that show clear morphological affinities to one another. Expanded descriptions are provided for the four species already named, and the two others are described as new (*Euphorbia haevermansii* and *Euphorbia nusbaumeri*), both from the Daraina region in north-eastern Madagascar. An identification key is provided to the species, which are characterized by having developed leaves, unarmed twigs (unlike most of Malagasy *Euphorbia*), leafy deciduous cyathophylls, and carunculate seeds. Members of the section differ from one another in their geographical distribution, habit, and the shape and the size of their leaves, glands, cyathia and cyathophylls, as well as the size, surface and number of locules of the fruits. The morphological affinities of these six species are discussed and preliminary conservation assessments are provided.

Introduction

The genus *Euphorbia* Linnaeus (1753: 450) (Euphorbiaceae, Malpighiales) is a giant among flowering plants: it has a worldwide distribution and comprises about 2000 species and infraspecific taxa (Haevermans 2003, Mabberley 2008). The island of Madagascar, with at least 170 taxa of *Euphorbia*, almost all endemic (Haevermans 2003), stands out as one of the main hotspots of the genus. Despite this remarkable diversity, the most recent global revision of the genus dates from the 19th century (Boissier 1862). Results from recent molecular phylogenetic analyses, based on both nuclear and plastid markers, have revealed many monophyletic groups and shown that traditional infrageneric systems of classification in large part fail to reflect evolutionary relationships (Steinmann & Porter 2002, Haevermans 2003, Bruyns et al. 2006, Zimmermann et al. 2010, Dorsey et al. 2013). These phylogenetic studies, however, provide a framework for an ongoing series of taxonomic revisions of well-supported, monophyletic groups. The present paper focuses on a distinctive clade endemic to Madagascar, *E* section *Pachysanthae* X.Aubriot & Haev. in Dorsey et al. (2013: 309). Although poorly sampled in the above-mentioned phylogenetic studies, this clade nevertheless forms a coherent group, both morphologically and geographically. It comprises four described species of trees [viz. *E. elastica* Jumelle (1905a: 1047), *E. mananarensis* Leandri (1945: 69), *E. mandravioky* Leandri (1957: 499) and *E. pachysantha* Baillon (1886: 624)] that share several features, including more or less pachycaul trunks, developed leaves, unarmed twigs, leafy deciduous cyathophylls and carunculate seeds.

When Baillon described *Euphorbia pachysantha* in 1886, he placed it in the highly heterogeneous group *E* section *Goniostema* Baill. ex Boissier (1862: 10). This section, lectotypified *a posteriori* with *E. lophogona*
Lamarck (1788: 417) (see Wheeler 1943), initially included all Malagasy species with well developed leaves and thus resulted in a “catch-all” group. Boissier (1862 and supplement in 1866) and Baillon (1886) expanded the section with the addition of numerous unarmed species. Bentham & Hooker (1880) later reduced this group to subsectional rank, placing it within section *Euphorbium* Bentham & Hooker (1880: 260), and subsequently Denis (1921) added the newly discovered *E. elastica*. In the same paper, Denis also proposed that four taxa with stipules forming laciniate ridges be transferred to *E*. subsect. *Diacanthium* (Boissier 1862: 10) Bentham & Hooker (1880: 260), which included all spiny *Euphorbia* from throughout the world. In 1945, Leandri, following Denis, excluded the species with stipules forming laciniate ridges and, without proposing a new name for the former subsect. *Goniostema* (Baill. ex Boiss.) Bentham & Hooker (1880: 260), included in it the newly discovered *E. manganarensis*. Subsequently, Leandri formally published a new name for the group: *E*. subsect. *Denisophorbia* Leandri (1957: 500), designating *E. pyrifolia* Lamarck (1788: 419) as the type. At the same time he described a new species, *E. mandravioky*, which he also placed in the subsect.

In a recent phylogenetic study based on molecular sequence data, Bruyns et al. (2006) proposed a new infrageneric classification for *Euphorbia* in southern Africa in which they expanded *E*. sect. *Goniostema* to include all of the species formally placed in subsects. *Goniostema, Diacanthium, Denisophorbia* and *Deuterocalli* Croizat (1972: 179). Several other studies have, however, shown that adopting such a broad circumscription results in a polyphyletic group (Horn et al. 2012, Aubriot 2012, Dorsey et al. 2013). In particular, *E. pachysantha* and its relatives, none of which was included in the study used by Bruyns et al. (2006), do not show a close affinity to the taxa assigned to the expanded sect. *Goniostema*, which are themselves intimately related to the spiny Afro-Asian species (sect. *Euphorbia* sensu Dorsey et al. 2013) and to the taxa heretofore placed in the genus *Monadenium* Pax (1894: 126) [sect. *Monadenium* (Pax) Bruyns (2006: 411) sensu Dorsey et al. 2013].

Notwithstanding these taxonomic inconsistencies based on sampling issues, all recent molecular phylogenetic studies that included more than one member of *Euphorbia* sect. *Pachysantheae* indicate that they form a distinct clade, separate from all other Malagasy taxa (Aubriot 2012, unpubl. data). Based on these studies and on the fact that *E*. sect. *Pachysantheae* forms a morphologically sound and coherent group, we present here a comprehensive taxonomic revision in which a total of six species are recognized, two of which are described as new. Each of the four previously described taxa was originally based on a very limited number of often fragmentary specimens, without illustrations or photos, and their protologues thus lacked clarity and accuracy. By using additional material collected during fieldwork in Madagascar conducted over the last decade, we have been able to standardize and amend the descriptions for these four species, two of which, *E. pachysantha* and *E. elastica*, are also lectotypified. The two new species, both collected within the last few years in the Loky-Manambato (Daraina) region of northeastern Madagascar, are described and illustrated. All six members of *E*. sect. *Pachysantheae* are assigned a preliminary conservation status.

**Material and Methods**

Morphological measurements were made on exsiccatae and alcohol-preserved material available in the herbaria in Geneva (G), Kew (K), University of Michigan (MICH), Saint Louis (MO), Paris (P), and Antananarivo (TAN). When historical collections lacked geographic coordinates, post-facto georeferencing (indicated in square brackets) was done using the “Gazetteer to Malagasy Botanical Collecting Localities” (Schatz & Lescot 2005) and other sources. Preliminary risk of extinction assessments were based on the calculations of the area of occupancy (AOO) and extent of occurrence (EOO), which were performed using the methods of Callmander et al. (2007). Conservation statuses were assigned using the IUCN Red List Categories and Criteria (IUCN 2012).

Digital images of all type specimens in the Paris herbarium are available via the Sonnerat/BryoMyco database (Sonnerat/BryoMyco 2013) and some images of the material in the Geneva herbarium can be accessed through the Catalogue des Herbiers de Genève (CHG 2013).
Results

Characterization and circumscription of *Euphorbia* sect. *Pachysanthe*


Small to medium-sized trees, 3–20 m tall; bark gray, smooth to wrinkled; trunk “bottle-shaped” and unbranched at the base [resembling *Adansonia* spp. (Malvaceae)], stems succulent, grouped at the top; leaves spirally arranged toward the ends of the twigs, blade obovate to lanceolate, more or less shiny and succulent, apex acuminate to mucronate, sometimes retuse, petioles more or less developed with two small stipular glands at the base. Sexual system difficult to determine given the fragmentary record of flowering stages, but apparently monoecious in most species with the cyathia bisexual and functionally protandrous. Inflorescences sub-terminal, cyathia solitary or grouped by 2 to 4 at the ends of the twigs, cyathophylls usually 2, developed, leafy, deciduous, glands and inter glandular bracts 5. Capsules erect or pendant, very variable in size, sometimes trilocular but more often 2- or 1-locular by abortion, green when young, smooth to weakly wrinkled; 1- to 3-seeded, testa smooth, lacking a caruncle.

Key to the species of *Euphorbia* sect. *Pachysanthe*

1. Small tree to 6 m tall, leaves small (2–3 × 1–1.5 cm), obovate, succulent; cyathia usually small (6–7 mm in diameter). Xeric bushland, south-eastern Madagascar (near Fort-Dauphin) ................................................................. *E. mananarensis*

- Small tree to 3–30 m tall), leaves large (generally >5 cm long), shape variable, from obovate to elliptic, more or less succulent; cyathia large (>8 mm in diameter). Deciduous or humid forest, northern, western and eastern Madagascar … 2.

2. Cyathium glands crescent-shaped, bearing appendices recurved towards the cyathium cup, glands attached to the cyathium cup by a short stalk (2 mm long), cyathium divided into 5 units separated by bracteoles, peduncle of cyathium 2–4 mm long; trees 3–6 m tall, humid forests, eastern Madagascar ............................................................. *E. pachysantha*

- Cyathium glands circular to reniform, never crescent-shaped, directly inserted on the cyathium cup, peduncle of cyathium 6–15 mm long; trees 3–30 m tall. Deciduous and semi-deciduous forests of northern and western Madagascar … 3.

3. Leaves succulent; fruit unilocular or bilocular, large (2.5–4 cm in diameter), pendulous when ripe ………. *E. mandravioky*

- Leaves not succulent or only slightly so; fruit unilocular to trilocular, never exceeding 2 cm in diameter when mature, erect when ripe .............................................................................................................................................. 4.

4. Fruits trilocular, spherical, surface smooth; bark thick, strongly desquamating (as in some species of *Prunus* L.); trees to 20(–30) m tall. Relictual forests, Ambongo plateau SE of Mahajanga (western Madagascar) .................... *E. elastica*

- Fruits unilocular or trilocular, trigonous or spherical, surface smooth or sulcate; bark smooth; trees 6–11 m tall. Semi-deciduous forests, north eastern Madagascar ..................................................................................................................... 5.

5. Fruits trilocular, trigonous, surface sulcate, solitary or borne in pairs, ca. 2 cm in diameter when mature; leaves large (generally >7 cm long) ................................................................................................................................................ *E. haevermansii*

- Fruits unilocular, spherical, surface smooth, usually 2 to 4 borne together, ca. 1 cm in diameter when mature; leaves small (generally <6 cm long) ................................................................................................................................................ *E. nusbaumeri*

*Euphorbia elastica* Jumelle (1905a: 1047) (Figure 1).


Trees 10–20(–30) m tall, monoecious, deciduous, pachycalxous, trunk straight, rounded at the unbranched base, to 30(–60) cm in diameter, weakly branched at the top; bark whitish-gray, exfoliating longitudinally by rolling into cylinders as in some *Prunus* spp., with large corky lenticels 0.8–2 cm in diameter; secondary branches slender, small. White latex present in all organs, having the consistence of rubber at the base of the trunk. Leaves simple, alternate, grouped at the ends of the twigs, blade light green abaxially, dark green adaxially, thin, obovate to spatulate, (7–)8–10(–11) × 4–5 cm, glabrous, primary and secondary veins light green to white, well impressed adaxially, base attenuate, margin entire, apex wide, strongly acuminate to mucronate; petioles 1(–1.5) cm long, light green to white, glabrous; stipules 2, gland-like. Cyathia pseudoterminal, solitary or 2 or 3 grouped at the top.
of the twigs, functionally protandrous, cupuliform, 1–1.8 cm in diameter when dry (including the glands), glabrous. Cyathia borne on peduncle 0.6–1.5 cm long; cyathophylls 2, deciduous, glabrous, spatulate to obovate, 1.5–2 × 0.9–1.1 cm, apex mucronate, inserted at the base of the peduncle (male phase cyathia) or ⅔ of the distance from the base of the peduncle (female phase cyathia), subopposite. Glands 5, fleshy, contiguous to slightly overlapping one another, almost twice as long as wide (5–6 × 2.5–4 mm), elliptic, strongly bilabiate, glabrous, gland margins minutely fimbriate. Inter glandular bracts straight, orbital (3 × 3 mm), greenish-yellow, with deeply laciniate margins. Stamineate flowers numerous, borne on pedicels 3–8 mm long, filaments very small to absent, anthers 1 mm in diameter; bracteoles hyaline, numerous, filamentous, lingulate. Pistillate flower erect, inserted in the center of the cyathium, tricarpellate, glabrous, styles 4 mm long, connate from the base to the middle, curved at the top, stigmas 3, bifid, brown. Young fruit solitary, erect, peduncle green, ribbed, 1–2.7 cm long; fruit green when fresh, bilocular by abortion, globular, 1–1.5 cm in diameter, stigmas persistent, recurved at the top, exocarp smooth, glabrous, covered by more or less prominent wrinkles. All known fruits aborted, seeds thus unknown.

**Distribution and ecology:**—Long considered possibly extinct, this species has been collected only four times, twice by Perrier de la Bâthie in 1904 (the type collection) and 1910 in relict High Plateau forest near Adranomavo (between 50 and 600 m elevation), in the vicinity of Antsirabe (southeast of Mahajanga), in central-western Madagascar, and then in 2011 and 2012 during expeditions to the dry forest of Beanka (in the vicinity of Bemaraha reserve), in central-western Madagascar, where it was collected on tsingy between 284 and 355 m elevation.

**Additional specimens examined:**—MADAGASCAR. Province de Majunga/Mahajanga: Beanka, partie sud, Sarodrano, 18°03′06″S, 44°32′06″E, 355 m, 25 February 2012, fr., Bollinger et al. RFB 255 (G); Province de Majunga/Mahajanga, Beanka, partie sud, Sarodrano, 18°03′45″S, 44°31′30″E, 284 m, 22 November 2011, fl., Gautier et al. LG 5701 (G); Ankissompo[b?]e près d’Ambatonihikina (Bemarivo) [unreadable and unobtainable locality], December 1910, fr., Perrier de la Bâthie 9756 (P).

**Conservation status:**—With an Area of Occupancy (AOO) of 18 km², just four known collections (one of them without interpretable locality data) and two subpopulations (one of which occurs within the tsingy forest of Beanka, an area targeted for protection by Biodiversity Conservation Madagascar), we have assigned *Euphorbia elastica* a preliminary status of “Critically Endangered” [CR C2a(i)+D] based on the IUCN Red List Categories and Criteria (IUCN 2012).

**Euphorbia haevermansii** X.Aubriot & Lowry, sp. nov. (Figure 2).

*E. elasticae et* *E. pachysanthae* affinis *est, sed prima corticalis laevi, atque secunda capsula 3-seminali, trigona, profunde sulcata, glandibus ellipticis in cyathio sessilibus differt.*


Small to medium-sized trees to 11 m tall, sexual system unclear; trunk to 14 cm in diameter, unbranched at the base; bark smooth, lenticelate; secondary branches slender and numerous, forming a crown at the ends of the twigs, young branches rounded, green. White latex present in all organs. Leaves simple, alternate, grouped at the ends of the twigs, blade shiny, light green abaxially, dark green adaxially, fleshy, obovate to spatulate, about twice as long as wide, (5–)7–8(–11) × 3–4(–5) cm, glabrous, primary vein light green, well impressed adaxially, secondary veins numerous, inconspicuous, base attenuate, margin entire, smoothly revolute, apex finely acuminate to mucronate; petiole (1–)1.5–1.7(–2) cm long, light green, glabrous; stipules 2, gland-like. Cyathia pseudo-terminal, solitary, less often in pairs, obconical and broadly spreading, 1 cm in diameter when dry (including the glands), glabrous. Cyathia at male phase borne on peduncles 4 mm long; cyathophylls 2, deciduous, glabrous, spatulate, 1 × 0.5–0.7 cm, apex mucronate, inserted at the base of the peduncle, borne on petioles 5 mm long. Glands 5, fleshy, thick, contiguous, 5 × 3 mm, elliptic to reniform, slightly bilabiate, outstretched, glabrous; surface light green, weakly dotted; margin yellow green, thickened, slightly revolute. Interglandular bracts upright, orbital (3 × 3 mm), glabrous, green, margin laciniate. Stamineate flowers numerous, organized in 5 cymes, surrounded by a network of numerous bracteoles, filamentous, lingulate, hyaline. Pistillate flowers well exserted from the cyathium cup at maturity, each borne on a pedicel 6 mm long, filaments thin, 3 mm long, anthers light-green, 0.5 mm in diameter. Cyathia at female phase solitary or in pairs, peduncles 1.2 cm long; cyathophylls 2, deciduous, inserted at the base of the cup. Female flower unknown. Mature fruit 1(or 2) borne at the ends of the fertile twigs, erect, peduncle
green, ribbed, 1.2 cm long, green when fresh, trilocular, 3-angled, sulcate, glabrous, 2 cm in diameter, stigmas 3, persistent, straight, borne at the apex of the fruit. Seeds 3, 3-angled, 1.2 × 1.2 cm, 2-lobed with a persistent hilum at maturity, testa smooth, brown, glabrous.

FIGURE 2. Euphorbia haevermansii. A. Habit. B. Leaf. C. Cyathium with cyathophylls. D. Cyathophyll. E. Detail of a fertile branch showing two terminal mature fruits. F. Fruits, the one on the left cut open to show the three locules and three seeds inside. G. Ventral, lateral and dorsal views of a seed. A–D after Ranirison & Nusbaumer PR 1035 (G, P), E–G after Nusbaumer LN 865 (G).
**Etymology:**—This new species is named in honor of our friend and colleague Thomas Haevermans as a mark of recognition for his invaluable contribution to improving our understanding of Malagasy *Euphorbia*. Thomas’ studies have opened the way for developing an improved classification of the group, and his research has been important in strengthening our understanding of the processes responsible for plants diversification in Madagascar.

**Distribution and ecology:**—Deciduous and semi-deciduous forests in the Daraina region of northeastern Madagascar, at 600–700 m elevation.


**Conservation status:**—*Euphorbia haevermansii* has an Extent of Occurrence (EOO) of ca. 20 km², an Area of Occupancy (AOO) of 27 km², and is known from two subpopulations (one of which occurs within the Loky-Manambato protected area). Consequently, we assign *E. haevermansii* a preliminary status of “Endangered” [EN B1ab(i,ii,iii)+2ab(i,ii,iii)] based on the IUCN Red List Categories and Criteria (IUCN 2012).

**Notes:**—*Euphorbia haevermansii* closely resembles to *E. pachysantha* and *E. elastica*. It differs from *E. elastica*, however, by several morphological characters: it is a small tree (up to ca. 10 m tall) with a smooth bark and trilocular fruits, whereas *E. elastica* is a large tree (20 m tall) with the bark rolled into cylinders (as in some species of *Prunus*) and has bilocular fruits (by abortion). *Euphorbia haevermansii* differs from *E. pachysantha* in having cyathium glands that are elliptic to reniform and directly inserted on the cyathium cup, rather than crescent shaped and borne on a stalk. *Euphorbia haevermansii* is known only from forests in the area near the Loky-Manambato reserve in northern Madagascar, whereas *E. elastica* grows in remnant dry, deciduous forest in western Madagascar and *E. pachysantha* occurs in rainforest in eastern Madagascar.

**Euphorbia mananarensis** Leandri (1945: 69) (Figure 3).

Type:—MADAGASCAR. Tolara Province: Vallée de la haute Mananara (limite orientale de l’Androy), pente gneissique, [24°49′S, 46°37′E], 25 November 1931, fl., *Decary 9413* (holotype P [P00078031]); isotypes K [K000185028], P [P00078032], TAN [TAN000553]).

Small trees to 6 m tall, monoeocious, pachycalous, trunk rounded at the base, to 40 cm in diameter, unbranched at the base; bark brown, slightly wrinkled; branches slender, small, pseudodichotomous, with blackish bark. Abundant white latex present in all organs. Leaves simple, alternate, grouped at the ends of the twigs, blade shiny, light green abaxially, dark green adaxially, thick, fleshy, elliptic to ovate, (0.9–)2–3×(4.3) cm, glabrous, primary and secondary veins forming light green dots, inconspicuous, secondary veins ca. 3 to 6 per side, base attenuate, margin entire, minutely revolute, apex wide and usually almost flat, acumen more or less developed (rarely absent); petiole very short (1–5 mm long) to absent (leaves sessile), light-green to white, glabrous; stipules 2, minute, gland-like. Cyathia pseudodterminal, solitary, functionally protandrous, cupform to obconical, (0.4–)0.6–0.7–(0.8) cm in diameter when dry (including the glands), glabrous. Cyathia at male phase borne on peduncles 2–4 mm long; cyathophylls not developed. Glands 5, fleshy, contiguous, almost as long as wide (4 × 3 mm), reniform to ovate, glabrous, margin smooth, revolute. Interglandular bracts 5, as long as wide (2 × 2 mm), orbicular, glabrous, with filamentous margins; staminate flowers numerous, divided into 5 clearly distinguishable cymes, pedicels 2 mm long, filaments thick, very small, 0.5 mm long, anthers 1 mm in diameter; stamine flowers weakly exserted from the cyathium cup at maturity, hyaline bracteoles numerous, united to the base of the stamine flowers, filamentous, lingulate. Cyathia at female phase with peduncle (4.5–)6–7–(8.5) mm long; cyathophylls 2, deciduous, glabrous, lingulate, 5 × 3 mm, inserted ½ of the distance from the base of the peduncle, subopposite; pistillate flower erect, in the center of the cyathium, bicapellate, glabrous, style very short, stigmas 2, bifid, brown. Mature fruit solitary, erect, peduncle green, smooth, 0.7–1 cm long; fruit green when fresh, usually unilocular (sometimes bilocular), comprising a large globose lobe 1.3–1.6 cm in diameter when dry plus an aborted lobe, conical to hemispherical, <7 mm high; exocarp hard, smooth, glabrous, covered by more or less prominent wrinkles, a sclerotic crest visible in longitudinal section. Seed 1( or 2), globular, smooth, brown, glabrous, 1.4 cm in diameter.
**Distribution and ecology:**—*Euphorbia mananarensis* grows in xeric bushland in southeastern Madagascar, near Fort-Dauphin (Tolagnaro), at 100–900 m elevation.

Additional specimens examined: — MADAGASCAR. Toliara Province. Flanc de colline, dans la forêt sèche, à 32 km au nord-est d'Ambosany, 24°53′15″S, 46°39′24″E, 457 m, 29 November 2009, fr., Aubriot et al. 55 (G, K, MICH, MO, P, TAN); Sud-ouest: Crête et flanc Sud-Est du massif du Vohimena, au S.W. d’Antamimiora, [24°52′S, 45°32′E], 7 July 1958, fl., Service Forestier (Capuron) 18692 (P); Toliara: Préfecture de Fort-Dauphin; forêt sèche de Mananarive; bush, [25°3′20″S, 46°52′12″E], 100 m, 17 October 1990, fl., Dumetz 1303 (P, TAN); Vallée de la Manambolo, rive droite (Bassin du Mandrare) aux environs d’Isanomano (confluent de la Sakamalio), [24°31′S, 46°37′E], 400–900 m, December 1933, fr., Humbert 13072 (P); Fort-Dauphin, Ambatoabo, Savoa, 2.5 km est d’Imonty, 24°47′48″S, 46°42′16″E, 200 m, 27 November 2009, fr., Ratovoson 1548 (P, TAN).

Conservation status: — Euphorbia mananarensis has an Extent of Occurrence (EOO) of ca. 3770 km², an Area of Occupancy (AOO) of 54 km², and is known from four separate subpopulations (only one of which occurs within a protected area, i.e. Andohahela National Park). Consequently, we have assigned a preliminary status of “Endangered” [EN B1ab(i,ii,iii)+2ab(i,ii,iii)] based on the IUCN Red List Categories and Criteria (IUCN 2012).

Euphorbia mandravioky Leandri (1957: 499) (Figure 4).


Trees 12–20 m tall, monoeocious, deciduous, pachycaulous, trunk straight, rounded at the base, similar to that of Adansonia spp., to 1 m in diameter at the unbranched base, weakly branched at the top; bark gray, smooth, with large corky lenticels >2 cm in diameter, these sometimes contiguous, forming transversal wrinkles round the trunk. White latex present in all organs. Leaves simple, alternate, usually arranged spirally at the ends of the twigs, blade light green abaxially, shiny green adaxially, thick, fleshy, obovate to obcordate, about twice as long as wide, (3.6–)5.8–7.5(–9.6) × (1.9–)3.2–4.1(–5) cm, glabrous, primary vein weakly impressed adaxially, secondary veins inconspicuous, ca. 7 per side, base attenuate, margin entire, smoothly revolute, apex wide, strongly acuminate or retuse; petioles 1(–1.5) cm long, light-green to white, glabrous; stipules 2, gland-like (0.5 mm in diameter). Cyathia inconspicuous, ca. 7 per side, base attenuate, margin entire, smoothly revolute, apex wide, strongly acuminate or retuse; petioles 1(–1.5) cm long, light-green to white, glabrous; stipules 2, gland-like (0.5 mm in diameter). Cyathia pseudoterminal, solitary or paired, functionally protandrous, cupuliform to obconical with a broadly spreading base, 0.7–0.8(–1) cm in diameter when dry (including the glands), glabrous, peduncles (1–)1.3–1.5 cm long; cyathophylls 2, deciduous, glabrous, spatulate, 6 × 3 mm, inserted ¼ of the distance from the base of the peduncles, subopposite. Glands 5, fleshy, thick, contiguous, in general two times longer than wide, 3–6 × 1.5–3 cm, distinctly reniform, strongly bilabiate, glabrous, gland margins undulate, slightly revolute, with inconspicuous appendices recurved towards the cyathium cup. Interglandular bracts straight, almost as long as wide (3 × 2 mm), orbicular to spatulate, margins fimbriate. Staminate flowers numerous, divided into 5 clearly distinguishable cymes, separated by a net of small hyaline bracteoles. Staminate flowers weakly exserted from the cyathium cup at maturity, pedicel 4 mm long, filaments thick, small, 1 mm long, anther 1 mm in diameter. Pistillate flower erect, inserted in the centre of the cyathium, bicarpellate, glabrous, style very short, stigmas 2, bifid, brown. Mature fruit solitary, pendulous, peduncle grey, woody, 1.7–2 cm long; green when fresh, unilocular or bilocular, globular, 2.5–4 cm in diameter when dry, coriaceous, exocarp slightly wrinkled, glabrous, with prominent longitudinal ridges. Seed 1, ovoid, smooth, brown, glabrous, 3 × 2.5 cm.

Distribution and ecology: — Deciduous and semi-deciduous forests of northern Madagascar (calcareous plateau of the Ankarana reserve, Montagne des Français near Diego Suarez, and the Daraina region), at 50–600 m elevation.

Additional specimens examined: — MADAGASCAR. Antsirana Province, forêt de Bekaraoka, près du Camp Tattersalli, à 6 km au nord-est de Daraina, 13°10′00″S, 49°42′26″E, 185 m, 14 May 2010, st., Aubriot et al. 107 (MO, P, TAN) and Aubriot et al. 108 (P, TAN); Montagne des Français, à 8 km au sud-est de Antsiranana (Diego-Suarez), 12°22′33″S, 49°20′27″E, 376 m, 20 May 2010, st., Aubriot et al. 134 (G, P, TAN); Antsiranana, sous préfecture de Vohemar, commune rurale de Daraina, forêt de Moramanga, 13°15′S, 49°37′E, 500 m, 6 November 2001, fr., Gautier & Ravelonarivo 4078 (K, P); Antsiranana, Vohemar, Ampisikinana, Tsaratanana, forêt Moramanga, 12°58′12″S, 49°41′42″E, 320 m, 7 November 2005, fr., Service Forestier (Capuron) 18692 (P); Amitava, Moromibo, 12°58′12″S, 49°41′42″E, 320 m, 7 November 2005, fr., Service Forestier (Capuron) 11254 (holotype P [P00078036]); isotypes P [P00078037], [P00078038]).

st., Humbert 18919 bis (P); Plateau calcaire de l'Ankarana du nord entre Ambilobe et Anivorano, [12°52'10"S, 49°13'43"E], 200–350 m, 4–9 March 1951, fl., Humbert 25539 bis (P); Collines et plateaux calcaires de l'Ankarana du nord, [12°50'32"S, 49°14'38"E], 30–350 m, 24 January–29 February 1960, st., Humbert 32456 (P); SAVA, Daraina, village plus proche Tsaratanana, forêt d'Ampondrabe à 3 km au nord de Tsaratanana, 12°57'42"S,
94°42′19″E, 23 September 2007, fl., fr., Randrianavoivo 1483 (P, TAN); Montagne des Français, forêt d'Antaolanaomby, forêt sèche, 12°22′25″S, 49°21′11″E, 385 m, 22 March 2007, fr., Ratovoson 1244 (MO, P, TAN); Ramena, Andavakoera, forêt d'Andranonakomba, à 4 km au sud-est d'Andavakoera, 12°21′03″S, 49°21′29″E, 50 m, 5 December 2007, fr., Ratovoson et al. 1435 (P, TAN); Anstiranana, Ramena, Montagne des Français, partie Andavakoera, 12°20′44″S, 49°21′9″E, 214 m, 13 August 2004, fr., Razafitsalama et al. 628 (K, P, TAN); Pic des Orchidées, village le plus proche Andranomainty, canton de Mahavanona, [12°22′12″S, 49°21′E], 600 m, 13 September 1963, st., Service des Eaux et Forêts 718R64 (P).

Conservation status:—With an Extent of Occurrence (EOO) of ca. 2850 km², an Area of Occupancy (AOO) of 99 km², and five severely fragmented subpopulations (one of which occurs within the Loky-Manambato protected area), Euphorbia mandravioky is assigned a preliminary status of “Endangered” [EN B1ab(i,ii,iii)+2ab(i,ii,iii)] based on the IUCN Red List Categories and Criteria (IUCN 2012).

Euphorbia nusbaumeri X.Aubriot & Lowry, sp. nov. (Figure 5).

E. haevermansii affinis est. sed cyathis pedunculis longioribus, capsula sphaerica 1-seminali et laevi, semine pisiformi differt.


Shrubs to small trees, to 6 m tall, monoecious; trunk to 18 cm in diameter, unbranched at the base; bark smooth, brown; secondary branches slender, forming a crown at the top of the trunk. White latex present in all organs. Leaves simple, alternate, grouped at the ends of the twigs, blade shiny, light green abaxially, dark green adaxially, fleshy, morphology very variable, elliptic to obovate, (4–)5–6–8 (–8.5) × 2–3–4 (–4), glabrous, primary vein light green, well impressed adaxially, secondary veins numerous, inconspicuous, base attenuate, margin entire, minutely serrate when young, thickened, undulate, apex mucronate; petiole small, (4–)6–8–(10) mm, light green to white, glabrous; stipules 2, gland-like. Cyathia pseudoterminal, 2 to 4 grouped together, less often solitary, functionally protandrous, cupuliform, slightly spreading, 0.6 cm in diameter when dry (including the glands), glabrous, peduncles 6–7 mm long; cyathophylls 2, deciduous, glabrous, spatulate, 0.6 × 0.4 cm, apex mucronate, subopposite (<0.5 mm from one another), inserted at the base of the cup. Glands 5, fleshy, contiguous, 3 × 2 mm, elliptic, recurved towards the cup, glabrous; surface light-green, weakly dotted when young, orange to reddish when mature; margin yellow-green, undulate. Interglandular bracts covering the cyathium cup when young, orbicular (2 × 2 mm), glabrous, green, margin laciniate. Stamine flowers numerous, grouped into 5 cymes, bracteoles numerous, filamentous, hyaline. Stamine flowers weakly exerted from the cyathium cup at maturity, pedicel 2 mm long, filaments thin, 1 mm long, anthers ca. 1 mm in diameter. Pistillate flower erect, inserted in the center of the cyathium, glabrous, style very short, stigmas 3, bifid, more or less recurved. Mature fruit (1 or)2–4 at the ends of the twigs, erect, peduncle green, ribbed; shiny green, unilocular, spherical, smooth, glabrous, ca. 1 cm in diameter, stigmas 3, persistent, minutely recurved, at the apex of the fruit. Seeds 1, pea-shaped, with two rounded basal lobes, 8 × 8 × 6 mm, apex pointed, testa smooth, green.

Etymology:—This new species is named in honour of Louis Nusbaumer, who contributed greatly to the inventory project of the once poorly-collected Loky-Manambato region. His constant help to the first author while making preparations for fieldwork conducted in Madagascar, especially in the northeastern part of the island, was invaluable.

Distribution and ecology:—Deciduous and semi-deciduous forests in the Daraina region of northeastern Madagascar, at 230–1000 m elevation.

Additional specimens examined (paratypes):—MADAGASCAR. Forêt de Sahafary S./P. Diégo-Suarez, 12°34′S, 49°26′E], 2 December 1970, fl., Debray 1558-D (P); Province of Diego-Suarez/Antsiranana: Sous-préfecture de Vohemar, commune rurale de Daraina, forêt de Solaniampilana-Maroadabo, 13°6′S, 49°35′E, 541 m, 5 February 2006, fr., Nusbaumer & Ranirison LN 2173 (G); Sous-préfecture de Vohemar, commune rurale de Daraina, forêt de Bekaraoka, partie nord, 13°6′S, 49°42′E, 230 m, 12 February 2004, fr., Nusbaumer & Ranirison LN 1156 (G, K, P); Sous-préfecture de Vohemar, commune rurale de Daraina, forêt de Solaniampilana-Maroadabo, 13°6′S, 49°35′E, 562 m, 2 February 2006, fr., Nusbaumer & Ranirison LN 1994 (G, P); SAVA, Vohemar, Andrafainkona, Ampisarahina, forêt dense sub-humide de moyenne altitude de Marohaniny, située à 5 km au nord d'Ampisarahina, 13°38′38″S, 49°32′51″E, 1090 m, 10 November 2007, fl., Randriambolomalamomalijy et al. 392 (MO, P, TAN).
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Conservation status:—Euphorbia nusbaumeri, with an Extent of Occurrence (EOO) <500 km², an Area of Occupancy (AOO) of 45 km², and 3 severely fragmented subpopulations (one of which occurs within the Loky Manambato protected area), is assigned a provisional status of “Endangered” [EN B1ab(i,ii,iii)+2ab(i,ii,iii)] based on the IUCN Red List Criteria (IUCN 2012).

Notes:—Euphorbia nusbaumeri most closely resembles to E. haevermansii, but differs in having 1-seeded, unilocular fruits that are smooth and borne in groups of 2 to 4, whereas E. haevermansii bears 3-seeded, trilocular fruits that are deeply sulcate and solitary or borne in pairs. Moreover, the seeds of E. nusbaumeri are pea-shaped, whereas those of E. haevermansii are 3-angled, and the cyathia of E. nusbaumeri are borne on peduncles 6–7 mm long, whereas E. haevermansii has peduncles 4 mm long. Finally, the cyathophylls of E. nusbaumeri are directly inserted at the base of the cyathium cup, whereas those of E. haevermansii are inserted at the base of the peduncle (no cyathophylls or insertion traces are visible on the peduncle).

Euphorbia pachysantha Baillon (1886: 624).

Euphorbia monocephala Baker ex Denis (1921: 43), nom. illeg. Lectotype (designated here):—MADAGASCAR. Central Madagascar, without precise locality, fl., Baron 4437 (lectotype P [P00078061]!; isolectotypes K [K000185237]!, P [P00078063]!).

Small to medium sized trees, 3–6 (–15) m tall, monoecious, deciduous, pachycaulous, trunk to 50 cm in diameter, unbranched at the base; bark smooth; secondary branches slender and numerous, forming a crown at the top of the trunk, young branches rounded, greenish brown. White latex present in all organs. Leaves simple, alternate, grouped at the ends of the twigs, light green abaxially, blade dark green to glaucous adaxially, thin, usually lanceolate to elliptic (very variable in shape), always 2–3 times longer than wide, (4–)6–10(–14) × 2–3.5(–5) cm, glabrous, primary vein light green, well impressed adaxially, secondary veins light green, numerous, usually almost perpendicular to the primary vein, base attenuate, margin entire, thickened, apex strongly acuminate, rarely retuse; petiole (0.5–)1–1.5(–2) cm long, light-green, glabrous; stipules 2, gland-like. Cyathia pseudoterminal, usually solitary, sometimes 2 or 3 grouped at the top of the fertile twigs, functionally protandrous, broadly obconical, 0.8–1 cm in diameter when dry (including the glands), glabrous, peduncles 2–4 mm long; cyathophylls 2 to 4, whitish-green, deciduous, glabrous, elliptic to obovate, very variable in size, inserted at the base of the cyathium peduncle. Glands (4 or)5, stalk short (2 × 2 mm), fleshy, not touching one another, 3.5–5 × 1 mm (dry and excluding the stalk), crescent-shaped, with appendices recurved towards the cyathium cup, gland margins smooth. Interglandular bracts curved towards the cyathium cup, as long as wide (about 2 × 2 mm), circular, glabrous, greenish-yellow, fimbriate on the upper side. Staminate flowers numerous, divided into 5 cymes subtended and covered by interglandular bracts; cymes separated completely from one another by one (or more) encircling bracteoles. Staminate flowers well exserted from the cyathium cup at maturity, pedicels 2 mm long, filaments thin, 2 mm long, anthers <1 mm in diameter. Pistillate flower erect, inserted in the center of the cyathium, tricarpellate, stigmas 3, bifid, short, thin, recurved and brown. Mature fruit solitary, erect, glabrous, smooth; fruit unilocular or bilocular, with an evident globular lobe 1.4 cm in diameter when dry plus a smaller aborted lobe, hemispherical, less than 7 mm in diameter. Seeds unknown.

Distribution and ecology:—Euphorbia pachysantha grows on soils derived from gneiss in humid forests and ravines in eastern Madagascar, in the vicinity of Lac Alaotra, near Toamasina, and south of Vatomandry, at 400–800 m elevation.

Additional specimens examined:—MADAGASCAR. Toamasina Province. Centre: Escarpements rocheux de la Mandraka, à la sortie des gorges (P.K. 70 de la route de Tananarive à Moramanga), [18°55'S, 47°50'5"E], 8 November 1957, fl., fr., Service Forestier (Capuron) 18409 (P); Menaloha (MEN-154), District d'Ambatondrazaka, [17°44'S, 48°28'E], September 1938, fl., fr., Cours 770 (P); Pentes à l'est du lac Alaotra, [17°33'25"S, 48°33'56"E], 800 m, October 1937, fl., Humbert 17573 (P); Anosivola (Manjobo) [Nosivolo (Mangoro)], [20°3'S, 48°8'E], 700 m, November 1911, fl., fr., Perrier de la Bâthie 9689 (K, P); Fianarantsoa Province. Mananjary, [21°14'18"S, 48°19'3"E], 400 m, December 1911, fr., Perrier de la Bâthie 9689 (P); Forêt orientale, près de Sevazy au S.W. de Vatomandry, [19°39'45"S, 48°31'59"E], December 1921, fl., Perrier de la Bâthie 14160 (P).
Conservation status:—Euphorbia pachysantha has an Extent of Occurrence (EOO) of ca. 16,100 km\(^2\), an Area of Occupancy (AOO) of 54 km\(^2\), and is known from six fragmented subpopulations (none of which occurs within the protected area network). This species has not been collected in 50 years. Consequently, we have assigned a preliminary status of “Endangered” [(EN B2ab(i,ii,iii)] based on the IUCN Red List Categories and Criteria (IUCN 2012).

Notes:—Considering that Rauh (1996) recently published detailed photos of a living specimen of Euphorbia pachysantha, we have refrained from including a line drawing as it would not have provided any new information.

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