

Omphalea (Euphorbiaceae) in Madagascar: A New Species and a New Combination

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ABSTRACT. *Omphalea ankaranensis*, a shrub endemic to limestone karst hills of northern Madagascar, is described and illustrated. The species is closely related to *Omphalea palmata* Leandri of western Madagascar but differs in its entire to coarsely crenate-dentate leaf blade margins, broader inflorescence bracts, lax cymules, and shorter pistillate flower pedicels. The new combination *Omphalea oppositifolia* (Willdenow) L. J. Gillespie is made for the widely distributed rainforest species of eastern Madagascar, previously known as *Omphalea biglandulosa* Persoon. A synopsis including new lectotypifications and a key to the four Madagascan species of *Omphalea* is provided.

Omphalea L. is a genus of ca. 17 species belonging to the Euphorbiaceae. Six species are canopy lianas, while the remaining species range in habit from shrubs to large canopy trees. The genus is known from the Neotropics, southeast Asia to northeast Australia, Tanzania, and Madagascar, with centers of diversity and endemism in the Caribbean (6 species, 5 endemic) and in Madagascar (4 species, all endemic). While several species are widespread, the majority have limited ranges and some are quite rare. Species occupy a diversity of habitats from lowland rainforest, wet montane forest, to dry forest and thicket on limestone and sandy soils.

The genus is characterized by an androecium of two or three stamens with connate filaments, styles that are completely fused into a usually massive stylar column, large foliaceous inflorescence bracts, and a complex inflorescence architecture. Inflorescences are technically thyrses and consist of spicate, racemose, or paniculate main axes that bear numerous cymules. These cymose units may be glomerate to lax and each is subtended by a usually foliaceous bract (note that bracteoles are defined as subtending axes within a cymose unit). Other features common in the genus but rarely found elsewhere in the family include red latex, liana habit with tendril-like climbing stems, mushroom-shaped androecia, and large fruits.

Omphalea has long been considered a well-de-

fined genus and one that is rather isolated in the Euphorbiaceae. The genus has been allied with genera that belong to all three uniovulate subfamilies in Webster's classification (1975, 1994). In the past *Omphalea* was usually placed in either tribe Hippomaneae (Baillon, 1858, as tribe Excaecarieae; Pax & Hoffmann, 1912), which is included in Webster's subfamily Euphorbioideae, or tribe Gelonieae (Mueller, 1866; Pax & Hoffmann, 1931; Hutchinson, 1969), a heterogeneous grouping of genera belonging to all three uniovulate subfamilies. More recently, Webster (1994) treated the genus as the monogeneric tribe Omphaleae, close to tribe Plukenetieae in subfamily Acalyphoideae. In contrast, Airy Shaw (1980) included the genus in his tribe Jatropheae (which comprises genera placed by Webster in subfamily Crotonoideae) in his tentative scheme for natural grouping of genera. Recent preliminary evidence from molecular and specialist herbivore phylogenetic studies appears to support a relationship with members of subfamily Crotonoideae (Wurdack & Chase, 1996; Lees & Smith, 1991). Its isolated position and unusual combination of plesiomorphic (e.g., extrastaminal disc, imbricate staminate sepals) and derived (e.g., presence of laticifers, foliaceous bracts, few connate stamens, entirely connate styles) character states suggest that *Omphalea* may represent a relatively early evolutionary branch within the uniovulate euphorbs (Gillespie, 1988b), perhaps near the base of subfamily Crotonoideae.

Three species of *Omphalea* were previously known from Madagascar. The east coast rainforest tree *O. oppositifolia* (Willdenow) L. J. Gillespie was first collected, illustrated, and described as the genus *Hecatea* by Du Petit-Thouars (1804a, 1804b, 1805) and formally named as a species by Willdenow (1805) in the early 1800s. Much later, Leandri (1938) described two dry forest species, *O. occidentalis* and *O. palmata*, from the west coast of Madagascar. A fourth species was recently discovered by the author on limestone karst in the Réserve Speciale Ankarana in northern Madagascar. A specimen of this new species from Montagne des

Français, just south of Antsiranana (Diego Suarez), was subsequently found in the Paris Herbarium.

Phylogenetic studies of the genus suggest that the Afro-Madagascan and neotropical species form a clade defined by a complex of male floral characters including a mushroom-shaped androecium (Gillespie, 1988a, b; Fig. 1D). There appear to be two major lineages within this clade based primarily on leaf architectural characters (for leaf architectural terminology refer to Hickey, 1975, 1979). The first culminates in leaves having palmate primary venation and highly organized secondary and higher order venation, while the second is characterized by leaves with pinnate primary venation and relatively disorganized secondary and higher order venation. These two lineages correspond (excluding the Australasian species) to Pax and Hoffmann's sections *Palmatinerviae* and "Penninerviae" (= sect. *Omphalea*) respectively. Both are represented in Madagascar. The east coast wet forest species *O. oppositifolia* is the sole palaeotropical member of the clade characterized by pinnately veined leaves. The three western and northern Madagascan dry forest species, *O. ankaranensis*, *O. occidentalis*, and *O. palmata*, together with the single African species *O. mansfeldiana* Mildbraed, comprise the palaeotropical members of the palmate clade. According to the above phylogenetic hypothesis the shrub/tree habit apparently evolved from the plesiomorphic state of liana habit at least three times in the genus (Gillespie, 1988b). All Madagascan species are shrubs or trees, while the Tanzanian species *O. mansfeldiana*, most closely related to the Madagascan dry forest species, is a liana. This suggests that the shrub/tree habit of *O. oppositifolia* may have evolved independently of that habit in the Madagascan dry forest species. A second character state that appears to have evolved more than once is foliar gland pair positioned abaxially at the blade-petiole junction (Fig. 5), the only state unique to all five Afro-Madagascan species (all neotropical and Australasian species have the gland pair positioned adaxially). The above phylogenetic hypothesis would suggest that the abaxial state was derived independently in the two lineages.

Omphalea has an interesting association with the moth subfamily Uraniinae. Species of the genus are the primary larval foodplants of the three large diurnal moth genera, *Urania* Fabricius, *Chrysiridia* Hübner, and *Alcides* Hübner (Lees & Smith, 1991). Secondary compounds present in *Omphalea* (such as polyhydroxy alkaloids, Kite et al., 1991) and selectively sequestered by the larvae are thought to have set the stage for the evo-

lution of the adult moths' aposomatic appearance (Coleman & Monteith, 1981; Lees & Smith, 1991). Larvae of the Madagascan endemic *Chrysiridia ripheus* (Drury) have been observed to feed on all four species of *Omphalea* in Madagascar (Lees & Smith, 1991; Lees & Gillespie, pers. obs.). This large colorful moth known as the Sunset Moth is both collected in the wild and raised commercially for the international butterfly trade. Individual moths appear to migrate throughout Madagascar apparently among populations and species of *Omphalea*, suggesting that *C. ripheus* may be dependent on all four Madagascan species of *Omphalea* for its survival.

- KEY TO THE SPECIES OF *OMPHALEA* IN MADAGASCAR
- 1a. Leaf blades elliptic, oblong or obovate, pinnately veined; bracteoles leaf-like, petiolate, to 3.5 cm long, resembling the bracts; inflorescence paniculate or sometimes racemose . . . 3. *O. oppositifolia*
 - 1b. Leaf blades cordiform to ovate, palmately veined; bracteoles triangular, less than 0.5 cm long; inflorescence spicate, racemose, or rarely paniculate (and then branches spicate).
 - 2a. Inflorescence spicate, cymes highly condensed and glomerate; bracts highly reduced, triangular, less than 0.5 cm long; plant mostly covered in a dense velvety pubescence; leaf blades 12–38 cm long 2. *O. occidentalis*
 - 2b. Inflorescence racemose, cymes condensed to lax; bracts elliptic to linear, mostly longer than 2 cm; plant glabrous to sparsely pubescent; leaf blades 6–16 cm long.
 - 3a. Cymes condensed, appearing glomerate; pistillate flower pedicel 2–4 mm long; bracts epetiolate, linear or very narrowly oblong; inflorescence strongly recurved at base, pendent; leaf blades sparsely pubescent or very sparsely pubescent, entire to often deeply palmately lobed 4. *O. palmata*
 - 3b. Cymes lax, flowers terminating divaricate axes ca. 0.4–1(–2) cm long; pistillate flower pedicel to 0.5 mm long; bracts petiolate, blade elliptic or lanceolate; inflorescence not recurved at base, erect to pendent; leaf blades glabrous or glabrescent, entire to sometimes coarsely crenate-dentate 1. *O. ankaranensis*

1. *Omphalea ankaranensis* L. J. Gillespie, sp. nov. TYPE: Madagascar. Prov. Antsiranana: Réserve Speciale Ankarana, limestone tsingy near Camp Anglais, 7 km SE of Matsaborimanga, 12°54'S, 49°07'E, ca. 150 m, 27 Nov. 1990 (fl), *Lynn Gillespie 4064* (holotype, MO; isotypes, CAN, K, P, TAN, US). Figures 1–4.

Differt a *O. palmata* Leandri foliis marginibus integris

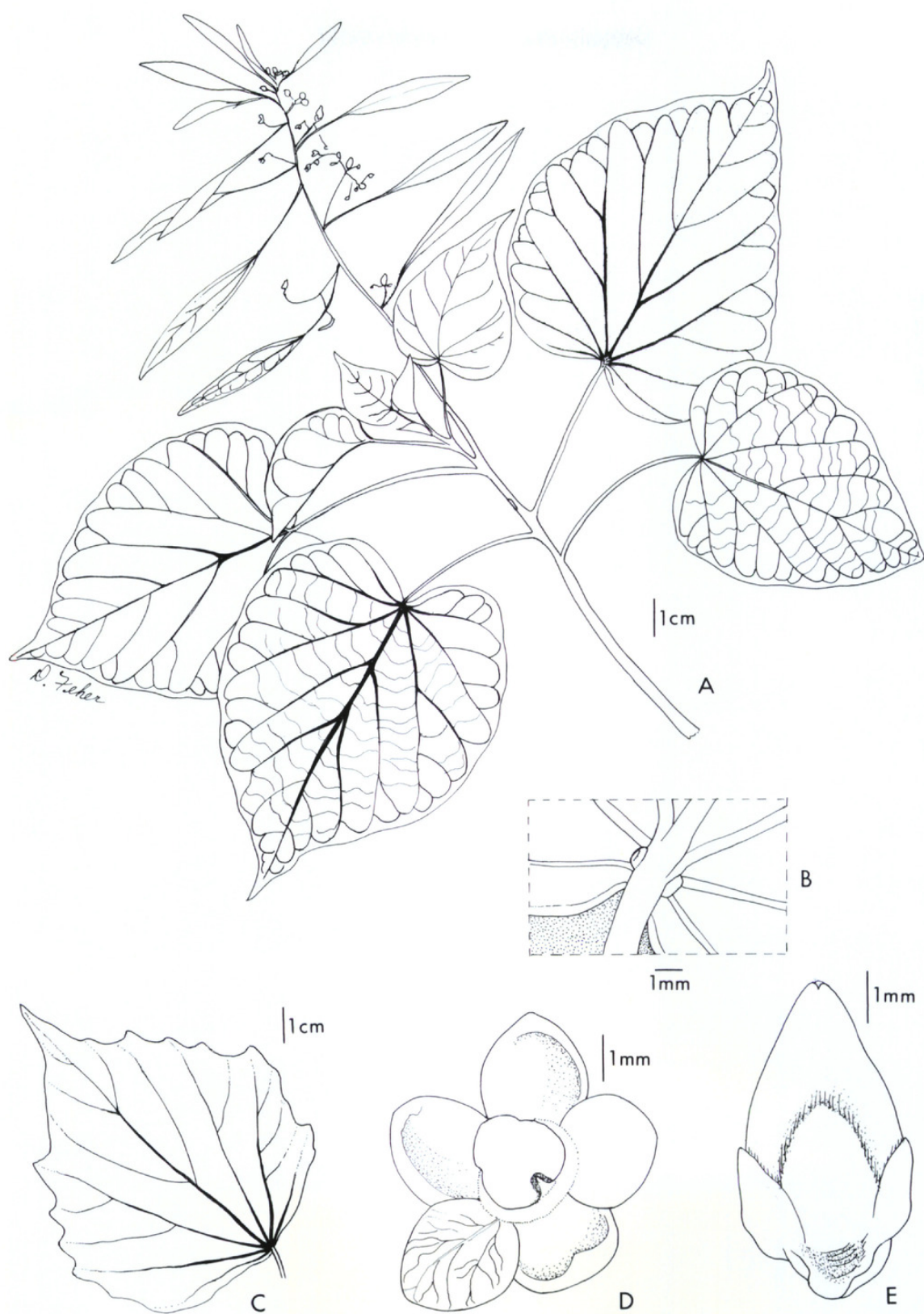
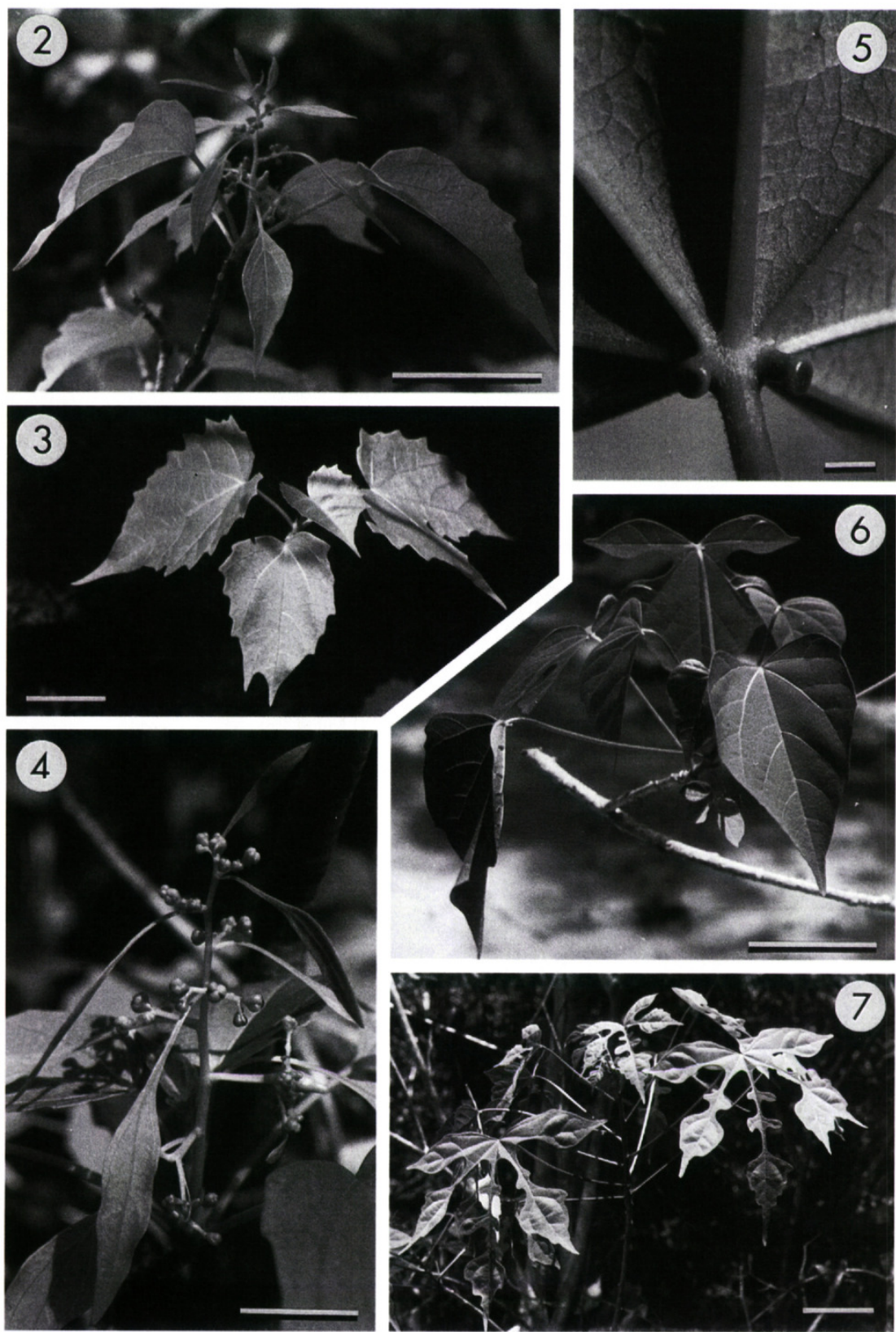


Figure 1. *Omphalea ankaranensis* L. J. Gillespie. —A. Flowering branch; note bracts subtending cymose units. —B. Gland pair on abaxial leaf surface. —C. Leaf with coarsely and irregularly crenate-dentate margins. —D. Staminate flower. —E. Pistillate flower. (A, B, D, E based on *Gillespie 4064*; C based on *Gillespie 4078*.)



Figures 2–7. 2–4. *Omphalea ankaranensis*. —2. Flowering branch. —3. Vegetative branch showing leaves with coarsely crenate-dentate margins. —4. Inflorescence. 5–7. *Omphalea palmata*. —5. Gland pair on abaxial leaf surface. —6. Vegetative branch with entire to lobed leaf blades. —7. Vegetative branch with deeply palmately lobed leaf blades. (2, Gillespie 4064; 3, 4, Gillespie 4078; 5, 6, Gillespie 4167; 7, Gillespie 4168). Scale bar = 5 cm in Figures 2, 3, 6, 7; bar = 2 cm in Figure 4; bar = 2 mm in Figure 5.

vel repandis vel crenato-dentatis, inflorescentiis basi non recurvatis, cymis laxis in axibus divaricatis, bracteis petiolatis lamina elliptica vel lanceolata et pedicellis florum femineorum brevioribus.

Shrub or small tree 1–7 m tall, trunk often enlarged and sometimes bulbous at base; branches slender, glabrous, brick-colored when dry with whitish leaf scars; young shoots glabrous; latex red; foliage deciduous, leaves spirally clustered on ascending branch tips. Leaf blade cordiform or narrowly cordiform, 7–16 cm long, 5–12 cm wide, attenuate or long-acuminate at apex, cordate at base with sinus 0.5–2.3 cm deep or rarely truncate with sinus absent, chartaceous, glabrous or glabrescent, margin entire, repand, or sometimes irregularly and coarsely crenate-dentate; venation palmate with 5 primary veins, basal veins 7; secondary veins brochidodromous, rarely craspedodromous and then only in crenate-margined leaves, intersecondary veins absent; tertiary veins weakly percurrent, sometimes forked or ramified, not strongly recurved; higher order veins random-reticulate or ramifying; glands elliptic or suborbicular in outline, 0.7–1.2 mm diam., cup-shaped, disciform, or slightly raised with flat surface, at junction of petiole and primary veins, abaxial; laminar glands absent or present at lobe apices in crenate-dentate margined leaves, suborbicular, ca. 0.4 mm diam., submarginal; petiole 3–10 cm long, slender, glabrous or glabrescent. Inflorescence a racemose thyrs, 3–13 cm long, erect to pendent, axes glabrous, main axis determinate and often terminating in either a staminate or pistillate flower. Cymes lax with 2–4 orders of branching, branches divaricate with angle of divergence 90° or more; primary cyme axis 4–11 mm long (to 20 mm long in basal cymes) with two terminal subopposite branches; secondary axes 3–10(–14) mm long with two terminal subopposite branches, higher order axes to 10 mm long with 1–2 terminal branches. Bracts (3–)4–8.5 cm long, green, glabrous; blade narrowly elliptic, narrowly rhombic, or lanceolate, (2–)3–5.5 cm long, (0.3–)0.5–1.4 cm wide, acute or attenuate at apex, decurrent at base, margin entire; venation pinnate, triplinerved at base, secondary veins brochidodromous, tertiary veins reticulate; basilar glands absent; petiole 1–3 cm long; basal-most bract often broader, elliptic or ovate, to 2.2 cm wide; bracteoles triangular or narrowly triangular, ca. 1 mm long, glabrous to sparsely pubescent at apex; primary bracteoles sometimes linear-triangular, to 3 mm long. Staminate flowers subsessile or pedicel to 1.6 mm long, glabrous, sometimes appearing long-pedicellate due to slender subtending cyme axis; sepals 5, 1.8–2.8 mm

long and wide, outer surface pale green, inner surface purplish pink or pale green with dark pink speckles, glabrous, usually ciliate-margined, thickened at base with membranous margin; outer sepals broadly ovate, obtuse or acute at apex; inner sepals suborbicular, rounded or obtuse at apex; disc annular, 1.8–2.5 mm diam., ca. 0.8 mm high, purplish pink or pale green with dark pink speckles; androecium mushroom-shaped; staminal column ca. 1 mm long, ca. 0.5 mm wide; cap 1.8–2.5 mm diam., 0.9–1.5 mm high, purplish pink or pale green with dark pink speckles, bearing 3 anthers. Pistillate flowers subsessile or pedicel to 0.5 mm long, glabrous; sepals 5, pale yellowish green, glabrous, often ciliate-margined, spreading slightly; outer sepals broadly ovate, 2.0–3.0 mm long, 1.8–2.5 mm wide, obtuse at apex; inner sepals suborbicular, 1.6–3.0 mm long and wide, rounded or obtuse at apex; gynoecium obpyriform, 4–6 mm long, 2.5–3.5 mm wide, green, glabrous; style conical or narrowly conical with rounded apex, 1.5–2.5 mm long, 1.2–1.8 mm wide. Fruit depressed globose, 3-lobed in cross section, 2–2.3 cm long, 2.4–2.8 cm diam. when dry, with slender conical beak at apex, 0.5–1.5 cm long, apparently separating into three mericarps; pericarp ca. 1 mm thick when dry, glabrous; fruiting pedicel 2–5 mm long; infructescence axis 1.5–4 cm long with 1–2 branches ca. 1 cm long. Seeds subglobose, somewhat radially compressed, ca. 1.7 cm long, 1.6–1.8 cm wide, 1.3–1.6 cm thick, ventral and dorsal surfaces convex; testa thin, persistent, whitish or pale brown with vascular bundles visible as slightly darker lines; tegmen brown, ca. 0.5 mm thick, minutely tuberculate.

Older seedlings with enlarged root apex, ca. 3 cm long, ca. 2 cm diam.; leaf blade cordiform, 4–6 cm long, 3–4 cm wide, attenuate at apex, cordate at base, membranous, glabrous with very sparse pubescence at base above, margin entire or repand, venation palmate; basilar glands absent or elliptic, ca. 0.3 mm wide, flat-surfaced; laminar glands absent; petiole 1–2.5 cm long, glabrous. Juvenile leaf blade as above except 6–11 cm long, 5–9 cm wide, membranous or chartaceous-membranous, margin repand to irregularly and coarsely crenate-dentate, rarely entire; basilar glands elliptic, 0.6–1 mm long, ca. 0.5 mm wide; tooth apices indistinctly glandular or with marginal, suborbicular laminar glands, to 0.4 mm diam.; petiole 2.5–6 cm long.

Distribution and ecology. Endemic to the karst ranges of Ankarana in Réserve Speciale Ankarana and Montagne des Français, located at the northern tip of Madagascar (Fig. 8). A deciduous shrub or

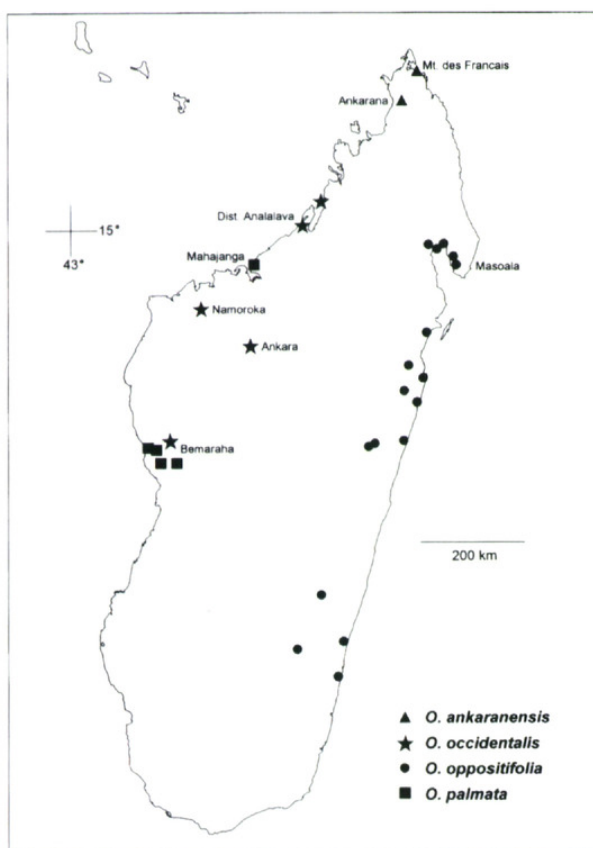


Figure 8. Distribution of *Omphalea* in Madagascar.

small tree found in open dry forest on heavily eroded limestone terrain ("tsingy"). Flowering November through January during the beginning of the wet season.

Local names and uses. None known. Seeds are apparently edible (pers. obs.).

This species is closely related to *Omphalea palmata*, sharing racemose inflorescences with elongate bracts, glabrous flowers and fruit, conical styles, glabrous or glabrescent branches and inflorescence axes, and medium-sized, chartaceous, palmately veined, heart-shaped leaf blades. They differ primarily in inflorescence and bract morphology, pistillate flower pedicel length, and leaf blade pubescence and margin with *O. ankaranensis* having inflorescences not recurved at their base, broader petiolate bracts, shorter pedicels, and glabrous or glabrescent leaf blades with entire or repand to irregularly and coarsely crenate-dentate margins (Figs. 1–4). Mature cymes are lax with conspicuously divaricate axes, each axis terminating in a flower and usually with two subopposite branches (Figs. 1A, 4). These two species together with *O. occidentalis* form a group of dry forest Madagascan species that is very distinct from the single wet forest Madagascan species, *O. oppositifolia*. This species group is characterized by deciduous

leaves with heart-shaped or ovate blades, palmate primary venation, weakly to strongly percurrent tertiary venation, and fruit with a conical apical beak.

Intrapopulational variation in the shape of the leaf blade margin was observed in the Réserve Ankarana population. The majority of individuals examined had leaf blades with entire to repand margins and brochidodromous (looped) venation (Fig. 1A). However, several mature individuals were observed with very distinctive irregularly and coarsely crenate-dentate blade margins (Figs. 1C, 3) and mixed brochidodromous-craspedodromous venation with veins often terminating the tooth apices. Juvenile individuals observed had leaves mostly with repand to coarsely crenate-dentate margins, occasionally with entire margins, while seedlings were observed to have primarily entire or repand margined leaf blades.

The species was collected only once from Montagne des Français in 1944. No recent collections are known nor have any individuals been found despite active searches by the author and D. Lees (1990–1991). This accessible limestone range is now mostly covered in heavily disturbed dry forest and thicket suggesting that the species may have been extirpated from the area as a result of habitat degradation.

Paratypes. MADAGASCAR. **Antsiranana:** calcaires du Mur de l'Ankarana, Capuron, *Serv. For.* 28716 (P); limestone tsingy near Camp Anglais, Réserve Speciale Ankarana, 7 km SE of Matsaborimanga, 12°54'S, 49°07'E, Gillespie 4052 (MO, P, TAN, US), 4053 (MO, TAN), 4054 (P, juvenile plant), 4056 (P, TAN, US), 4058 (MO), 4059 (DAV, K, MO, P, TAN), 4060 (DAV, NY), 4061 (US, juvenile plant), 4068 (TAN, MO, seedlings), 4070 (CAN, MO, US), 4078 (CAN, MO, P, TAN, NY), 4081 (P, US), 4082 (MO, K, TAN, juvenile plant), 4086 (K); Montagne des Français, *Homolle* 386 (P); Plateau Ankarana, *Vaucoulon* 92 (P, fruit only).

2. *Omphalea occidentalis* Leandri, *Bull. Soc. Bot. France* 85: 529, Fig. 1.26–30. 1938. **TYPE:** Madagascar. Prov. Mahajanga: Ambongo, rocaillies calcaires de Namoroka, Dec. 1926 (fl), *Perrier* 17854 (lectotype, designated here, P; isolectotype, P).

Distribution and ecology. Endemic to the karst ranges or plateaus of Bemaraha, Namoroka, and Ankara (a single collection from the early 1900s) in the central part of western Madagascar (Fig. 8). A deciduous shrub or small tree found in dry forest on limestone outcrops. Flowering September through December, when plants are leafless or with young leafy shoots during the latter half of the dry season to beginning of the wet season. Fruits have been collected in December and January when mature leaves are present during the wet season. An

additional more northerly and somewhat distinct population (*Capuron, Serv. For. 18826*) is found in dry coastal forest (substrate unknown) in Analalava District northwest of Mahajunga (flowering October–November).

Local names and uses. Beravy (*Rakotonao, RN 6408*), Ravintsingy (*Capuron, Serv. For. 18826*). Seeds reported to have a fleshy, white, edible testa (Leandri, protologue).

This species may be easily distinguished from the related dry forest species, *Omphalea ankaranensis* and *O. palmata*, by its larger, more coriaceous leaves, stout branchlets, and dense velvety yellowish pubescence on most plant parts (branchlets, leaves, inflorescence axes, bracts, sepals, gynoecia, and fruit; see below for exceptions). The spicate inflorescences have glomerate cymes, very small, non-foliaceous bracts, and are typically pendent with a strongly recurved base. This is the only species of *Omphalea* that does not have conspicuous foliaceous inflorescence bracts.

Leaf blades of adult plants are mostly entire-margined or sometimes remotely dentate near the apex. In contrast, juvenile plants have leaf blades that vary from repand to coarsely and irregularly crenate-dentate to sometimes distinctly three-lobed. Ontogenetic variation in leaf morphology is characteristic of the majority of species in the genus (Gillespie, 1988b).

Omphalea occidentalis was described from two collections made by Perrier de la Bâthie. *Perrier 17854* is here designated as the lectotype; the two specimens include inflorescences, flowers, and leaves. The three syntype specimens labeled *Perrier 1326* lack a specific date but do contain the information, “Fl. septembre—Fr. janvier.” They appear to represent two separate collections, one consisting only of leafless flowering branches presumably collected in September and the other of branches with mature leaves and fruit collected in January.

A collection from dry coastal forest in Analalava District, Mahajunga Province (*Capuron, Serv. For. 18826*), may represent a distinct subspecies or closely related species. Although closely resembling typical *Omphalea occidentalis*, it differs in its erect inflorescences with glabrous to sparsely pubescent axes and bracts, and glabrous fruit. *Decary 14870*, a sterile collection from nearby Ile de Nosy Lava, is tentatively considered to be part of this geographically isolated northern population. Further collections are needed to clarify the status of these collections.

Additional specimens examined. MADAGASCAR. **Mahajanga:** District Analalava, Canton Antonibe, Forêt d'Ambondro-Ampasy, *Capuron, Serv. For. 18826* (P—2 sheets); Ile de Nosy Lava, *Decary 14870* (P); District Soal-

ala, Namoroka, Réserve Naturelle 8, *Decary 15840* (P); limestone tsingy near Ambodiriana, 9 km E of Antsalova, 18°39'S, 44°43'E, *Gillespie 4133* (MO, TAN, seedlings), *4135* (CAN, seedling), *4138* (MO, TAN); along Antsalova-Ambondro track ca. 3 km E of Ambodiriana, 9 km E of Antsalova, 18°39'S, 44°43'E, *Gillespie 4145* (MO, P, TAN), *4146* (DAV, MO, P, TAN, US), *4147* (MO, P, seedlings); ca. 1.5 km E of Ambodiriana, 9 km E of Antsalova, 18°39'S, 44°43'E, *Gillespie 4148* (CAN, MO, TAN, US, juvenile plants), *4150* (P), *4151* (NY, P, juvenile plant); limestone tsingy forest opening SW of Ambodiriana, 9 km E of Antsalova, 18°39'S, 44°43'E, *Gillespie 4155* (CAN, DAV, K, MO, NY, P, TAN, US), *4156* (US), *4157* (CAN, MO, NY, P, TAN), *4158* (CAN, K, MO, NY, TAN), *4162* (K, MO, juvenile plants), *4163* (MO, US); calcaires de l'Antsingy vers Ambodiriana, E d'Antsalova, *Leandri et al. 2124* (P), *2176* (P); Plateau d'Ankara, *Perrier 1326* (syn-types, P—3 sheets); District Soalala, Canton Amatomavo, Réserve National 8 (Namoroka), *Rakotonao, RN 6408* (P).

3. *Omphalea oppositifolia* (Willdenow) L. J. Gillespie, comb. nov. Basionym: *Hecatea oppositifolia* Willdenow, Sp. Pl. 513. 1805. *Hecatea biglandulosa* Persoon, Syn. Pl. 2: 588. 1807. *Omphalea biglandulosa* (Persoon) Baillon, Étude Euphorb. 528. 1858. *Omphalandria oppositifolia* (Willdenow) Kuntze, Rev. Gen. Pl. 2: 609. 1891. TYPE: Madagascar. “Dans le voisinage de la mer,” *Du Petit-Thouars s.n.* (holotype, P; fragment of holotype with original illustration, P; isotype, P).

Hecatea alternifolia Willdenow, Sp. Pl. 514. 1805. *Omphalea alternifolia* (Willdenow) Baillon, Étude Euphorb. 528. 1858. TYPE: Madagascar, *Du Petit-Thouars s.n.* (holotype, P).

Distribution and ecology. Endemic to eastern Madagascar, from the Masoala Peninsula to just south of Farafangana (Fig. 8). An evergreen large shrub to medium-sized (to ca. 30 cm diam.) tree found in lowland to montane wet tropical forest, from near sea level to 1200 m. Flowering (August) September to November (December) in Toamasina sub-prefecture and November to January in Fianarantsoa sub-prefecture. Fruiting specimens have been collected between December and February.

Local names and uses. Fianarantsoa: Hitsebo (Antaifasy dialect), mandrésy, ramoha, varanahy. Toamasina: Malambovony fotsy, salihy, salehy, salejy, tsalehy, voantsalehy, valahakoho, vaolokoa, voalokoho, voalohakoho, voalatakakoho. Province unknown: Huzo-malay.

The species is cultivated on a small scale as a foodplant for rearing *Chrysiridia ripheus* larvae (Lees, pers. comm.). Leaves from wild collected and to a lesser extent cultivated plants provide the main food supply for these commercially raised larvae. Other occasional local uses are as a mediocre quality construction wood (*Serv. For. 12078*) and as a

living fence post (Lees, pers. comm.). Seeds are reported to be edible (*Cours* 2534; *Martin, RN* 6667), with one collector suggesting they are edible after removal of the cotyledons (*Serv. For.* 26671).

This species is distinct from all other Madagascan species in having evergreen leaves with elliptic, obovate, or oblanceolate, pinnately veined blades. Leaf blades are entire-margined and subcoriaceous to coriaceous and often somewhat succulent in texture. Venation is relatively disorganized with secondary veins diverging at a wide, usually variable angle and tertiary venation random-reticulate. The conspicuous pendent inflorescences have white, cream, or greenish white bracts and small whitish flowers that are sometimes tinged with dark pink or red. A unique character is the paired foliaceous whitish bracteoles that resemble bracts in size, shape, and color, in contrast to the typically very small triangular green bracteoles found in most other species of the genus (except *O. mansfeldiana*, which may have enlarged epetiolate bracteoles).

Adult leaf blades are variable in size (6–25 cm long and 3–10 cm wide) and shape within a population and to a lesser extent on an individual, with flowering branches usually bearing smaller leaves than vegetative branches or individuals. Ontogenetic variation in leaf blade shape occurs with juvenile individuals having proportionately narrower leaf blades that are oblanceolate to linear-oblanceolate in shape and usually lobed apically with one to two pairs of rounded to acute lobes.

Willdenow's specific epithet *oppositifolia* appears to be somewhat of a misnomer. The name was apparently based on Du Petit-Thouars's (1804a) inaccurate description of the leaves as opposite or verticillate in threes. Leaves are alternate and never strictly opposite but may sometimes be subopposite or subverticillate, as depicted in Du Petit-Thouars's illustration (1804a: tab. 5; 1804b: tab. 5; 1805: tab. 3).

Although the species has been known throughout most of its history as *Omphalea biglandulosa*, a name change to *O. oppositifolia* is necessary since Willdenow's publication of the species predates that of Persoon by two years. The former name was nomenclaturally superfluous when published, since it was based on the same type as *O. oppositifolia*, a collection by Aubert du Petit-Thouars. Kuntze (1891) recognized this and published the new combination *Omphalandra oppositifolia* in his list of all new combinations associated with Patrick Browne's newly restored genus *Omphalandra*. Pax and Hoffmann (1912, 1931) did not follow Kuntze's lead and retained the name *O. biglandulosa*. Although

recognizing that *Hecatea oppositifolia* has priority, Pax and Hoffmann (1912) mentioned that the name had apparently not been cited since the time of Willdenow. Both Willdenow and Persoon appear to have based their new species on Du Petit-Thouars's detailed description and illustration (1804a: tab. 5) of the first species under his new genus *Hecatea*. Du Petit-Thouars did not provide specific epithets for either this species or for a second related species.

Willdenow named a second species in the genus *Hecatea*, *H. alternifolia*, and distinguished it from *H. oppositifolia* on the basis of its alternate, much larger leaves (i.e., much larger than 11 cm long and 4 cm wide), and racemose inflorescences. This diagnosis was based on a brief description by Du Petit-Thouars (1804a) of a second species in his new genus *Hecatea*, which he promised to describe in a later publication but never did. Though recognized by Baillon (1858), this species was reduced to synonymy under *O. biglandulosa* (= *O. oppositifolia*) by Mueller (1866) who correctly recognized that in the latter species leaf size and shape vary considerably, inflorescence structure varies both among individuals and ontogenetically, and the leaves are never strictly opposite but rather alternate with a tendency to be clustered and appearing subopposite, particularly just below the terminal inflorescence.

Recent collectors have remarked on what appear to be two different forms of the species occurring in separate populations in the Masoala Peninsula and neighboring Makira region. One form is a gracile understory shrub, to 3 m tall, with slender racemose or few-branched paniculate inflorescences and pale green or greenish white bracts. Flowers are pale green or greenish white in bud, the staminate flower sepals becoming dark reddish at anthesis. The other more common typical form is a small to medium-sized tree, often densely branched and foliose, with more branched inflorescences, and cream-white bracts and flowers. The status of these two forms, whether ecological variants or otherwise, needs to be further investigated in the field.

Selected specimens examined. MADAGASCAR. **Fianarantsoa:** environs d'Ivohibe, *Armand* 60 (P); Andrambovato, à l'est de Fianarantsoa, *Capuron, Serv. For.* 11592 (P); forêt à l'est d'Ivohibe, *Humbert* 3162 (P); Andrambovato, à l'est de Fianarantsoa, *Humbert & Capuron* 28507 (P); district Farafangana, canton Thorombe, forêts à l'ouest immédiat de Manombo, *Ratoimbazafy* 353 (P); Manombo, Thorombe, *Serv. For.* 9485 (P). **Toamasina:** Fanovana, "Andevorante Prov.," 24 Oct. 1912, *Afzelius s.n.* (S); Forêt de l'Analamazaotra, Dec. 1905, *Alleizeite s.n.* (L); Tamatane, near the capital, *Baron* 6011 (K, P); Ambila Lemaitso, *Capuron, Serv. For.* 8570 (P); Réserve

Naturelle 1 (Betampona), Dist. Tamatave, *Capuron*, *Serv. For.* 8578 (P); Massif d'Andriandavibe, près d'Anevoka, à l'est de Périnet, *Capuron*, *Serv. For.* 24161 (P); Canton Vavatenina, Ambalahady, *Cours* 1541 (P); Réserve 1, Betampona, poste Rendrisandry, sommet de Vohimarangitire, *Cours* 2534 (P); itinéraire de Didy à Brickaville, *Cours* 4779, 4788, 4797, 4828 (P); 8 km ESE of Périnet (= Andasibo), 18°57'S, 48°30'E, *Gillespie* 4000 (CAN, K, MO, P, TAN), 4002 (MO, P, juvenile plant), 4003 (MO, US); 6 km ESE of Périnet (= Andasibo), along Anevoka River, 18°57'S, 48°28'E, *Gillespie* 4005 (NY, juvenile plant), 4007 (MO, P, TAN, US), 4009 (P), 4010 (TAN), 4014 (CAN, MO, NY, P, TAN), 4016 (K, MO), 4017 (MO, TAN), 4018 (P, juvenile plant), 4019 (K, juvenile plant), 4020 (CAN, juvenile plant), 4021 (MO, juvenile plant), 4022 (MO, US, juvenile plant), 4030 (K, NY, TAN), 4031 (DAV, MO, P, TAN, US), 4032 (CAN, MO, TAN); Andriandavibe, 6 km ESE of Périnet (= Andasibo), 18°57'S, 48°28'E, *Gillespie* 4023 (MO), 4028 (DAV, K, TAN, US), 4029 (CAN, MO, NY, P, TAN); Foulepointe, *Humboldt s.n.* (P); coast to capital, *Kitching s.n.* (K); Réserve National 1, Tamatave, *Martin*, *RN* 6667, *RN* 6677 (P); Baie d'Antongil, *Perrier* 8682 (P); 160 Route de Tamatave, *Rajerison s.n.* (P); Fanovana, *Rakatozafy* 407 (P, TAN); Nosy Mangabe, an island in the Bay of Antongil, 5 km S of Maroantsetra, 15°30'S, 49°46'E, *Schatz* 2771 (MO, P); Masoala Peninsula, ca. 3 km NE of Antalavia, along Antalavia River, 15°47'S, 50°02'E, *Schatz et al.* 2791 (MO); Nosy Mangabe, an island in the Bay of Antongil, 5 km S of Maroantsetra, 15°30'S, 49°46'E, *Schatz & Carlson* 2958 (MO); Farankaraina, near Andranofotsy, District Maroantsetra, *Serv. For.* 12078 (P); Canton Périnet, Nanda, near Ambalovola, *Serv. For.* 26671 (P); Forêt d'Analamazoatra, Nov. 1888, *de Viders s.n.* (P). Without precise locality: *Chapelier s.n.* (P); *Sep.*, *Perrot s.n.* (P); *Herb. Poivre* (P).

4. *Omphalea palmata* Leandri, Bull. Soc. Bot. France 85: 530, Fig. 1.22–25. 1938. TYPE: Madagascar. Prov. Mahajanga: "bas bassin du Manambolo," Oct. (fl), *Perrier* 9849 (lectotype, designated here, P; isoelectotypes, P—3 sheets). Figures 5–7.

Distribution and ecology. Endemic to Réserve Naturelle Bemaraha west to the coast and to the vicinity of Mahajanga along the central west coast of Madagascar (Fig. 8). A deciduous few-branched shrub or small tree found in dry forest on sandy soils and on eroded limestone terrain. Flowering July through October while plants are leafless during the dry season; young vegetative shoots produced sympodially at the inflorescence base may be present during the latter part of the flowering season. Fruiting collections have been made in October and December while plants are in leaf (October collections have only young leaves present). Larvae of the Sunset Moth (*C. ripheus*) were found feeding on foliage and fruit (Lees & Gillespie, pers. obs.); herbivory damage was moderately heavy in the population sampled.

Local names and uses. Sarihasy (Léandri 469).

Seeds have a pleasant flavor and are reported to be very oily (*Perrier* 16809; pers. obs.).

The species differs from the closely related *Omphalea ankaranensis* by its frequently deeply lobed leaf blades (Fig. 7), extreme variation in blade shape from entire to very deeply palmately lobed (Figs. 6, 7), linear or narrowly oblong, epetiolate inflorescence bracts, condensed cymes, longer pistillate flower pedicels, and inflorescences that are strongly recurved at the base. Although overlapping in distribution and habitat with *O. occidentalis*, the species may be easily recognized by its smaller (less than 16 cm long), chartaceous, often lobed leaf blades, racemose inflorescences, and bracts to 8 cm long.

The most distinguishing feature of *Omphalea palmata* is the leaf blade shape and its high degree of variation, from entire to very deeply palmately lobed (Figs. 6, 7). Deeply lobed leaves have primary lobes constricted basally, acute or acuminate apically, with each lobe itself often pinnately lobed with one to several pairs of small usually asymmetrical lateral lobes and a larger acuminate terminal lobe (Fig. 7). The lowermost leaves on a branch may occasionally be coarsely crenate-dentate either apically or along the entire margin (similar to *O. ankaranensis*). *Omphalea trichotoma* Mueller Argoviensis, a species of dry thicket on limestone terrace in Cuba, is also characterized by variably lobed adult leaf blades, from entire to very deeply palmately lobed; however, these differ considerably in shape, having linear-oblong lobes not constricted basally and with blunt apices.

In the protologue Perrier described the leaves as initially entire, becoming very deeply lobed. Indeed, the type collection with fruit made in December (*Perrier* 16809) has very deeply lobed mature leaves, while all new shoots bear young, very small, entire leaves. However, the two type collections made in October (*Leandri* 469, *Perrier* 9849) have new shoots that bear only immature, very deeply lobed leaves. In the population examined by the author in detail (vicinity of Antseranandraka, *Gillespie* 4167–72, 4178–79) leaf blade shape varied from entire to deeply lobed on a single individual. The degree of lobing varied considerably among individuals with some having predominantly one leaf shape, such as shallowly lobed, and others having a much greater range from entire to deeply lobed. Ontogenetic or positional factors did not appear to influence degree of lobing.

Leandri designated two collections, *Perrier* 9849 and *Perrier* 16809, as syntypes (*Leandri* 469 is a paratype). Only *Perrier* 9849 includes flowering

material; the specimen with fruit, in addition to inflorescences and leaves, is selected as lectotype.

Additional specimens examined. MADAGASCAR. **Mahajanga:** dunes à Ampazony, au N de Majunga, *Capuron*, *Serv. For.* 18528 (P); 1–3 km SW of Antseranan-draka, along road to Ambereng between Lakes Bemamba and Masama, ca. 30 km SW of Antsalova, 18°50'S, 44°24'E, *Gillespie* 4167 (CAN, MO, P, TAN, US), 4168 (P, US), 4169 (CAN, MO, P, TAN, US, older seedlings), 4170 (CAN, NY, TAN), 4171 (MO, P, TAN), 4172 (MO, P, TAN, juvenile plants), 4178 (MO, NY), 4179 (DAV, K, TAN); Trangahy, bas bassin du Manambolo, *Leandri* 469 (paratypes, P—2 sheets); Forêt de Tsiampihy et forêts cotières près de Besaraha de Bemihia et de Soahanina, *Leandri et al.* 2264 (P); near Majunga, *Perrier* 16809 (syntypes, P—2 sheets); forest between Ambereng and Lac Masama, SW of Antsalova, 18°51'S, 44°27'E, *Phillipson* 2266 (DAV, K, MO, P, TAN); Réserve Naturelle 9 (Bemaraha), *Bekobaka, Rakotozafy* 1012 (TAN).

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