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A revision of *Homalium* sect. *Odontolobus* (Salicaceae) endemic to Madagascar

Wendy L. Appleyquist

Abstract

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Homalium sect. *Odontolobus* Warb. (Salicaceae) is endemic to Madagascar and formerly included three species. In this revision, nine species are recognized, three of them newly described (*Homalium densispicatum* Appleyq., *Homalium masoalense* Appleyq., *Homalium ovatifolium* Appleyq.) and three transferred from *Homalium* sect. *Blackwellia* Benth. *Homalium densispicatum* has highly reduced flowers like those of *Homalium moniliforme* H. Perrier, but the leaves are larger and the inflorescences thicker, with flowers in elongated many-flowered glomerules. *Homalium masoalense* and *Homalium ovatifolium* are northern species that have frequently ovate leaves and long styles and filaments; the flowers of *Homalium masoalense* are larger, with longer sepals, while *Homalium ovatifolium* has often canescent inflorescences. Two new subspecies are described: *Homalium moniliforme* subsp. *littorale* Appleyq. and *Homalium planiflorum* subsp. *roseiflorum* Appleyq. A key for identification of the species of *Homalium* sect. *Odontolobus* is provided.

Résumé

APPLEQUIST, W.L. (2018). Révision de *Homalium* sect. *Odontolobus* (Salicaceae) endémique de Madagascar. *Candollea* 73: 27-48. En anglais, résumés anglais et français. DOI: <http://dx.doi.org/10.15553/c2018v731a4>

Homalium sect. *Odontolobus* Warb. (Salicaceae) est endémique de Madagascar et comprenait trois espèces. Dans cette révision, neuf espèces sont reconnues, dont trois sont nouvellement décrites (*Homalium densispicatum* Appleyq., *Homalium masoalense* Appleyq., *Homalium ovatifolium* Appleyq.) et trois sont transférées de *Homalium* sect. *Blackwellia* Benth. *Homalium densispicatum* possède des fleurs très réduites comme *Homalium moniliforme* H. Perrier, mais ses feuilles sont plus grandes et ses inflorescences plus épaisses, avec des glomérules allongés à fleurs nombreuses. *Homalium masoalense* et *Homalium ovatifolium* sont des espèces du nord avec des feuilles généralement ovales et de styles et filets allongés. Les fleurs de *Homalium masoalense* sont plus grandes, avec des sépales plus longs, tandis que *Homalium ovatifolium* possède des inflorescences souvent canescentes. Deux sous-espèces nouvelles sont décrites: *Homalium moniliforme* subsp. *littorale* Appleyq. et *Homalium planiflorum* subsp. *roseiflorum* Appleyq. Une clé de détermination des espèces de *Homalium* sect. *Odontolobus* est proposée.

Keywords

SALICACEAE – *Homalium* – *Homalium* sect. *Odontolobus* – Madagascar – New species – Taxonomy

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Introduction

Homalium Jacq. is a pantropical woody genus traditionally placed in *Flacourtiaceae*; along with a large portion of that formerly recognized family, its proper affinities are now known to be with the taxa placed in an expanded *Salicaceae* (CHASE et al., 2002). The genus includes over 150 currently recognized species (see APPLEQUIST, 2013). Characters these species have in common include hermaphroditic flowers with two perianth whorls, semi-inferior ovaries, oppositipetalous stamens, single conspicuous large glands at the base of each sepal, and very small fruits with few maturing seeds; in other floral characters, they encompass an unusual degree of diversity.

Madagascar is perhaps the primary center of diversity of *Homalium*. WARBURG (1894) published a complex classification of the genus that recognized two subgenera and nine sections. With some emendations and additions such as the publication of *Homalium* sect. *Rhodonisa* (Tul.) Sleumer, that classification has been mostly maintained since. The subgenera, defined by whether stamens were only one per petal (*Homalium* subg. *Blackwellia* (Benth.) Warb.) or fasciculate (*Homalium* subg. *Homalium*), were implicitly known by early authors to be artificial and were apparently accepted and maintained for convenience. The present author (APPLEQUIST, 2016) has proposed to emend this classification to recognize ten sections and omit recognition of subgenera, since the relationships among some sections are unclear. Of those ten sections, six are found in Madagascar and five are endemic there.

One of these endemic Malagasy sections is *Homalium* sect. *Odontolobus* Warb., which traditionally is characterized by a reduction of the sepals to tiny deltoid teeth; the flowers are usually sessile and quite small, in two species much reduced and borne in clusters, and the filaments and styles are unusually short. WARBURG (1894) initially included two species, *H. parkeri* Baker and *H. lucidum* Scott-Elliott, in this section. PERRIER DE LA BÂTHIE (1940) did not recognize *Homalium* sect. *Odontolobus*; he included these two species within *Homalium* sect. *Blackwellia* Benth. and described another species in that section, *H. moniliforme* H. Perrier, that was later transferred to *Homalium* sect. *Odontolobus* by SLEUMER (1973), author of the most recent treatment of the Malagasy species of *Homalium*. Recent study of existing herbarium material has indicated that several additional, unrecognized taxa are assignable to this section. Moreover, three species traditionally placed in *Homalium* sect. *Blackwellia* were more similar to members of *Homalium* sect. *Odontolobus* in overall morphology, though lacking the extreme sepal reduction. A modernized treatment of *Homalium* sect. *Odontolobus* was thus needed and is herein presented.

Material and methods

Herbarium specimens at P and MO (herbarium acronyms according to INDEX HERBARIORUM, 2018) were examined, as were then-undistributed duplicates for exchange available at those herbaria and images available through JSTOR Global Plants website [<http://plants.jstor.org>] of types held by other institutions. Most recent collections have duplicates at TAN or TEF, including all those derived from the Missouri Botanical Garden's Madagascar program. As these were not seen they are not listed among material examined; however, the locations of many such duplicates are available through TROPICOS (2018).

Species were defined according to a taxonomic species concept (e.g., GRANT, 1981), the most widely used and usually most practical approach in plant taxonomy, with three morphological features differing among groups of populations considered sufficient to warrant recognition at the species level. Flowers undergo little expansion in fruit, but are usually caducous at or before fruit maturity. Because fruits with mature seeds are rarely seen, only flowering characters are used in species delimitation. In descriptions of taxa, character states or size ranges given in parentheses are uncommon.

Known distributions and habitat are described for each species or subspecies. To save space, locality data are not provided for all specimens seen of common taxa, and those that are provided are edited for brevity, especially when full label data are available from TROPICOS (2018). "Fkt." is used throughout as an abbreviation for "fokontany". A complete index of specimens seen is provided as an appendix. Maps of georeferenced specimens may also be generated within the MADAGASCAR CATALOGUE (2018), which is continually updated with new determinations and specimens.

A preliminary, unofficial assessment of conservation status using the categories and criteria of IUCN (2012) is provided for each taxon recognized. In instances when the extent of occurrence (EOO) and area of occupancy (AOO) might affect the assessed status, GeoCAT (BACHMAN & MOAT, 2012) was used to estimate those values. Geographic coordinates were taken from label data or from the Missouri Botanical Garden's gazetteer (TROPICOS, 2018).

Taxonomic treatment

Homalium sect. *Odontolobus* Warb. in Engl. & Prantl, Nat. Pflanzenfam. III(6a): 35. 1894.

Typus (designated by SLEUMER, 1973: 306): *Homalium parkeri* Baker.

Trees (occasionally shrubby in *H. parkeri*). *Stipules* axillary, free. *Inflorescences* spicate to racemose (partly paniculate with racemoid branches in *H. planiflorum* subsp. *roseiflorum*) with most flowers borne in small clusters or glomerules (singly in *H. brachystylis*); bracts small, often broad, usually persistent;

bracteoles caducous or persistent (rapidly caducous or possibly absent in *H. masoalense*), minute to broad and larger than bracts, usually thick-textured, in 2 species fleshy, approaching subterete at base. *Leaves* alternate (sometimes opposite or subopposite), glabrous (occasionally glabrate with few trichomes on midrib or sparsely pubescent when young). *Flowers* sessile or short-pedicellate, pedicels not articulated; perianth 5-8-merous. *Sepals* reduced to minute deltoid teeth or small and ligulate to lanceolate-oblong, not at all accrescent; calyx tube broadly funnellform (to narrowly so in *H. lucidum*), in fruit becoming nearly hemispherical; sepal glands rounded (to elliptical), densely pubescent (to sparsely so, usually with age). *Petals* ovate, sometimes broadly to transversely so, or narrowly oblong-lanceolate to oblong-elliptical, sometimes quite small but always larger than sepals, spreading, not or very little accrescent; sepals and petals lacking cilia, ciliolate, or ciliate with sometimes long, wavy, fine trichomes. *Stamens* 1 per petal, inserted between glands (filaments usually short); anthers basifixed, broader than long, very small, with subglobose locules diverging at a wide angle, dehiscent by short slits at or near the apex. Upper surface of *ovary* broad and nearly flat (to convex or broadly conical) in flower, in fruit becoming convex to hemispherical; styles 2-4(-5), free, often quite short. Locule of *fruit* subglobose to obovoid, sparsely pubescent to glabrate; seeds 1 per fruit, subglobose, occupying the entire locule (sometimes several-seeded, the seeds then possibly not maturing).

Distribution. – *Homalium* sect. *Odontolobus* is endemic to Madagascar, where its members occur throughout much of the island.

Notes. – *Homalium* sect. *Odontolobus* has been expanded to include three species formerly placed in *Homalium* sect. *Blackwellia* (APPLEQUIST, 2016). It is characterized by its small open flowers borne in spicate or racemose inflorescences (or seldom panicles with racemiform branches), which are sessile to short-pedicellate and have a usually relatively short, broad calyx tube, a broad upper ovary surface that is nearly flat (sometimes to convex, but not narrowly conical) at anthesis, sometimes highly reduced sepals, and small anthers dehiscing towards the apex. The styles and filaments are often short; the locule of the ovary is subglobose to obovoid, with little or no internal pubescence, and there is usually only one large seed per fruit, though mature fruit is rarely seen.

Key to the species of *Homalium* sect. *Odontolobus*

1. Sepals reduced to small teeth, barely visible from above2
- 1a. Sepals from nearly as long as petals to less than half as long, sometimes quite small but readily visible from above.....5
2. Inflorescences canescent; most flowers borne in elongated, many-flowered clusters inserted close together on a thick rachis..... 2. *H. densispicatum*
- 2a. Inflorescences glabrous or sparsely or minutely pubescent; flowers in few-flowered clusters or subglobose moniliform clusters mostly separated on rachis.....3
3. Flowers mostly in groups of 2 or 3, sessile or petiolate; petals lanceolate (narrowly ovate) to oblong-lanceolate or narrowly elliptical (elliptical), 1.5-2.5(-3.1) mm long, margin ciliolate, apex acute 4. *H. lucidum*
- 3a. Flowers in subglobose, often moniliform clusters, sessile; petals ovate (or somewhat oblong) to transversely ovate, not over 1.5 mm long, margin not ciliolate, apex acute or rounded (to obtuse).....4
4. Petals transversely ovate (seldom very broadly ovate or oblong-ovate), 0.5-0.7(-0.8) mm long, apex rounded (rounded-obtuse)6. *H. moniliforme*
- 4a. Petals ovate (oblong-ovate), 0.7-1.5 mm long, apex acute to rounded 8. *H. parkeri*
5. Flowers solitary; filaments and styles 0.3-0.6 mm long 1. *H. brachystylis*
- 5a. Flowers at least partly in clusters of 2 or more; filaments and styles (0.4-)0.6-1.9 mm long.....6
6. Inflorescences canescent (to in part moderately pubescent); bracteoles densely pubescent, fleshy to subterete at the base; petals 0.8-1.2 mm long; sepals (0.3-)0.4-0.5(-0.6) mm long, deltoid to ovate or narrowly deltoid7
- 6a. Inflorescences moderately to sparsely short-pubescent; bracteoles in 1 species glabrous or minutely pubescent, flat; petals 1-1.7 mm long; sepals 0.5-0.9(-1.1) or 1.2-1.4 mm long, oblong-lanceolate to narrowly oblong or lanceolate (ovate)8
7. Leaves irregularly elliptical to broadly elliptical or ovate (lanceolate), (3.2-)3.5-7.5 × 1.6-3.3(-4.8) cm; base convex to rounded (attenuate at extreme base); margins irregularly crenate apically to crenate-serrate for most of length; apex acute to obtuse or rounded (short-acuminate); petals oblong to somewhat obovate, pubescent on both surfaces, densely so abaxially and usually at base adaxially; SE Madagascar 3. *H. longistaminum*

- 7a. Leaves ovate (elliptical), (4.2-)6.2-10.2 × (2.1-)3.1-5.2 cm; base rounded; margins irregularly crenate-serrulate, sometimes with only 1 tooth per side, to slightly wavy or subentire; apex acute to acuminate; petals narrowly oblong, abaxially pubescent, mostly glabrous adaxially; N Madagascar 7. *H. ovatifolium*
8. Leaf blade ovate to lanceolate (elliptical) with acuminate (acute, emarginate) apex, convex to rounded base; flowers sessile or subsessile with pedicels to 0.5 mm long; petals 1.5-1.7 mm long, sepals 1.2-1.4 mm long; Masoala Peninsula..... 5. *H. masoalense*
- 8a. Leaf blade narrowly elliptical to elliptical or oblanceolate with acute to acuminate (rounded, emarginate, cuspidate) apex, convex (cuneate, attenuate) base; flowers pedicellate with pedicels (0.4-)1.3-3(-3.5) mm long; petals 1-1.7 mm long, sepals 0.5-0.9(-1.1) mm long 9. *H. planiflorum*

Taxonomy

1. *Homalium brachystylis* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 573. 1886 [as *brachystylum*].

= *Blackwellia brachystylis* Tul. in Ann. Sci. Nat., Bot. ser. 4, 8: 59-60. 1857.

Lectotypus (designated by SLEUMER, 1973: 246): **MADAGASCAR. Prov. Antsiranana:** Forêts à l'entrée de la Baie de Vohémar, 1837, fl. & fr., *Richard 63* (P [P04679017]!; isolecto-: G [G00018411] image seen, L [L0010889, L0010890] images seen). **Syntypi:** **MADAGASCAR. Prov. Antsiranana:** Vohémar, 1846, fl. & fr., *Richard 110* [= *Boivin 2568*] (P [P04734119]!). **Sine loco:** "Sud de Madagascar [?]", s.d., fr., *Richard 561* (P [P04734120]!); *Herb. Galldich* [cl. *Jaubert*] 40 (not found).

= *Homalium humbertii* H. Perrier in Mém. Mus. Natl. Hist. Nat. 13: 290. 1940 [as *humberti*]. **Lectotypus** (first step designated by SLEUMER, 1973: 247; second step designated here): **MADAGASCAR. Prov. Toliara:** bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, au Vatazo (S d'Imonty), 900-950 m, II.1934, fl., *Humbert 14077* (P [P04734112]!; isolecto-: B [B100153995] image seen, G [G00018412] image seen, P [P04734111, P04734113, P04734114]!, PRE [PRE0297345-0] image seen, TAN [TAN000242] image seen). **Syntypi:** **MADAGASCAR. Prov. Toliara:** vallée moyenne du Mandrare près d'Anadabolava, Mont Vohitrotsy, 700-850 m, XII.1933, fl., *Humbert 12655* (G [G00018413, G00018414, G00018415] images seen, P [P04734115, P04734116, P04734117, P04734118]!, S [S10-10143] image seen).

Tree to 12 m tall, 15 cm dbh; bark sometimes described as platanoid; young twigs glabrous or sparsely pubescent, later becoming glabrous. *Leaves:* petiole (1-)1.5-2.5(-4) mm long, glabrous (sparsely pubescent); blade narrowly elliptical to narrowly oblong-elliptical or elliptical (somewhat obovate), 2.5-7.7 × 0.5-2(-3.4) cm; base convex to cuneate; margins shallowly serrulate to crenulate, usually with few teeth, or subentire; apex acute to rounded (slightly acuminate, obtuse). *Inflorescences* racemose, 2-7.7 cm long, glabrous or with small patches of pubescence near the point of insertion of flowers (rarely sparsely and minutely pubescent on much of the inflorescence or with small patches of yellowish scaly indument around flowers); flowers solitary, sessile; bracts broadly to transversely ovate, thick-textured; bracteoles transversely to broadly ovate, broadly elliptical, or irregularly transversely oblong, thick-textured. *Flowers* (5-)6-7(-8)-merous, white to cream-colored, yellow or yellowish green (browning after anthesis); sepals narrowly deltoid to oblong-lanceolate or ligulate, 0.8-1.8 mm long; petals narrowly oblong to narrowly oblong-elliptical or oblong-lanceolate (to somewhat oblanceolate, in north), 1.1-1.8(-2.3) mm long, margins ciliate, otherwise glabrous (adaxial surface rarely pubescent), apex acute (to rounded); filaments 0.3-0.6 mm long; upper surface of ovary moderately villous or pubescent; styles 2(-3), 0.3-0.6 mm long.

Vernacular names. – "Ampolilaha" (*Service Forestier 14092*); "Mantsapoty" (*Service Forestier 9872, 10080*); "Somontsohihy" (*Be et al. 42*); "Tsohontsobe" (*Humbert 19161*).

Distribution, ecology and conservation status. – *Homalium brachystylis* is widespread in dry seasonal low to moderate-elevation forests and is reported from limestone, sand and silica substrates and in acid soil. It is noteworthy that the single specimen (*Andriamibajarivo et al. 293*) from the high-elevation quartzite massif [Itremo] near the town of Ambatofinandrahana has much larger leaves than other specimens in the southern part of this species' range. This massif is an unusual locality that is home to a relatively large number of endemic species, e.g., *Andropogon itremoensis* Voronts. (VORONTSOVA et al., 2013), *Buxus itremoensis* G.E. Schatz & Lowry (SCHATZ & LOWRY, 2002), *Streptocarpus lanatus* MacMaster (MACMASTER et al., 2005), *Xerochlamys diospyroidea* (Baill.) F. Gérard and *X. itremoensis* Hong-Wa et al. (HONG-WA, 1999). Thus this specimen may be suspected of representing a genetically distinct population that merits further investigation.

The species is widely distributed from the Antsiranana province in the north to the Toliara province in the south and is relatively common with many localities within the protected area network. *Homalium brachystylis* is therefore assigned a preliminary assessment of conservation status of "Least Concern" [LC].

Notes. – In most of its range, including much of the northern province of Antsiranana, *H. brachystylis* usually has narrowly elliptical or oblong-elliptical leaves, seldom to elliptical or aberrantly obovate, which are 0.5–2 cm broad (after the exclusion of one large-leaved specimen from Ambatofinandrahana), and has petals that are usually less than 1.8 mm long. A few older collections made in the Vohémar region of northeastern Madagascar have elliptical leaves at maturity, which are 1.9–3.4 cm broad, and unusually large flowers, with petals to 2.3 mm long. They also have relatively narrow bracteoles, short pubescence on the calyx cup, and small patches of indument on the inflorescence rachis above flowers, all features that likewise occur in some narrow-leaved material, though the latter is rare. The protologue of *Blackwellia brachystylis* indicated that the original material came from the Vohémar region; not all available syntypes are labeled as such (one was later, in another hand and probably erroneously, labeled as “Sud de Madagascar”), but their morphology is consistent with the claim. All original material of *Homalium humbertii*, which SLEUMER (1973) synonymized with *H. brachystylis*, is from southern Madagascar and has narrow leaves. The possibility therefore had to be considered that *H. brachystylis* and *H. humbertii* should be distinguished from one another at some rank. However, no recent collections from around Vohémar reflect the extreme morphology of the older broad-leaved specimens; a couple of recent collections have elliptical leaves and relatively narrow bracteoles, but the flowers are not large, nor is the calyx cup pubescent. Therefore, it appears that there is no clear evidence of a persistent, clearly distinguished taxon endemic to the Vohémar region, and the unusual older specimens represent local genetic variation that does not warrant formal recognition.

The epithet of this species, once transferred to *Homalium*, is usually given incorrectly as *brachystylum*. Epithets such as *brachystylis* should properly be treated as nouns in apposition, which are not declined as adjectives according to the gender of the genus name (STEARN, 1992: 96–97). Since many authors do treat them as adjectives, the decision to do so is not correctable. However, since the author of the basionym (*Blackwellia brachystylis* Tul.) did choose to use a form correct for a noun in apposition, that choice should be preserved.

SLEUMER (1973) designated *Humbert 14077* in the Paris herbarium as the lectotype of *Homalium humbertii*; there are in fact four sheets of this collection at P, and he made no selection among them. The International Code of Nomenclature [ICN] (McNEILL et al., 2012: Art. 9.17) recommends that a second-stage lectotypification be published to designate a single sheet as the lectotype. The selected sheet is one of the better duplicates, in terms of the size and completeness of the material, and it bears a complete original label.

Selected material examined. – **MADAGASCAR. Prov. Antsiranana:** env. de RS d'Analamera, 12°40'40"S 49°32'43"E, 127 m, 17.I.1995, fl., *Andri-anantoanina et al. 738* (BR, G, K, MO, P, WAG); massif de l'Ankarana, 12°57'09"S 49°09'01"E, 120 m, 26.I.2003, fl. & fr., *Bardot-Vaucoulon et al. 1325* (MO); Sahafary, 12°34'30"S 49°27'32"E, 200 m, 25.VII.2004, fl., *Be et al. 42* (MO, P); Analamera, 50–400 m, I.1938, buds, *Humbert 19161* (P [3 sheets]); forêt d'Antsahabe, 10 km à l'W du village d'Ankarafa, 13°12'38"S 49°33'29"E, 471 m, 29.X.2005, *Rakotondrajara et al. 335* (MO); Sahafary be, 3 km à l'E de Saharenana, 12°35'09"S 49°27'34"E, 235 m, 11.IX.2004, fr., *Rakotondrajaona et al. 336* (MO, P); Ankarongana, forêt d'Andranomadiro, 12°36'18"S 49°26'34"E, 258 m, 7.XI.2006, fl., *Ranaivojaona et al. 1519* (MO); Vohemar, forêt de Binara, 13°14'09"S 49°37'22"E, 300 m, 31.III.2004, fl., *Ranirison 551* (MO); Fkt. Saharenana, forêt d'Andranomadiro, 12°36'18"S 49°26'35"E, 300 m, 14.II.2005, fl., *Schatz et al. 4264* (MO); Diégo-Suarez, Ankara JB8, 27.VII.1954, buds, *Service Forestier 10426* (P); plateau de l'Ankarana près d'Ambondromifehy, 4–6.X.1954, *Service Forestier 11257* (MO); Diégo-Suarez, Ankara, 24.III.1955, fl., *Service Forestier 13208* (P); Ankarana à l'W d'Ambondromifehy, 24.IV.1963, fl., *Service Forestier 22695* (MO, P [3 sheets]); rebord S du plateau de Mahory, au SW de Marotaolana (Anivorano-Nord), 3.IV.1964, fl., *Service Forestier 23376* (P); massif de l'Ankitakona, au S de la Baie d'Ambararata, 25–265 m, 25.IV.1966, fl., *Service Forestier 24673* (P); massif du Bezavona entre la Fanambana et la Manambery, pentes inférieures de la rive droite de l'Andilana, 20.III.1967, fl., *Service Forestier 27537* (MO, P). **Prov. Fianarantsoa:** Ambatofinandrahana, 20°30'03"S 46°50'51"E, 1451 m, 20.III.2004, fl., *Andriamibajarivo et al. 293* (MO); haute vallée de la Menarahaka à l'E d'Ihosy, 700–800 m, 28.I.1955 & 10.IV.1955, fl., *Humbert 28538* (MO, P); between Ankazobetroka and Ambararata, ca. 25 km NE of Ihosy, 22°15'S 46°15'E, 750 m, 11.IV.1971, fl., *Mabberley 910* (P); Ihosy, 800 m, VI.1953, fl. & fr., *Perrier de la Bâthie 19272* (P [2 sheets]); forêt de Kitranga, à 12 km au N d'Ihosy, I.1955, fl., *Service Forestier 11611* (P [2 sheets]); Zasafofisy, Ihosy, 21.VII.1954, buds, *Service Forestier 14482* (P); Kitranga, entre Ambararata et Ivandrika, 22.II.1970, fl., *Service Forestier 29063* (P). **Prov. Mahajanga:** Bemanevika, forêt d'Analafaly, 17°13'50"S 46°59'58"E, 640 m, 9.V.2005, fr., *Andrianjafy et al. 1038* (MO, P). **Prov. Toliara:** Andohahela RNI parcelle 2, path E to Ambohivory massif, 24°56'23"S 46°38'40"E, 120 m, 9–12.V.1997, fr., *Birkinshaw et al. 427* (MO); W du Tsimelaha, Andohahela RNI, 24°56'S 46°35'E, 345 m, 22.III.1995, fl., *Eboroke 985* (G, K, MO); forêt de Zombitsy (Sakaraha), 600–850 m, 26–29. III.1955, fl. & fr., *Humbert et al. 29567* (P); Andohahela, Parcelle 3, 25°04'S 46°41'E, 100–300 m, 8–10.IV.1993, fr., *Randriamampionona 302* (MO, P); RN XI [Andohahela], 18.I.1951, fl., *Réserves Naturelles 2756* (MO, P [2 sheets]); Tulear, forêt d'Analavelona, 7.IV.1954, fr., *Service Forestier 9872* (MO, P); Mahaboboha, forêt d'Thera, 9.IV.1954, fr., *Service Forestier 10080* (P); forêt de Zombitsy, 700 m, III.1955, fl., *Service Forestier 11912* (P); Andranolava, forêt Vohibasia, 27.V.1955, fl., *Service Forestier 14092* (P); Forêt de Zombitsy, 700–800 m, 20.VI.1958, fl. & fr., *Service Forestier 18593* (P).

2. *Homalium densispicatum* Appleg., **spec. nova** (Fig. 1).

Holotypus: MADAGASCAR. **Prov. Toliara:** Anosy, Fort Dauphin, Iabokoho, Antsotso, forêt d'Ivohibe, 24°34'14"S 47°12'10"E, 230 m, 2.IV.2008, fl., *Rabenantoandro et al. 1884* (MO–6474628!; iso-: P [P06171672]!, TAN).

Homalium densispicatum differs from *H. moniliforme* *H. Perrier* in having larger leaves, (5.5–)7–15 (–17) × (1.5–)2.1–6(–6.9) cm (vs (1.8–)2.7–6.8 × 0.7–2.6(–3) cm); inflorescences canescent (vs minutely pubescent or glabrous); and flowers borne in elongated many-flowered glomerules along most of the rachis (vs in well-separated, moniliform glomerules).



Fig. 1. - *Homalium densispicatum* Appleg. **A.** Flowering branch; **B.** Flower cluster.
[Rabenantoandro et al. 1884, TAN] [Drawing: R.L. Andriamiarisoa]

Tree to 12 m tall; young twigs glabrous. *Leaves*: petiole 2.5–20(–30) mm long, glabrous; blade narrowly elliptical to elliptical (oblanceolate to oblong-oblanceolate, obovate), (5.5–)7–15(–17) × (1.5–)2.1–6(–6.9) cm; base cuneate to attenuate or convex, usually attenuate at extreme base; margins crenate-serrulate (subentire, crenate-serrate or crenulate), often slightly revolute; apex rounded to acute or cuspidate (shallowly emarginate, short-acuminate). *Inflorescences* spicate with a thick rachis, 1.4–7 cm long, canescent; flowers in elongated many-flowered clusters, sessile; bracts transversely (to very broadly) oblong, deltoid or ovate, often irregular; bracteoles reduced to minute teeth, caducous. *Flowers* (6–)7(–8)-merous, white or greenish; sepals ovate to oblong or broadly ovate-deltoid, 0.2–0.3(–0.4) mm long; petals broadly (transversely) oblong-elliptical to oblong-ovate, (0.4–)0.5–0.8 mm long, glabrous (pubescent abaxially but not ciliate), apex rounded; filaments 0.1–0.4(–0.5) mm long; upper surface of ovary densely short-tomentose; styles (2–)3, 0.1–0.4 mm long.

Distribution, ecology and conservation status. – *Homalium densispicatum* is primarily native to humid forests in south-eastern Madagascar at low (seldom to moderate) elevations. As herein circumscribed, it includes one disjunct population from northern Madagascar. Only eight distinct locations are known for *H. densispicatum* (if the Antsiranana collection is included). Most low-elevation forest in Madagascar is now badly fragmented. However, most collections are from two protected areas (Manombo, Tsitongambarika) where the species seems not to be rare and further decline in habitat extent or quality may be avoidable. Therefore it is suggested that an appropriate preliminary assessment of conservation status would be “Least Concern” [LC].

Notes. – *Homalium densispicatum* shares extremely reduced, tightly clustered flowers with *H. moniliforme*, and some specimens have previously been assigned to that species. However, the leaves are much larger, with numerous veins and sometimes much longer petioles, the inflorescences are much more densely pubescent, and the flowers are borne on a thick rachis in elongated many-flowered clusters that at their termini are mostly close to one another on alternating sides of the rachis, giving the inflorescence a uniformly thick, rather than moniliform appearance.

The distribution is primarily southeastern. One small-leaved collection (*Razakamalala et al. 55*) is known from Antsiranana, far to the north; though this distribution is suspicious, the specimen is overall morphologically consistent with *H. densispicatum* and not with *H. moniliforme*, e.g., in having thick inflorescences with elongated, nearly contiguous glomerules. A second northern collection, *Service Forestier 28807* from Ile Sainte-Marie (partie S de la forêt de Kalalao, 16.V.1969, fr., P [2 sheets]), has leaves to 9.7 × 4.1 cm, yet

in other features it seems to resemble *H. moniliforme* more than *H. densispicatum*; it is therefore treated as *incertae sedis*. Specimens from Fianarantsoa province have smaller leaves than those from Toliara; one of the latter, *Razafimandimbison et al. 223*, has unusually narrow and strongly toothed leaves and might represent a distinctive local variant.

Paratypes. – MADAGASCAR. **Prov. Antsiranana:** Fiv. Antalaha, Fkt. Sahafary, 15°17'34"S 50°22'07"E, 173 m, 18.II.2001, fl., *Razakamalala et al. 55* (MO). **Prov. Fianarantsoa:** Ranomafana, XII.1963, fl., *Chabonis s.n.* (P); Fkt. Manombo, Réserve Spéciale de Manombo, 23°01'19"S 47°43'56"E, 30 m, 14.XI.2001, fr., *Rabenantoandro et al. 780* (MO); forêt de Manombo, à 30 km au S de Farafangana, J.B. 16, 26.VI.1954, fl. & fr., *Service Forestier 9205* (MO, P [7 sheets]); Ihorombe, Manombo, 21.VII.1955, fr., *Service Forestier 15240* (P). **Prov. Toliara:** Fkt. Antsotso, Ivohibe forest, 24°34'10"S 47°12'37"E, 41 m, 24.V.2006, fl., *Antilahimena et al. 4846* (P); Fkt. Iaboakoho, forêt d'Ampasina, 24°34'30"S 47°08'35"E, 119 m, 25.I.2015, fl., *Randrianarivony et al. 623* (MO); village d'Antsotso, forêt de Bemangily, 24°35'33"S 47°12'52"E, 22.V.2006, fl., *Randriatafika et al. 672* (MO, P); forêt de Manantantely à 15 km au NW de Fort-Dauphin, 24°59'S 46°55'E, 50–100 m, 24.VI.1996, fl., *Razafimandimbison 223* (BR, G, K, MO, P [2 sheets]); Antsotso Avaratra, forêt Tsitongambarika, 24°34'16"S 47°12'05"E, 271 m, 1.IV.2008, fl., *Razakamalala et al. 4113* (MO, P). **Sine loco:** s.d., fl., *Service Forestier 71-R-176* (P).

3. *Homalium longistaminum* H. Perrier in Mém. Mus. Natl. Hist. Nat. 13: 287. 1940.

Lectotypus (designated here): MADAGASCAR. **Prov. Toliara:** vallée de la Manambolo, rive droite (bassin du Mandrare) aux env. d'Isomono (confluent de la Sakamalio), 400–900 m, XII.1933, buds & fl., *Humbert 12914* (P [P04679979]); isolecto-: L [L0010953] image seen, P [P04679980]!

Tree to 12 m tall, 30 cm dbh; young twigs glabrous or minutely pubescent. *Leaves*: petiole 4–11 mm long, glabrous (sparsely, minutely pubescent); blade irregularly elliptical to broadly elliptical or ovate (lanceolate), (3.2–)3.5–7.5 × 1.6–3.3(–4.8) cm; base convex to rounded (attenuate at extreme base); margins irregularly crenate apically to crenate-serrate for most of their length; apex acute to obtuse or rounded (short-acuminate). *Inflorescences* racemose, (2.2–)4–6.5 cm long, canescent or in part moderately pubescent; flowers often borne in clusters of 2 or 3, on pedicels 0.3–1.4 mm long; bracts transversely to broadly deltoid; bracteoles very thick, to subterete at base, densely pubescent (absent or rapidly caducous). *Flowers* 6- or 7-merous, pale or yellowish green; sepals deltoid to ovate, (0.3–)0.4–0.5(–0.6) mm long; petals oblong to somewhat obovate, 0.8–1.2 mm long, margins short-ciliate and both surfaces pubescent, densely so abaxially and usually at base adaxially, apex rounded or obtuse; filaments 1.1–1.7 mm long; upper surface of ovary canescent; styles (3–)4(–5), 1.1–1.7 mm long.

Vernacular names. – “Tsimalagnilamba” (*Eboroke 980*); “Tsimalamba” (*Humbert 12914*).

Distribution, ecology and conservation status. – *Homalium longistaminum* is confined to a limited area in southeastern Madagascar, where it occurs mostly in low-elevation humid forests. The fact that very few collections are available, although both Andohahela and Ranopiso are relatively well-collected, suggests that the species is rare in its native range. Four collections are known, pertaining to only three distinct localities, and giving an AOO of no more than 12 km². Two of these three are in the area of Andohahela RNI, hence protected. However, the species should be considered “Vulnerable” [VU B1ab(iii)+B2ab(iii)] based on its small AOO (< 20 km²) and number of locations (≤ 5).

Note. – In publishing this species, PERRIER DE LA BÂTHIE (1940) did not note that there were two sheets of the type collection at P; Sleumer incorrectly marked both as “holotype”. The sheet numbered P04679980 has a determination label by Perrier, while the sheet numbered P04679979 has notations on the label in the same handwriting that read “*Homalium* (*Blackwellia*) *longistaminum* H. Perr.”, with the addition of “n. sp.”, and “Type” (double underlined). The latter sheet is in better condition, having a fragment packet that contains partially open flowers; it would certainly be a more suitable type and Perrier de la Bâthie probably intended it as such. However, since both sheets were used by Perrier de la Bâthie and no distinction between them was made in the protologue, they are regarded as syntypes and it is therefore necessary to designate a lectotype.

Additional material examined. – MADAGASCAR. **Prov. Toliara:** RNI d’Andohahela, parcelle n° 2, 24°49’49”S 46°32’15”E, 30–50 m, 16.III.1994, *Andrianarisata et al. 101* (MO [2 sheets]); Ranopiso, Evasia, 24°46’S 46°41’E, 350 m, s.d., post-fl., *Eboroke 980* (G, MO); Andohahela, parcelle n° 2, Ihazofotsy, 24°50’S 46°33’E, 50–200 m, 2–5.III.1993, fr., *Randriamampionona 152* (MO, P).

4. *Homalium lucidum* Scott-Elliot in J. Linn. Soc., Bot. 29: 24. 1891.

Lectotypus (designated by SLEUMER, 1973: 307): MADAGASCAR. **Prov. Toliara:** Fort Dauphin, V.1889, fl., *Scott Elliot 2661* (K [K000231842] image seen; isolecto-: P [P04704037]!)

Tree to 30 m tall, 60 cm dbh; bark dark gray-brown, sometimes slightly fissured or peeling, with a bright yellow slash; young twigs glabrous. *Leaves:* petiole 3–10(–19) mm long, glabrous (glaucous, peeling); blade elliptical to lanceolate (narrowly lanceolate, aberrantly broadly elliptical), 3.5–11.5 × 1.5–3.8(–4.3) cm; base convex; margins serrulate to crenate-serrulate (shallowly crenate, subentire); apex acute to acuminate (emarginate, rounded-cuspidate). *Inflorescences* racemose, (2.5–)4–10(–12) cm long, glabrous; flowers proximally often in clusters of 2 or 3, sessile (pedicellate with pedicels to 2 mm long); bracts ovate to broadly ovate; bracteoles ovate, minute,

caducous. *Flowers* 6–7(–8)-merous, pale green to white, cream or yellowish, or brown with age (once described as red); sepals deltoid, 0.3–0.4(–0.5) mm long; petals lanceolate (narrowly ovate) to oblong-lanceolate or narrowly elliptical (elliptical), 1.5–2.5(–3.1) mm long, ciliate, otherwise glabrous (or adaxial surface sparsely short-pubescent), apex acute; filaments 0.3–0.7 mm long; upper surface of ovary sparsely to moderately short-pubescent; styles 2–3, 0.3–0.5 mm long.

Vernacular names. – “Fotsakara (g[rands] f[euilles])” (*Service Forestier 2718, 2737*); “Hazofotsy” (*Antilahimena et al. 4835*); “Hazokoaky” (*Service Forestier 13942*); “Mafaikoditra” (*Antilahimena et al. 1139*); “Maroampotolia” (*Réserves Naturelles 3668*); “Menavahatra” (*Antilahimena et al. 7110*); “Ramisaona” (*Service Forestier 14569, 14608*).

Distribution, ecology and conservation status. – *Homalium lucidum* is widely distributed in humid regions of Madagascar and occurs from near sea level to over 1400 m elevation. The species is widely distributed from Antananarivo province in the center to Toliara province in the south and is relatively common with many localities within the protected area network (i.e., Andohahela, Anjozorobe, Betampona, Makira, Nosy Mangabé and Tsitongambarika). *Homalium lucidum* is therefore assigned a preliminary assessment of conservation status of “Least Concern” [LC].

Note. – *Homalium lucidum* was described from only one collection. As for other species published by Scott Elliot, the duplicate at K, where he worked, has been informally considered to be the “holotype.” However, as other duplicates of his own collections were certainly available to him, and the publication did not specify that specimens cited were held at K, the two known duplicates of *Scott Elliot 2661* should be regarded as syntypes under Art. 9.5 of the ICN (McNEILL et al., 2012). SLEUMER’S (1973) subsequent statement that the K and P duplicates were the “holotype” and “isotype”, respectively, was an effective selection of the former as lectotype, with the use of “holotype” being a correctable error under Art. 9.9.

Selected material examined. – MADAGASCAR. **Prov. Antananarivo:** 3.0 km NW of Ambohitsaratelo-Bebao (NW of Tsiroanomandidy), 1100–1200 m, 16.I.1985, fl., *Dorr et al. 3587* (MO, P); Bongolava, 1300 m, VII.1974, fl. & fr., *Morat 4639* (MO [2 sheets], P [4 sheets]); Fkt. Ambaravarana, 18°25’S 45°40’E, 1190–1200 m, 25.VI.1997, fr., *Rakotomalaza et al. 1344* (G, K, MO); forêt de Besofina à 8 km au S de Betatao, 18°15’10”S 47°53’27”E, 1386 m, 9.III.2000, fl., *Randrianaivo et al. 517* (MO, P); 7 km E of Anjozorobe, 18°22’S 48°00’E, 1300 m, 11.V.1987, fl., *Schatz et al. 1380* (MO, P). **Prov. Fianarantsoa:** Fkt. Iabomaro, 23°11’07”S 47°42’32”E, 24 m, 19.VI.2004, fr., *A. Randrianasolo et al. 878* (P); Vangaindrano, 20.I.1950, fl., *Service Forestier 2737* (P); Manakara, Vakoary, 11.V.1955, fr., *Service Forestier 14569* (P); Manakara, forêt Belambo, 11.V.1955, *Service Forestier 14608* (P). **Prov. Mahajanga:** 9.6 km NW of Ambohitaratelo-Bebao, 1200 m, 14.I.1985, fl., *Dorr et al. 3535* (MO, P); 5 km à l’E de Bandabe, 15°31’08”S 49°06’00”E, 3696’, 25.IV.2007, fr., *Ravelonarivo et al. 2253* (MO, P). **Prov. Toamasina:**

5 km du village d'Anony, vers Ankarefobe, 17°12'26"S 48°33'13"E, 1164 m, 22.IV.2005, fl., *Andriamijabarivo et al.* 577 (MO); Fkt. Andranofotsy, 15°25'14"S 49°48'51"E, 140 m, 14.VII.2002, fr., *Antilabimena et al.* 1139 (MO, P); Fkt. Ampitambe, Ambatovy, Andranoverly, 18°52'43"S 48°17'38"W, 1010 m, 10.VI.2009, fl., *Antilabimena et al.* 7110 (G, K, MO, P); Andapanomby, près de la rivière Ampandisanana, Makira NW, 15°21'48"S 49°07'06"E, 25.IV.2007, fr., *Bernard & Birkinshaw* 462 (G, MO, P); Nosy Mangabé, 15°30'S 49°45'E, 17.IV.1988, fl. & fr., *Leeuwenberg* 13933 (MO, P); confluence de l'Onive et du Mangoro, 600 m, IX.1926[?], fl., *Perrier de la Bâthie* 17012 (P); entre Moango et Antanamarina, 17°33'57"S 48°53'58"E, 740 m, 27.X.2000, fr., *Randrianjanaka et al.* 586 (MO, P); entre Manakambahiny Est et Nonokambo, 17°45'34"S 48°42'04"E, 7.III.2001, fl. & fr., *Randrianjanaka et al.* 606 (MO, P); RN 1 [Betampona], 20.III.1952, fl., *Réserves Naturelles* 3668 (MO, P [2 sheets]); Nosy Mangabe, 15°30'S 49°46'E, 0-330 m, 13-23.IV.1988, fl., *Schatz & Gentry* 2055 (MO, P); Bassin de la Manonga (effluent [rive gauche] de la Rantabe), env. de Sahajinja, 700 m, 5.III.1954, fl., *Service Forestier* 9107 (P). **Prov. Toliara:** Fkt. Antsotso, Ivohibe forest, 24°34'10"S 47°12'37"E, 41 m, 24.V.2006, fr., *Antilabimena et al.* 4835 (P); Andohahela [NP], parcelle 1, Eminiminy, 24°40'S 46°48'E, 200-700 m, 4-24.V.1993, fr., *Randriamampionona* 309 (MO, P); *ibid. loco*, 4-24.V.1993, fl., *Randriamampionona* 376 (MO, P); Imonty, 3.VIII.1955, fr., *Service Forestier* 13942 (P).

5. *Homalium masoalense* Appleg., **spec. nova** (Fig. 2).

Holotypus: MADAGASCAR. **Prov. Toamasina:** Masoala Peninsula, trail along coast 3-6 km S of Ambanizana, 15°39'S 49°58'E, 0-20 m, 30.X.1992, fl., *Schatz et al.* 3367 (MO-6703444!; iso-: BR!, G!, K!, P!, TAN, USMS).

Homalium masoalense Appleg. differs from *H. longistaminum* H. Perrier in having leaves mostly ovate to lanceolate (vs elliptical to broadly elliptical, less often ovate or seldom lanceolate), with the apex usually acuminate (vs acute to obtuse or rounded, rarely short-acuminate) and the petiole shorter, 3-5.5 vs 4-11 mm long; inflorescences longer, 5-11 cm long (vs (2.2-)-4-6.5 cm long), moderately pubescent with the surface visible (vs at least partly canescent), the flowers sessile or subsessile with pedicels to 0.5 mm long (vs pedicellate with pedicels 0.3-1.4 mm long); sepals oblong-lanceolate to narrowly oblong, 1.2-1.4 mm long (vs deltoid to ovate, at most 0.6 mm long); petals narrowly oblong, 1.5-1.7 mm long, only modestly longer than sepals, with the apex acute (to narrowly rounded) (vs oblong to somewhat obovate, 0.8-1.2 mm long, much longer than sepals, with the apex rounded to obtuse).

Tree to 16 m tall; young twigs glabrous. *Leaves:* petiole 3-5.5 mm long, glabrous; blade ovate to lanceolate (elliptical), (3.5-)-5-9.1 × (1.8-)-2-4.2 cm; base convex to rounded with the extreme base attenuate; margins irregularly crenulate to slightly undulate, usually for most of their length, or subentire; apex acuminate (acute, emarginate). *Inflorescences* racemose, 5-11 cm long, moderately pubescent with short erect trichomes that are often relatively dense but leave the surface visible; flowers mostly in clusters of up to 4, sessile or subsessile with pedicels to 0.5 mm; bracts transversely oblong to transversely oblong-ovate; bracteoles rapidly caducous (or possibly absent?). *Flowers* (6-)-7-merous, greenish yellow;

sepals oblong-lanceolate to narrowly oblong, 1.2-1.4 mm long; petals narrowly oblong, 1.5-1.7 mm long, margins ciliate, abaxial surface pubescent, mostly glabrous adaxially, apex acute (to narrowly rounded); filaments (0.7-)-1.5-1.9 mm long; upper surface of ovary moderately pubescent with long trichomes; styles 3-4, (1.1-)-1.3-1.6 mm long.

Distribution, ecology and conservation status. – *Homalium masoalense* is known from a single collection, made in coastal forest of the Masoala Peninsula in northwestern Madagascar just outside the Masoala protected area in an area with human activities. Since accessible coastal areas of Masoala have been relatively well collected, the new species is likely to be rare. The new species should be considered "Vulnerable" [VU D2] based on its rarity and its probable occurrence within the Masoala protected area even if no collection has yet been made there.

Notes. – *Homalium masoalense* and another new species, *H. ovatifolium* Appleg., which is discussed below, have clear affinities to *H. longistaminum*, previously placed in *Homalium* sect. *Blackwellia*, which likewise has unusually long stamens and styles compared to most species of *Homalium* sect. *Odontolobus*. All three have ciliate petals that are relatively long compared to most species of *Homalium* sect. *Odontolobus*.

Homalium masoalense and *H. ovatifolium* are most readily distinguished from *H. longistaminum* by having usually ovate leaves (in the former species frequently to lanceolate) with the apex usually acuminate or long-acute.

Homalium masoalense is distinguished from both *H. longistaminum* and *H. ovatifolium* by having larger flowers and in particular, much longer sepals both proportionately and in absolute measurements (1.2-1.4 mm long, more or less narrowly oblong, versus at most 0.7 mm long and deltoid to ovate in the other two species). The flowers are thereby more similar in proportion to those of *H. brachystylis*, which has smaller, more or less elliptical leaves and solitary flowers, than to those of any other species in *Homalium* sect. *Odontolobus*.

Homalium longistaminum and *H. ovatifolium* both have thickened pubescent bracteoles; no bracteoles were observed on the type collection of *H. masoalense*.

6. *Homalium moniliforme* H. Perrier in Mém. Mus. Natl. Hist. Nat. 13: 291. 1940.

Lectotypus (designated by SLEUMER, 1973: 308): **MADAGASCAR. Prov. Fianarantsoa:** Vondrozo, province de Farafangana, s.d., fl., *Decary* 5469 (P [P04679983!]; isolecto-: K [K000231481] image seen, L [L0010965] image seen). **Syntypus:** **MADAGASCAR. Prov. Toamasina:** Tampina, 25.VIII, fr., *Louvel* 53 (P [P04679987!])

Tree to 13 m tall, 30 cm dbh; young twigs moderately pubescent with minute hairs or glabrous (glabrate). *Leaves:*



Fig. 2. - *Homalium masoalense* Appleq. **A.** Flowering branch; **B.** Flowers.
[Schatz et al. 3367, TAN] [Drawing: R.L. Andriamiarisoa]

petiole 1-7(-10) mm long, glabrous (minutely pubescent); blade narrowly elliptical to elliptical (oblanceolate) or obovate to elliptical, (1.8-)2.7-6.8 × 0.7-2.6(-3) cm; base cuneate to attenuate or convex; margins serrulate to crenate-serrate, shallowly wavy or subentire, sometimes slightly revolute; apex rounded-acute to rounded (slightly acuminate, rounded-cuspidate, aberrantly emarginate). *Inflorescences* spicate, (2-)4-7(-10) cm long, minutely pubescent or glabrous; flowers in several-flowered glomerules, sessile; bracts transversely oblong, often irregular; bracteoles reduced to minute teeth, rapidly caducous. *Flowers* 6-7(-8)-merous, greenish (corolla pale yellow); sepals deltoid to ovate, 0.1-0.3 mm long; petals transversely (very broadly) ovate (very broadly oblong-ovate), 0.5-0.7(-0.8) mm long, glabrous, apex rounded (rounded-obtuse); filaments 0.2-0.4(-0.6) mm long; upper surface of ovary densely short-pubescent; styles (2-)3, 0.2-0.3(-0.5) mm long.

Notes. – *Homalium moniliforme* displays geographic variation in its vegetative morphology and ecological preferences. Collections from the southern provinces of Toliara and Fianarantsoa occur consistently at low altitudes on sand and have small, short-petioled, often narrowly elliptical to elliptical leaves and minutely pubescent twigs. This form extends to coastal forests in Toamasina province. Inland collections from moderate-elevation humid forests, which occur on more diverse substrates, range from Antsiranana to Toamasina provinces and rarely Fianarantsoa province. These have somewhat larger leaves that are longer-petioled and usually mostly obovate, less often elliptical; the twigs are glabrous or glabrate, rarely papillate at the extreme apices. The two geographically distinct forms are usually readily distinguishable. It therefore seems appropriate to recognize them as subspecies. The lectotype is from Fianarantsoa province at a low-moderate elevation, in a region where no other material of the species has been collected. Its morphology is somewhat intermediate between the two forms, with mostly narrow, oblanceolate leaves, and the leaves dry relatively pale, which is much more common in the small-leaved subspecies (though that is not a fully reliable character in any related group observed to date). However, it is overall more similar to material from the moderate-elevation populations, for which it would represent a substantial range extension. These populations are therefore herein recognized as subsp. *moniliforme*, and the coastal subspecies is described below as subsp. *littoralis* Appleg., to which the other syntype (*Louvel* 53) belongs.

The original publication of *Homalium moniliforme* did not explicitly cite specimens, but did enumerate the vernacular names provided on the labels of both *Decary* 5469 and *Louvel* 53, which were the only two collections cited in the Flora treatment six years later (PERRIER DE LA BATHIE, 1946). SLEUMER (1973) therefore termed them syntypes. That interpretation could be questioned, since they were only indirectly

cited, but they are certainly original material, and he appropriately designated the P duplicate of *Decary* 5469 as lectotype.

Key to the subspecies of *Homalium moniliforme*

1. Young twigs glabrous (glabrate, minutely papillate at the apex); petiole 2-7(-10) mm long; leaf blade obovate to elliptical, narrowly elliptical, or oblanceolate, 3-6.8 × (1.1-)1.3-2.6(-3) cm; mid- to low-elevation humid forests 6a. subsp. *moniliforme*
- 1a. Young twigs moderately minutely pubescent; petiole 1-3 mm long; leaf blade narrowly elliptical to elliptical (oblanceolate), (1.8-)2.7-4.7(-5.6) × 0.7-1.6(-1.9) cm; littoral or low-elevation coastal forests 6b. subsp. *littorale*
- 6a. *Homalium moniliforme* subsp. *moniliforme*

Young twigs glabrous (glabrate, minutely papillate only at extreme apex). *Leaves*: petiole 2-7(-10) mm; blade obovate to elliptical, narrowly elliptical, or oblanceolate, 3-6.8 × (1.1-)1.3-2.6(-3) cm; margins shallowly wavy to crenate-serrate or subentire, often slightly revolute; apex rounded to acute (rounded-cuspidate, slightly acuminate, aberrantly emarginate).

Vernacular names. – “Hazombato” (*Razakamalala et al.* 55); “Mafaikoditre” (*Antilahimena et al.* 2171); “Matrambody” (*Razanatsima & Céléstin* 712); “Menahihy” (*Iambana & Arsène* 208, *Iambana* 270); “Rohitra” (*Decary* 5469); “Tamehaka madinindravina” (*Andrianjafy et al.* 189); “Tendrompony” (*Razanatsima* 859).

Uses. – Wood is used for construction (*Andrianjafy et al.* 189).

Distribution, ecology and conservation status. – *Homalium moniliforme* subsp. *moniliforme* is native to mid- to low-elevation humid forests in Antsiranana, Toamasina, and rarely Fianarantsoa provinces. It is reported to occur on laterite, humus soil with rocky substrate, and on ferricrete, sometimes near water. Because it is relatively widespread and occurs in four protected areas (i.e., Zahamena, Masoala, Betampona, Makirovana-Tsihomanaomby), the preliminary assessment of its conservation status is “Least Concern” [LC].

Notes. – *Homalium moniliforme* subsp. *moniliforme* has on average larger leaves than subsp. *littorale*, but its leaves usually do not exceed 6.8 × 2.6(-3) cm. Collections from lower-elevation sites, e.g., in Betampona, seem more often to have acute or cuspidate leaves while those at higher elevations have more rounded leaf apices and the leaves are more strongly coriaceous; at the highest elevations the margins are generally revolute.

Two specimens from northern Madagascar with very large leaves (to 9.7×4.1 cm) (*Service Forestier 28807* and *Razakamalala et al. 55*) are tentatively placed with the large-leaved, usually southern *H. densispicatum* but may have affinities to *H. moniliforme*.

Selected material examined. – **MADAGASCAR. Prov. Antsiranana:** Ambo-divoapaza, forêt de Makirovana-Tsihomanambo, $14^{\circ}08'33''\text{S } 49^{\circ}55'06''\text{E}$, 593 m, 23.V.2009, post-fl., *Randrianarivony et al. 154* (MO); Antanandava, Makirovana, $14^{\circ}10'01''\text{S } 49^{\circ}57'12''\text{E}$, 685 m, 4.V.2010, fr., *Razakamalala et al. 5447* (MO). **Prov. Toamasina:** Zahamena PN, $17^{\circ}38'27''\text{S } 48^{\circ}52'32''\text{E}$, 700–1040 m, 4.X.2001, fr., *Andrianjafy et al. 189* (MO, P); Ampokafo, village Ambatolodama, $15^{\circ}17'\text{S } 50^{\circ}00'\text{E}$, 15.VIII.2003, fr., *Antilahimena 2046* (G, MO); Fkt. Anjahely, $15^{\circ}24'19''\text{S } 49^{\circ}30'28''\text{E}$, 360 m, 28.VI.2004, fl., *Antilahimena 2597* (P); Masoala NP, Ambohitsitondroina Mahalevona, $15^{\circ}25'37''\text{S } 49^{\circ}57'24''\text{E}$, 1158 m, 10.X.2003, fr., *Antilahimena et al. 2171* (P); Fkt. Anjian'i Madirano, $15^{\circ}54'08''\text{S } 49^{\circ}27'44''\text{E}$, 829 m, 22.VII.2007, post-fl., *Antilahimena et al. 5616* (MO); Betampona RNI, piste principale 2 à 4 km, $17^{\circ}55'\text{S } 49^{\circ}13'\text{E}$, 21.IV.1999, fr., *Iambana & Arsène 208* (MO, P); Vatomaniry, $19^{\circ}09'16''\text{S } 48^{\circ}34'56''\text{E}$, 686 m, 22.XI.2004, old fls., *A. Randrianasolo et al. 947* (MO); Brickaville, vers le sommet d'Ankerana, $18^{\circ}25'24''\text{S } 48^{\circ}47'06''\text{E}$, 896 m, 22.III.2011, fl., *Ravelonarivo et al. 3785* (MO); Fkt. Ambatolampy, forêt d'Ankerana, $18^{\circ}23'51''\text{S } 48^{\circ}47'53''\text{E}$, 948 m, 25.I.2012, fl., *Ravelonarivo et al. 4194* (MO); Sahanonaka, forêt de Vohibe, $19^{\circ}10'49''\text{S } 48^{\circ}32'27''\text{E}$, 763 m, 2.VI.2010, post-fl., *Razanatsima 859* (BR, G, K, MO, WAG); Ambinanindrano II, forêt de Vohibe, $19^{\circ}09'19''\text{S } 48^{\circ}35'04''\text{E}$, 655 m, 5.IV.2009, fl., *Razanatsima & Céléstin 712* (MO [2 sheets]); Fkt. Ambatolampy, forêt d'Ankerana massif de Beanjada (N de la presqu'île Masoala), 1000 m, I.1954, fr., *Service Forestier 8825* (P).

6b. *Homalium moniliforme* subsp. *littorale* Appleg., **subspec. nova** (Fig. 3).

Holotypus: MADAGASCAR. **Prov. Fianarantsoa:** Fiv. Fara-fangana, firaisam-pokontany Mahabo Mananivo, fkt. Nosy ala, forêt d'A[gnalazaha], $23^{\circ}10'13''\text{S } 47^{\circ}43'27''\text{E}$, 22 m, 26.VII.2003, fl., *Rabehevitra et al. 516* (MO-04810771!; iso-: G [G00418523] image seen, P [P04705768]!, TEF).

Homalium moniliforme subsp. *littorale* Appleg. differs from *H. moniliforme* *H. Perrier* subsp. *moniliforme* in having young twigs moderately pubescent with minute trichomes (vs glabrous to glabrate or minutely papillate at apex), and leaves with the petiole 1–3 mm (vs 2–7(–10) mm) and the blade usually narrowly elliptical to elliptical, (1.8–)2.7–4.7(–5.6) \times 0.7–1.6(–1.9) cm.

Young twigs moderately pubescent with minute hairs. *Leaves:* petiole 1–3 mm; blade narrowly elliptical to elliptical (oblanceolate especially when young), (1.8–)2.7–4.7(–5.6) \times 0.7–1.6(–1.9) cm; margins serrulate to crenate-serrate or subentire; apex rounded-acute to rounded (slightly acuminate with rounded tip).

Vernacular names. – “Fotsiakara” (*Ludovic et al. 870*); “Fotsiakara mainty” (*Ludovic 649*); “Fotsiakara minty” (*Ludovic et al. 696*);

“Fotsikara minty” (*Ludovic 761*); “Hazontsindrano” (*Louvel 53*).

Uses. – Wood is used for construction (*Ludovic et al. 696, 870*).

Distribution, ecology and conservation status. – *Homalium moniliforme* subsp. *littorale* is native to littoral or low-elevation coastal forests from Toamasina to Toliara provinces; it is reported to occur on sand. Coastal forest, where not protected, is one of the most threatened habitat types in Madagascar. The habitat is in fact quite fragmented; three locations are within the protected area network (i.e., Mahabo/Agnalazaha, Mandena, and Ste. Luce) but continuing decline in habitat area and quality can be expected for the remainder. There are only seven distinct locations, three of which (from Tular) are very close together. The EOO is estimated by GeoCAT as c. 10.5 km², and the AOO as 56 km². The preliminary assessment of conservation status suggests that a status of “Vulnerable” [VU B1ab(iii)+B2ab(iii)] would be appropriate, though one could argue for “Endangered” [EN] on the grounds that the habitat might be considered “severely fragmented.”

Paratypes. – **MADAGASCAR. Prov. Fianarantsoa:** Fkt. Vohimasy, forêt d'Agnalazaha, bloc Agnanto, $23^{\circ}10'09''\text{S } 47^{\circ}41'51''\text{E}$, 28 m, 23.III.2004, fl., *Ludovic 649* (MO); Fkt. Nosiala, forêt d'Agnalazaha, bloc de Betaindambo, $23^{\circ}08'42''\text{S } 47^{\circ}42'18''\text{E}$, 31 m, 22.IV.2004, fl., *Ludovic 761* (MO); Fkt. Nosiala, bloc forestier d'Ampandramadinika, $23^{\circ}12'13''\text{S } 47^{\circ}42'41''\text{E}$, 21 m, 8.IV.2004, fl., *Ludovic et al. 696* (MO); Nosiala, forêt d'Ampitavananima, $23^{\circ}11'10''\text{S } 47^{\circ}43'02''\text{E}$, 30 m, 5.VIII.2004, fr., *Ludovic et al. 870* (MO); Mahabo-Mananivo, forêt de Mahabo, $23^{\circ}10'20''\text{S } 47^{\circ}42'23''\text{E}$, 29 m, 23.IX.2002, fr., *Rabenantoandro et al. 961* (MO, P); *ibid. loco*, $23^{\circ}10'37''\text{S } 47^{\circ}43'\text{E}$, 10 m, 25.IX.2002, fl., *Rabenantoandro et al. 990* (MO, P); Trail E of Vohimasy Ankorabe, W edge of Ampanasanay forest, $23^{\circ}10'56''\text{S } 47^{\circ}42'00''\text{E}$, 24 m, 19.VI.2004, fr., *A. Randrianasolo et al. 853* (MO, P); Mahabo-Mananivo, Sahalava, 4 km à l'E du gîte MBG, $23^{\circ}11'27''\text{S } 47^{\circ}42'39''\text{E}$, 4 m, s.d., fl., *Razafitsalama et al. 1004* (G, MO, P). **Prov. Toamasina:** Fkt. Tanambao Ambodimanga, forêt de Menagisy 500 m du village Antanandava Martin, $16^{\circ}47'\text{S } 49^{\circ}43'\text{E}$, 26.V.2010, fl., *Leavana & Zackarie 692* (MO); Tampina, s.d., fr., *Louvel 53* (P); Fénériver, forêt à Mahambo, 12.VIII.1961, fl., *Peltier & Peltier 3419* (P); Vohibola, à l'W de Tampina, 12–14.VIII.1957, fl., *Service Forestier 18072* (P); Mahambo, au S de Fénériver, 30.VIII.1957, fl. & fr., *Service Forestier 18146* (MO, P [3 sheets]). **Prov. Toliara:** Mandena, $24^{\circ}57'\text{S } 47^{\circ}02'\text{E}$, 10 m, 13.I.1990, fl., *Dumetz 1184* (MO, P); forêt au NE de la rivière Antorendrika avant Belavenona, $24^{\circ}52'\text{S } 47^{\circ}07'\text{E}$, 0–20 m, 22.III.1989, fl., *Rabevohitra et al. 1781* (MO, P); Forest of Ste. Luce (Manafiafy), 2 km NW of Ambandrika village, $24^{\circ}46'\text{S } 47^{\circ}12'\text{E}$, 0–10 m, 9.VI.1994, fl., *A. Randrianasolo 343* (MO, P).

7. *Homalium ovatifolium* Appleg., **spec. nova** (Fig. 4).

Holotypus: MADAGASCAR. **Prov. Antsiranana:** Ambilobe, Marivorahona, village le plus proche Betsimiranja, forêt d'Andohan'Antsohiy, Ambohibe, RN6 à 1 km au SE d'Ambilomagodra, $13^{\circ}02'31''\text{S } 49^{\circ}09'19''\text{E}$, 100 m, 17.VII.2005, fl., *Randrianarivo et al. 1206* (MO-6082912!; iso-: CNARP, P [P04679126]!, TAN).

Homalium ovatifolium Appleg. differs from *H. longistaminum* *H. Perrier* in having leaves larger, (4.2–)6.2–10.2 \times (2.1–)



Fig. 3. - *Homalium moniliforme* subsp. *littorale* Appleg. **A.** Flowering branch; **B.** Flowers; **C.** Inflorescence; **D.** Leaf (upper surface); **E.** Leaf (lower surface). [Rabehevitra et al. 516, TEF] [Drawing: R.L. Andriamiarisoa]



Fig. 4. - *Homalium ovatifolium* Appleq. **A.** Flowering branch; **B.** Flowers.
[Randrianaivo et al. 1206, TAN] [Drawing: R.L. Andriamiarisoa]

3.1–5.2 cm (vs (3.2–)3.5–7.5 × 1.6–3.3(–4.8) cm), ovate (to elliptical) (vs irregularly elliptical to broadly elliptical, ovate or rarely lanceolate) with the base rounded (vs convex to rounded), margins less toothed, sometimes subentire (vs irregularly crenate apically to crenate-serrate for most of their length), apex acute to acuminate (vs acute to obtuse or rounded, rarely short-acuminate), and petals narrowly oblong (vs oblong to obovate), the abaxial surface pubescent and the adaxial surface largely glabrous (vs both surfaces pubescent, the abaxial surface densely so and often the base of the adaxial surface densely so). It differs from *H. masoalense* Appleq. in having possibly broader leaves, ovate or rarely elliptical (vs often lanceolate), with the petiole longer, 5–11 mm long (vs 3–5.5 mm long); inflorescences shorter, (2.2–)4–6.5 cm long (vs 5–11 cm long), often canescent (vs moderately pubescent), the flowers more often pedicellate with pedicels 0.5–1 mm long (vs absent or up to 0.5 mm long); sepals ovate to deltoid or narrowly deltoid, (0.3–)0.4–0.5(–0.7) mm long (vs oblong-lanceolate to narrowly oblong, 1.2–1.4 mm long); petals 0.8–1.2 mm long (vs 1.5–1.7 mm long), much longer than sepals (vs only moderately longer).

Tree to 10 m tall, 50 cm dbh; young twigs glabrous. *Leaves*: petiole 5–11 mm long, glabrous; blade ovate (elliptical), (4.2–)6.2–10.2 × (2.1–)3.1–5.2 cm; base rounded; margins irregularly crenate-serrulate, sometimes with only 1 tooth per side, to slightly wavy or subentire; apex acute to acuminate. *Inflorescences* racemose, (2.2–)4–6.5 cm long, canescent to moderately pubescent; flowers often in clusters of 2 or 3, pedicellate, with pedicels 0.5–1 mm long, or subsessile; bracts broadly ovate to deltoid or transversely oblong; bracteoles very thick, to subterete at base, densely pubescent, often caducous. *Flowers* 7–8-merous; sepals ovate to deltoid or narrowly deltoid, (0.3–)0.4–0.5(–0.7) mm long; petals narrowly oblong, 0.8–1.2 mm long, margins long-ciliate, abaxial surface pubescent, mostly glabrous adaxially, apex rounded; filaments 1.4–1.9 mm long; upper surface of ovary densely pubescent to moderately so in fruit; styles 3–4, 1.3–1.8 mm long.

Vernacular name. – “Taindalitra” (Guittou et al. 160).

Distribution, ecology and conservation status. – *Homalium ovatifolium* is known from only two collections and a single location in deciduous forests at low elevation in extreme northern Madagascar in the western edge of the Andrafiama Andavakoera protected area. Even if the only known location is within the protected area network, the new species is under threat and can be affected by a single event (e.g., fire), so its conservation status should be considered “Vulnerable” [VU D2].

Notes. – *Homalium ovatifolium* has clear affinities to *H. longistaminum*, which likewise has a canescent or mostly densely

pubescent inflorescence, fleshy, densely pubescent bracteoles and long filaments and styles. It differs in its larger leaves, (4.2–)6.2–10.2 × (2.1–)3.1–5.2 cm (vs (3.2–)3.5–7.5 × 1.6–3.3(–4.8) cm), which are more usually ovate with a rounded base, often long-acute to acuminate apex and few-toothed, shallowly wavy or subentire margins, and its narrow, less pubescent petals.

Interestingly, the two taxa are found at the opposite extremes of latitude, *H. ovatifolium* being confined to the extreme north of Madagascar and *H. longistaminum* to the southeast. It also is likely to be closely related to *H. masoalense*, which is from northeastern Madagascar and shares the unusual character of often ovate, acuminate leaves, as well as long filaments and styles. *Homalium masoalense* has often lanceolate, short-petiolate leaves and larger flowers (petals 1.5–1.7 mm long) with the sepals more similar to the petals in length (1.2–1.4 mm long) and narrowly oblong to oblong-lanceolate.

Paratypes. – MADAGASCAR. **Prov. Antsiranana:** Ambilobe, Tanambao Marivorahona, Betsimiranja, Andohan'Antsohy, 4 km au NE de Betsimiranja, 13°02'32"S 49°09'24"E, 76 m, 2.VII.2005, fl. & fr., Guittou et al. 160 (MO, P, TAN).

8. *Homalium parkeri* Baker in J. Linn. Soc., Bot. 20: 150. 1883.

Lectotypus (designated by SLEUMER, 1973: 309): MADAGASCAR. **Prov. Antananarivo:** Andrangolaoka, s.d., *Parker s.n.* (K [K000231480] image seen). **Syntypus:** MADAGASCAR. **Prov. Antananarivo:** forests of Imerina, s.d., *Baron 1295* (K [K000231479] image seen, TAN [TAN000592] image seen).

Tree to 20 m tall, 36 cm dbh, or shrub; young twigs glabrous (glabrate). *Leaves*: petiole 2.5–7(–8) mm long, glabrous (glabrate); blade elliptical to narrowly elliptical (to narrowly obovate, ovate or obovate), (2.8–)4–7.3(–9.3) × 1.3–3.1(–3.4) cm; base cuneate (moderately convex, attenuate); margins serrate with rounded tooth apices; apex acute (rounded, aberrantly emarginate). *Inflorescences* spicate, (1.8–)3–7(–11.5) cm long, minutely pubescent (glabrate); flowers clustered, sessile; bracts broadly to transversely deltoid; bracteoles deltoid, minute, caducous. *Flowers* 5–7-merous, pale green to yellowish; sepals deltoid (ovate), 0.2–0.4(–0.5) mm long; petals ovate (oblong-ovate), 0.7–1.5 mm long, glabrous (sparsely pubescent on abaxial surface), apex acute to rounded; filaments 0.3–0.6 mm long; upper surface of ovary short-pubescent, usually densely; styles (2–)3(–4), 0.2–0.5 mm long.

Vernacular names. – “Hazombato” (*Anonymous 19, Hong-Wa et al. 392, Lehavana et al. 487, Service Forestier 16807, 19957, 28755*); “Hazombatofotsy” (*Louvel 43*); “Hazombatomainty” (*Service Forestier 16010, 16822*); “Hazomby” (*Service Forestier*

595, 1043, 3926, 6006, 10370, 15990); “Hazompoza” (*Service Forestier* 7592); “Moara” (*Réserves Naturelles* 9460); “Romaindafa” [?] (*Réserves Naturelles* 10472); “Ranga” (*Service Forestier* 15873).

Distribution, ecology and conservation status. – *Homalium parkeri* is widespread in humid forests of eastern Madagascar, extending to high-elevation montane moss forest. A preliminary assessment of its conservation status should be “Least Concern” [LC].

Selected material examined. – **MADAGASCAR. Prov. Antananarivo:** Ambohitately RS, 1620 m, 18°11'52.5"S 47°17'03"E, 7.III.2004, fl., *Almeda et al.* 8645 (MO); Angavokely (Carion), V.1956, fl., *Bosser* 9575 (P); PK 138 de la route Tananarive-Majunga, 8.VII.1971, post-fl., *Cremers* 1636 (MO); W Imerina, Andrangolaoka, III.1881, fl. & fr., *Hildebrandt* 4102 (P [2 sheets]); Firarazana, forêt de Manjato, 18°06'19"S 47°14'43"E, 1447 m, 6.VII.2005, fl., *Hong-Wa et al.* 392 (MO, P); 7 km E of Anjozorobe, 18°22'S 48°00'E, 1350 m, 2.IV.1988, fl., *Lowry & Randrianasolo* 4419 (MO, P); Ambatolaona, 1700 m, VII.1914, fl., *Perrier de la Bâtie* 6720 (P); Tsinjoarivo, Ambatotsipihina, 22.XI.1949, fl., *Service Forestier* 1043 (P); Antsahambavy, Manjakandriana, 14.V.1956, fl., *Service Forestier* 15873 (P); Ambohidraondriana, Ankazobe, 3.V.1956, fl., *Service Forestier* 15990 (P); Ambatondradama au N d'Ambohimanga, 30.IV.1957, fl., *Service Forestier* 18027 (P); Tsiacompaniry, forêt d'Ambohimangakely, 6.IV.1961, fl., *Service Forestier* 19894 (P); Ibity massif W, Vohipisaka, 20°09'42"S 46°58'54"E, 1423 m, 29.II.2004, fl., *Skema et al.* 22 (MO); SW Andranofeno Sud village, 18°04'59"S 47°10'26"E, 1407 m, 5.IV.2004, fl., *Skema et al.* 54 (MO). **Prov. Antsiranana:** Manongarivo RS, 14°05'S 48°23'E, 1470-1570 m, 14-15.IV.1992, fl., *Malcomber et al.* 1495 (MO, P); SW edge of Anjanaharibe-Sud Reserve, 14°48'15"S 49°26'45"E, 1000-1100 m, 6.VIII.1997, fr., *McPherson* 17257 (MO); Anjanaharibe-Sud, 14°47'45"S 49°27'54"E, 1161 m, 22.V.1995, fl., *Ravelonarivo & Rabesonina* 811 (G, K, MO, P); Andranomilolo, 13 km à l'W du village d'Andranopositra, 14°19'16"S 49°17'56"E, 1462 m, 10.XI.2006, fl., *Ravelonarivo et al.* 2015 (MO, P); Befingotra, Andranotsarabe, 14°45'11"S 49°28'49"E, 762 m, 21.IV.1997, fl., *Razafindramora et al.* 26 (MO). **Prov. Fianarantsoa:** Andringitra, 26.II.1938, fl., *Herb. Jard. Bot.* 3141 (P [2 sheets]); Ranomafana, W side of Namorona riv., 21°16'S 47°21'E, 1080 m, 6.III.1992, fl., *Malcomber et al.* 1317 (MO, P); Ambalamanakana, 30 km S d'Ambositra sur RN 7, 20°44'06"S 47°11'37"E, 1650 m, 26.III.1996, fl., *Rakotomalaza et al.* 678 (MO); Ranomafana, parcelle n° 3, 21°15'30"S 47°25'E, 900-1100 m, 14.VI.1994, fr., *J. Randrianasolo et al.* 65 (MO). **Prov. Mahajanga:** Ambalotsangana, forêt de Makira, 15°31'S 49°05'E, 1169 m, s.d., fl., *Lehavana et al.* 487 (MO, P). **Prov. Toamasina:** Fkt. Ampita[m]be, Ambatovy, Ampanatovana forest, 18°51'17"S 48°19'07"E, 1085 m, 9.VI.2008, fl., *Antilabimena et al.* 6277 (G, MO); Andapanomby, près de la riv. Ampandisanana, Makira NW, 15°21'17"S 49°06'25"E, 25.IV.2007, fr., *Bernard & Birkinshaw* 456 (G, MO, P); Fkt. Ambohibato, forêt de Rianani Galy, 18°39'32"S 47°57'56"E, 1291 m, 10.IV.2005, fl., *Raharijaona et al.* 72 (MO); Mantadia PN, Andranomanamponga, 18°50'23"S 48°26'31"E, 1110 m, 19.III.2013, fl., *Ramahenina et al.* 224 (G, MO, P); Zahamena PN, campement Analentitra, 17°32'47"S 48°44'21"E, 1235-1400 m, 29.IX.2001, fr., *Randriananjana et al.* 629 (MO); Fkt. Ampitambe, Ambatovy, forêt d'Analamay, 18°49'07"S 48°19'26"E, 1138 m, 5.IX.2011, fl., *Ravelonarivo* 3950 (G, MO); Ambatondrazaka, Manaka Est, 27.VII.1960, fl., *Réserves Naturelles* 10472 (P); Bekiritsika [?], Lakato, 8.X.1953, fl., *Service Forestier* 7592 (P [2 sheets]); Perinet, km 7 Antaniditra, 5.V.1954, fl., *Service Forestier* 10370 (P); W du massif de l'Ampahana, à l'E de Fierenana, 950-1300 m, 10-16.III.1969, fl., *Service Forestier* 28755 (MO, P).

9. *Homalium planiflorum* (Tul.) Baill. in Bull Mens. Soc. Linn. Paris 1: 574. 1886.

≡ *Blackwellia planiflora* Boivin ex Tul. in Ann. Sci. Nat., Bot. ser. 4, 8: 64. 1857 [nom. conserv. prop.; APPELQUIST, 2017].

≡ *Blackwellia gracilis* Blume in Mus. Bot. Lugd.-Bat. 2: 26. 1856.

Holotypus: MADAGASCAR: “Ile Ste. Marie”, s.d., *Richard* 297 (L [L0010991] image seen; iso-: G [G00018396] image seen, P [P00375177, P00375178]!)

Tree to 30 m tall, 60 cm dbh; bark young twigs glabrous (minutely pubescent when very young). *Leaves:* petiole (2-)3-8(-14) mm long, glabrous (to sparsely and minutely pubescent); blade narrowly elliptical to elliptical or oblanceolate (aberrantly obovate), (2.8-)3.5-10.3 × 1-4 cm; base convex (cuneate to attenuate); margins crenate-serrate to serrulate, at least apically (partly subentire); apex acute to acuminate (to rounded, emarginate, cuspidate). *Inflorescences* racemose (paniculate with a few long branches, racemiform panicles), sometimes clustered terminally, (2.2-)5-10(-22) cm long, moderately to sparsely short-pubescent; flowers mostly in small clusters, pedicellate with pedicels (0.4-)1-3(-3.5) mm long; bracts broadly ovate-deltoid to transversely ovate; bracteoles ovate to deltoid, small, not thickened, caducous. *Flowers* 7-8 (-9)-merous, whitish to pale green, pale yellow or cream-colored or pink to reddish; sepals lanceolate to narrowly oblong-lanceolate (ovate), 0.5-0.9(-1.1) mm long; petals oblanceolate (to broadly spatulate, narrowly obovate, to somewhat oblong or narrowly elliptical), 1-1.7 mm long, margins ciliate and both surfaces sparsely pubescent to glabrate, apex acute to rounded; filaments (0.5-)0.6-1.2(-1.4) mm long; upper surface of ovary moderately pubescent; styles 3-4, (0.4-)0.8-1.4 mm long.

Notes. – Most specimens assigned to *H. planiflorum* have white to pale green or yellowish flowers. A group of specimens from southeastern Madagascar that are characterized by pink or reddish flowers are herein segregated as subsp. *roseiflorum* Appleg. While specimens of subsp. *planiflorum* have sometimes large leaves and racemes usually borne along the length of the twigs, those of subsp. *roseiflorum* often have relatively small leaves and relatively large (though not long) distal clusters of racemes, or occasionally paniculate inflorescences borne well below twig apices; however, these characters are not fully consistent. Several specimens from the extreme southeast, where both subspecies occur, are not assigned to either subspecies, though these collections generally have narrow leaves of modest size, typical of subsp. *roseiflorum*. One is sterile and two are only weakly flowering with one or two racemes, so subspecies identity cannot be confidently assigned

without information on flower color. Two other collections are described as having possibly reddish flower color (“terre brûlée” according to Cloisel and “fulvo-rosei (sordid)” according to Bernardi) but the distribution of their well-developed inflorescences appears to be more consistent with subsp. *planiflorum*, and flowers may brown as they turn to fruit. The inability to assign identities to some specimens in the zone where these taxa are sympatric supports a view that they are not fully genetically isolated, and that the distinctions between them are not adequate to justify recognition at the species level. Alternatively, the intermediate specimens could be interpreted as hybrids between two distinct species; however, because three fixed differences between the two morphological forms have not been observed, the conservative approach of treating them as conspecific has been preferred.

Service Forestier 9952 (Andovolava, Nosy-Varika, 14.XI.1953) is a specimen in poor condition with few flowers; the leaves are very large and broad (up to at least 10 × 5.5 cm). It may represent a regional variant, an aberrant individual, or an undescribed species; the available material is inadequate to clarify its status. Additional collections from this population would be highly desirable.

Blackwellia planiflora was published in 1857, the year after *B. gracilis* Blume, though its author, Tulasne, was apparently unaware of the latter publication. The citation of *Richard 297* in the protologue of *B. gracilis* explicitly referred only to the duplicate at L, which is therefore its holotype. The protologue of *B. planiflora* cited two syntype gatherings, *Boivin 1847* and *Richard 297*; three duplicates each of the former are present at P and G, and two of the latter at P. PERRIER DE LA BÂTHIE (1946: 92) chose *Boivin 1847* as “type” (i.e., the lectotype) without selecting among the available duplicates. Under Art. 52.2 of the ICN (McNEILL et al., 2012), the citation of *Richard 297*, which included the holotype of *B. gracilis*, in the protologue of *B. planiflora* would appear to make the latter a superfluous and illegitimate name. Past literature has implicitly treated it as being the citation only of duplicates that were available to Boivin and Tulasne, not the duplicate at L that they presumably did not have access to (e.g., SLEUMER, 1973: 248). By that view, *B. planiflora* need not be treated as illegitimate. However, Art. 9.5 of the ICN states that the citation of a gathering, if not qualified or limited, is equivalent to the citation of all duplicates of that gathering, even those not seen or known of. Tulasne did not indicate that only material at P was used. The informal practice of treating a duplicate in an author’s home institution as a holotype despite the absence of a qualifying statement is seen in the literature (see *Homalium lucidum* above), but normally in cases that do not involve questions of legitimacy. Hence *Blackwellia planiflora* is illegitimate due to the citation of the holotype of *B. gracile*, which is therefore also the obligate type of *B. planiflora*, regardless of Perrier de la Bâthie’s attempt to select another gathering as the (lecto)type.

This creates serious problems, because under the ICN, the species under question here would have no legitimate name. *Blackwellia gracilis* Blume cannot now be transferred to *Homalium* and retain that epithet because of the existence of *H. gracile* Briq., a replacement name for *Blackwellia gracilis* Vieill. [nom. illeg., non Blume]. However, because *Homalium gracile* had not yet been published when *H. planiflorum* was described, *H. planiflorum* as a replacement name credited to Baillon would also be illegitimate (see Art. 58, Note 1, of the ICN; McNEILL et al., 2012). The publication of a new name would therefore be required. However, since this is the most common species of its section, introducing an entirely unfamiliar name would cause some confusion among botanists. A proposal to conserve *Blackwellia planiflora* to permit the continued use of *Homalium planiflorum* (the preferable approach, since Prop. 235 to amend the ICN to permit this (WIERSEMA et al., 2016) was accepted at the 2017 Botanical Congress) has therefore been offered (APPLEQUIST, 2017) but will not be considered by the relevant Committees for some time yet.

Key to the subspecies of *Homalium planiflorum*

1. Inflorescences usually racemose (rarely a racemiform or few-branched panicle), usually borne along much of the length of small twigs; flowers whitish to pale green, pale yellow, or cream-colored; widely distributed 9a. subsp. *planiflorum*
- 1a. Inflorescences racemose, usually clustered near twig ends, or paniculate with few long racemoid branches; flowers pink to reddish; confined to southeastern Madagascar 9b. subsp. *roseiflorum*

9a. *Homalium planiflorum* subsp. *planiflorum*

Leaves narrowly elliptical to elliptical (oblancoolate, aberrantly obovate), (2.8-)3.8-10.3 × (1.1-)1.3-4 cm. *Inflorescences* almost always racemose (rarely a racemiform or few-branched panicle), usually borne along length of twigs. *Flowers* whitish to pale green, pale yellow or cream-colored, 7-8-merous.

Vernacular names. – “Fotsakara” (*Service Forestier 15282*); “Fotsakara (petits feuilles)” (*Service Forestier 2719*); “Haraka” (*Louvel 68*); “Hazombalovary” (*Louvel 146*); “Hazombarorana” (*Cours 2965*); “Hazombato” (*Ludovic & Rakotoarivony 213, Rabevohitra et al. 3876, Réserves Naturelles s.n., Service Forestier 1577, 1789, 5693, 5858, 5866, 16862, 17810*); “Hazombato mena (lahy)” (*Réserves Naturelles [Dumazer] s.n.*); “Hazomboangy” (*Service Forestier 11070*); “Hazondrano” (*Service Forestier 2861*); “Marimbody” (*Service Forestier 10155*); “Maroankoditra” (*Service Forestier 8916*); “Masonambatsy” (*Service Forestier 14449, 17999*); “Menavony” (*Réserves Naturelles 8807*); “Moranga ala” (*Réserves Naturelles 3344*);

“Rodrano” (*Service Forestier 14404*); “Tsimahamasatsokina” (*Service Forestier 16259*); “Tsofofonjahana” (*Bernard 126*); “Voangiala” (*Service Forestier 15183*); “Zanganitofotsy” (*Service Forestier 8090*); “Zora” (*Rakotoavao 4713*).

Uses. – Wood is used for construction (*Service Forestier 16259, 17810, 17999*).

Distribution, ecology and conservation status. – *Homalium planiflorum* subsp. *planiflorum* occurs most commonly in littoral and coastal eastern forests on sand, though it also occurs in low-elevation humid forests and rarely in mid-elevation forests (to 706 m) or dry forests. It is often described as occasional, but is common enough to be frequently collected. The preliminary assessment of its conservation status is “Least Concern” [LC].

Note. – *Homalium planiflorum* subsp. *planiflorum* has been reported to be visited by bees (*Ludovic & Rakotoarivony 213*).

Selected material examined. – MADAGASCAR. **Prov. Antsiranana:** Ambohitralalana, Masoala PN, 15°18'45"S 50°20'30"E, 75–150 m, 24.XI.1995, fl. & fr., *Bernard 126* (G, K, MO, P); Parc Masoala, forêt Ambodipont, 15°44'45"S 50°19'25"E, 0–10 m, 3.X.1996, fl., *Bernard 361* (G, MO, P); vallée inférieure de l'Androranga, affluent de la Bemarivo (NE) aux env. d'Antongondriha, 100–250 m, 1–24.XI.1950, fl., *Humbert & Capuron 23979* (P); Between Mandena and the Reserve Integral de Marojejy, 14°27'S 49°17'E, 100–200 m, 30.IX.1988, fl., *J. Miller et al. 3311* (MO [2 sheets], P); Sambava, au N d'Antalaha, XI.1912, fr., *Perrier de la Bâthie 6699* (P); Andravainambo, forêt de Tsihomanaomby, 14°06'S 50°01'E, 225 m, 3.II.2014, fl., *Rakotonirina et al. 446* (MO); Sambava, forêt d'Ambodivohitra, 14°24'42"S 49°51'49"E, 148 m, 20.X.2010, fl., *Ravelonarivo & Rabarivelo 3541* (MO, P); vallée de l'Ampalohandrano, affluent de l'Anohoranga, aux env. d'Antongondriha, 150 m, 9.XI.1950, fl., *Service Forestier 794* (P); Antsambalahy, Vohémar, 2.XII.1955, fl., *Service Forestier 15228* (P); env. S d'Analamanara (près de Tsaratanana), entre Sambava et Antsirabe-Nord, 2–7.XII.1966, fl., *Service Forestier 27184* (P); massif du Bezavona, entre la Fanambana et la Manambery, basse vallée de l'Andilana, 13.XII.1966, fl., *Service Forestier 27226* (P). **Prov. Fianarantsoa:** route Farafangana-Vangaindrano, XII.1963, fl., *Bosser 18580* (P); Province de Mananjary, zone côtière, III–IV.1909, fl., *Geay 7855* (P); Manombo RS, parcelle n° 2, 23°02'31"S 47°46'24"E, 20 m, 18.VIII.1995, fl., *Rakotomalaza et al. 410* (MO, P); Fkt. Marohita, forêt d'Alimamba, 21°28'04"S 48°17'43"E, 13 m, X.2004, fl., *Razakamalala et al. 1646* (G, MO, P); Mananjary, Rindrimbolo, 23.XII.1954, fl., *Service Forestier 14404* (MO); Analamarina, Fort-Carnot, 15.X.1955, fl., *Service Forestier 15282* (P); Evato, village le plus proche Loharano, forêt d'Analavory, 10.XI.1955, fl. & fr., *Service Forestier 16259* (P). **Prov. Toamasina:** Fkt. Ambanizana, between Andranobe & Tampolo, 15°42'12"S 49°57'38"E, 1 m, 27.X.2004, fl. & fr., *Antilabimena 2993* (G, K, MO, P); 0–2 km E of Andavakimemarana (location of ferry to cross Pangalanes), 18°52'34"S 49°08'12"E, 1–10 m, 14–16. II.1999, fl., *Birkinshaw et al. 559* (MO, P); Ile Ste. Marie, X.1849, *Boivin 1847* (P [3 sheets]); Maroantsetra, IX.1923, fr., *Louvel 68* (P); Masoala peninsula, Antalavia, coastal path leading S, 15°46'S 50°01'E, 25 m, 17.IV.1987, fl., *Nicoll et al. 553* (MO, P); Pointe à Larrée, forêt Menagisy, 16°46'39"S 49°41'32"E, XI.2008, fl., *Nikolov 1815* (MO); bassin inférieur du Mangoro, X.1922, fl., *Perrier de la Bâthie 18262* (P); entre Bedinta et Andranobe, 15°39'30"S 49°57'30"E, 350–500 m, 24–26.XI.2001, fr., *Rabevohitra 4006* (P); Tampolo forestry station, 17°17'S 49°23'E, 10 m, 11.X.1999, fl., *A. Randrianasolo et al. 603* (G, K, MO, P); Ambila-Lemaitso, W of Brickaville-Ambila road,

18°49'S 49°08'E, 0–5 m, 11.XI.1999, fl., *A. Randrianasolo & Ranivojoana 649* (G, K, MO, P); trail to Andranokoditra from Ambodivonanto, 18°33'39"S 49°14'33"E, 27 m, 28.X.2002, fr., *A. Randrianasolo et al. 746* (G, MO, P); Fkt. Ambalavontaka, forêt d'Antaimby, 20°22'21"S 48°33'15"E, 13 m, 27.IX.2004, fl., *Razakamalala et al. 1518* (G, MO, P [3 sheets]); RN II [Masoala], cton Ambohitralana[na], 21.I.1953, fr., *Réserves Naturelles 4932* (P); [Ile Ste. Marie], s.d., fl., *Richard 260* (P); Masoala Peninsula, N of Antalavia, 15°47'S 50°02'E, 200–380 m, 13–16.XI.1989, fl. & fr., *Schatz et al. 2780* (MO, P); poste forestier de Mananara-Nord, 4.XII.1953, fl., *Service Forestier 8090* (P); Tenina, au S de Rantabe, I.1954, fl. & fr., *Service Forestier 8916* (P); Tampina, s.d., fr., *Ursch s.n.* (P). **Prov. Toliara:** massif de l'Andohahel[a] (SE), vallée de Ranohela, 300–1200 m, 18–26.X.1928, fl. & fr., *Humbert 6244* (P [2 sheets]); Sainte Luce, forêt de Beboaka, 24°40'25"S 47°12'00"E, 13 m, 25.XI.2011, fl., *Miandrimanana 535* (MO); Ivorona, forêt de Mamoareny, 24°49'S 46°56'E, 706 m, 30.XI.2009, *Razakamalala et al. 5021* (MO); Fort Dauphin, VI.1889, fl., *Scott Elliot 2824* (P).

9b. *Homalium planiflorum* subsp. *roseiflorum* Appleq., subspec. nova (Fig. 5).

Holotypus: MADAGASCAR. **Prov. Toliara:** Anosy, Taolagnaro, Ampasy Nahampoana, forêt littorale d'Ambavarano-Mandena, 24°57'S 47°00'E, 5 m, 13.V.2006, fl., *Rabenantoandro & Ramisy 1765* (MO–6450859!; iso-: G [G00418622] image seen, P [P00806077]!, TAN).

Homalium planiflorum subsp. *roseiflorum* Appleq. differs from *H. planiflorum* (Tul.) Baill. subsp. *planiflorum* in having inflorescences mostly clustered at twig ends and occasionally paniculate (vs scattered along twigs and almost always racemose), and pink to reddish flowers (vs whitish to greenish or yellowish flowers).

Leaves narrowly elliptical to oblanceolate (aberrantly obovate), 3.5–7.7(–8.7) × 1–2.3(–2.9) cm. Inflorescences racemes, often clustered near twig ends, or occasionally panicles with a few long branches. Flowers pink to reddish, commonly 8-merous, less often 7-merous (9-merous).

Vernacular names. – “Hazofotsy” (*Faliniana et al. 2, Randriatafika et al. 319, Réserves Naturelles s.n., Soanary 26*); “Zora” (*Rabenantoandro et al. 336, Ratovoson 1731*); “Zora fotsy” (*Ratovoson 1629, 1692*).

Uses. – Wood of *H. planiflorum* subsp. *roseiflorum* is reported to be hard and to be used for construction and to make tool handles (*Randriatafika et al. 319, Ratovoson 1629, 1692, 1731, Réserves Naturelles s.n.*).

Distribution, ecology and conservation status. – *Homalium planiflorum* subsp. *roseiflorum* is confined to coastal forests in southeastern Madagascar. All collections are from a very small portion of Toliara province; most are from the protected areas of Mandena and Sainte Luce, with single collections from four other localities in close proximity (all within ca. 13 km of one of the significant populations). GeoCAT calculates an



Fig. 5. - *Homalium planiflorum* subsp. *roseiflorum* Appleq. **A.** Flowering branch; **B.** Flower clusters; **C.** Leaf (lower surface). [Rabenantoandro & Ramisy 1765, TAN] [Drawing: R.L. Andriamiarisoa]

EOO as c. 320 km² and an AOO of 40 km². Since there may be six distinct populations, the species cannot be formally assessed as “Vulnerable” [VU D2]. However, all localities are so close together that they could easily be affected by a single event such as a typhoon, and habitat outside the rather limited boundaries of the protected areas is at high threat of anthropogenic damage. A status of “Near Threatened” [NT] is therefore recommended to call attention to this concern.

Notes. – *Homalium planiflorum* subsp. *roseiflorum* is distinguished from the typical subspecies by its flower color (pink to red) and, to some extent, by inflorescence morphology (often clustered near twig apices, occasionally paniculate). Its leaves are on average somewhat narrower and more likely to tend to oblanceolate than those of subsp. *planiflorum*, and the average number of sepals and petals per flower is slightly greater (more often eight than seven, and rarely nine, whereas seven- and eight-petaled flowers are about equally common in subsp. *planiflorum*). However, these latter characters overlap too much to be taxonomically useful.

Paratypes. – **MADAGASCAR. Prov. Toliara:** Mandena, étude parcelles campement, 24°57'S 47°00'E, 0–10 m, 17.IV.1989, ster., *Dumetz et al.* 666 (P); Sainte Luce, 24°47'S 47°10'E, 0–10 m, 20.X.1989, fl., *Dumetz et al.* 754 (MO, P); Mandena, 24°57'S 47°00'E, 6.XII.1989, fl. & fr., *Dumetz & McPherson* 1127 (MO, P); Mandena, 0–10 m, 24.I.1990, fr., *Dumetz* 1236 (MO, P); Sainte Luce, 24°46'46"S 47°10'17"E, 10 m, 15.XII.2000, fl., *Faliniaina et al.* 2 (MO); Sainte Luce, proposed QIT mining conservation area, 24°46'42"E 47°10'15"E, 0 m, 13.X.2000, fl., *Hoffmann et al.* 209 (MO [2 sheets]); Near Mandena beyond QIT camp, 24°57'S 47°00'E, 25 m, 31.X.1989, buds, *McPherson & Dumetz* 14339 (P); *ibid. loco*, 20 m, 4.XI.1989, fl., *McPherson* 14369 (MO, P); M7, Taolagnaro, M 7 [Mandena], 24°57'31"S 47°00'02"E, 0–10 m, 6.X.2000, fl., *Rabenantoandro et al.* 336 (G, MO, P); Sainte Luce, près du campement QMM, 24°46'47"S 47°10'17"E, 3 m, 29.X.2003, buds, *Rabenantoandro et al.* 1522 (MO, P); Mandena, 24°57'S 47°02'E, 10 m, 13.I.1990, fr., *Rabevohitra* 2123 (MO, P); Taolagnaro, à 1 km au N d'Evatra, 24°57'S 47°06'E, 17.I.1990, fl. & fr., *Rabevohitra* 2153 (MO, P); Sainte Luce, forêt d'Analavinaky à l'W d'Ambandrika, 24°46'30"S 47°09'00"E, 21 m, 24.XI.2009, post-fl., *Rakotovoao* 4737 (MO); Fkt. Fenoambony, E du village Androangabe, 24°53'S 46°59'E, 58 m, 5.XII.2009, post-fl., *Rakotovoao et al.* 5042 (MO); Sainte Luce, S5 [forest parcel], 24°47'S 47°11'E, 2.II.2008, post-fl., *Ramison & Rabevohitra* 561 (MO); Sainte Luce, 4–5 km N of Manafyfy along main trail into forest, 24°47'S 47°09'E, 0–10 m, 19.XI.1996, fl., *A. Randrianasolo* 567 (G, MO, P); Fkt. Ampasy-Nahampona, Station forestière de Mandena (M3), 3.X.2001, fl., *Randriatafika et al.* 319 (MO); Sainte Luce, S10, 3 km au N d'Ambandrika, 24°44'39"S 47°10'45"E, 50 m, 19.XI.2011, fl., *Ratovoson* 1629 (MO); Sainte Luce, S11, 3.1 km au N d'Ambandrika, 24°44'26"S 47°10'38"E, 20 m, 21.XI.2011, fl., *Ratovoson* 1692 (MO); Mahatalaky, Belavenoko, S5, 1 km E de Belavenoko Forêt, 24°49'51"S 47°06'49"E, 20 m, 23.XI.2011, fl., *Ratovoson* 1731 (MO); Mandena (route Nancy), 6.XII.1949, fl., *Réserves Naturelles (Ranjatson)* s.n. (P); Sainte Luce, QMM Forestry Station, parcel S9, 24°46'05"S 47°10'16"E, 11 m, 23.I.2006, fl., *Rogers et al.* 970 (G, MO); forêt de Vinanibe, près de Fort Dauphin, 10.XII.1961, fl., *Service Forestier* 20513 (P [2 sheets]); Fkt. Ampasinahampoana, forêt de Mandena, block M15, 24°57'09"S 47°00'10"E, 6.XII.2001, fl., *Soanary et al.* 26 (MO).

Intermediate or unidentifiable specimens. – **MADAGASCAR. Prov. Toliara:** vicin. Fort-Dauphin, 15.XI.1967, fl., *Bernardi* 11517 (P); Fort-Dauphin, s.d., fl., *Cloisel* 120 (P); Fort-Dauphin, Ambinanibe, 28.II.1973, fl., *Debray* 1985 (P); Petriky forest, N of NE corner of Lake Andranany, NW of large dune at end of road, 25°03'S 46°53'E, 0–10 m, 12.IV.1989, ster., *Gereau et al.* 3365 (P); Fort Dauphin, VI.1889, fl., *Scott Elliot* 2835 (P).

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Appendix

Index to collectors. Collections are listed alphabetically by first collector's last name, with determinations indicated by numbers corresponding to those of species in the taxonomic treatment; types are indicated in boldface.

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