



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

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

Anna C. Wassel & Wendy L. Applequist

Abstract

WASSEL, A.C. & W.L. APPLEQUIST (2020). A revision of *Homalium* sect. *Nisa* (Salicaceae) endemic to Madagascar. *Candollea* 75: 1–23. In English, English & French abstracts. DOI: <http://dx.doi.org/10.15553/c2020v751a1>

Homalium sect. *Nisa* (Noronha ex Thouars) Baill. is endemic to Madagascar and has included four recognized species. A new revisionary treatment of the section is presented and an identification key is provided. Eleven species are recognized, including eight that were formerly part of the *Homalium nudiflorum* (DC.) Baill. species complex. Four species and one subspecies are newly described: *Homalium antilahimenae* Wassel & Appleq., *Homalium mandenense* Wassel & Appleq., *Homalium pachycladum* Wassel & Appleq., *Homalium tenue* Wassel & Appleq., and *Homalium stelliferum* subsp. *andapense* Wassel & Appleq. *Homalium ciliolatum* (Sleumer) Wassel & Appleq. is newly recognized at species level and the new combination *Homalium retusum* (Blume) Wassel & Appleq. is further published. Four lectotypes are designated including a second step. Taxonomic novelties are provided with line drawings or scans of their holotypes. Risk of extinction assessments indicate that three taxa are “Endangered” and three “Vulnerable”. Occasional hybridization is observed. Some specimens are not classifiable and it is possible that other unrecognized species exist.

Résumé

WASSEL, A.C. & W.L. APPLEQUIST (2020). Révision de *Homalium* sect. *Nisa* (Salicaceae) endémique de Madagascar. *Candollea* 75: 1–23. En anglais, résumés anglais et français. DOI: <http://dx.doi.org/10.15553/c2020v751a1>

Homalium sect. *Nisa* (Noronha ex Thouars) Baill. est endémique de Madagascar et comprenait quatre espèces reconnues. Une nouvelle révision de la section est présentée et une clé de détermination est proposée. Onze espèces sont reconnues, dont huit faisant partie anciennement du complexe d'espèces d'*Homalium nudiflorum* (DC.) Baill. Quatre espèces et une sous-espèce sont nouvellement décrites: *Homalium antilahimenae* Wassel & Appleq., *Homalium mandenense* Wassel & Appleq., *Homalium pachycladum* Wassel & Appleq., *Homalium tenue* Wassel & Appleq., et *Homalium stelliferum* subsp. *andapense* Wassel & Appleq. *Homalium ciliolatum* (Sleumer) Wassel & Appleq. est nouvellement reconnue au rang d'espèce et la nouvelle combinaison *Homalium retusum* (Blume) Wassel & Appleq. est publiée. Quatre lectotypes sont désignés incluant une deuxième étape. Les nouveautés taxonomiques sont accompagnées de dessins au trait ou de scans de leur holotypes. Une évaluation du risque d'extinction indique que trois taxons sont «Vulnérable» et trois sont «En danger». L'hybridation est observée occasionnellement. Quelques échantillons ne peuvent pas être classés et il est possible que d'autres espèces non reconnues existent.

Keywords

SALICACEAE – *Homalium* – *Nisa* – Madagascar – Taxonomy

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Introduction

Homalium Jacq. (Salicaceae) is a pantropical woody genus, historically included within the polyphyletic family *Flacourtiaceae* (CHASE et al., 2002). The genus is distinguished by two perianth whorls, a large gland on the adaxial base of each sepal, a semi-inferior ovary and oppositipetalous stamens arranged either singularly or in fascicles. It is currently arranged into ten sections (APPLEQUIST, 2016a). Two subgenera were formerly recognized, but the sole distinguishing feature of a solitary stamen per petal (subg. *Blackwellia* (Benth.) Warb.) vs. fasciculate stamens (subg. *Homalium*) appears to be homoplasious. Before recent re-evaluation of the Malagasy species, about 150 species had been recognized within the genus (APPLEQUIST, 2013). Madagascar and Malesia are the two primary centers of diversity. The most sectional diversity is ascribed to Madagascar, with six sections, five of which are considered endemic following the recent restriction of sect. *Eumyriantheia* to only Malagasy species (APPLEQUIST, 2016a, 2016b).

The Malagasy endemic *Homalium* sect. *Nisa* (Noronha ex Thouars) Baill. is distinguished by solitary stamens, sepals usually accrescent and much larger than the petals both at anthesis and especially during fruit maturation (Fig. 1), large persistent bracts and bracteoles, and stipules usually fused opposite the petiole (APPLEQUIST, 2016a). The last taxonomic revision of *Homalium* sect. *Nisa* (SLEUMER, 1973) reported it to include four species. However, in the intervening decades far more herbarium material has been collected from Madagascar, so that recent revisionary studies have described multiple new species in every section so far treated (APPLEQUIST, 2016b, 2018a, 2018b). Additionally, three of the recognized species – *Homalium louvelianum* H. Perrier, *H. stelliferum* H. Perrier, and *H. intercedens* Sleumer – have distinctive morphological features and are consistent and well-distinguished. However, *H. nudiflorum* (DC.) Baill., as treated by SLEUMER (1973), incorporated substantial morphological diversity, including multiple taxonomic synonyms: distinctive specimens with very densely pubescent flowers were described as *H. nudiflorum* var. *ciliolatum* Sleumer, while *Nisa retusa* Blume, *H. scleroxylon* (Tul.) Baill., and *H. confertum* Baker were included in var. *nudiflorum*. There was reason to suspect that this circumscription was overly broad and that some of these should be removed from *H. nudiflorum*, and that additional unnamed taxa existed within the *H. nudiflorum* complex. Therefore, a new modern revision based on available herbarium collections was necessary.

Materials and Methods

Materials examined included herbarium specimens at MO, duplicates of MO collections not yet distributed, and specimens from P received on loan or seen during a visit. In

addition, images of specimens at P were available through SONNERAT (2020), and images of types held by other institutions available through the JSTOR Global Plants website [<http://plants.jstor.org>] were observed. Standard taxonomic procedures were followed consistent with the recent revision of other sections of *Homalium* in Madagascar (APPLEQUIST, 2016a, 2018a, 2018b).

Special comment is necessary regarding certain morphological features in this section. Bark characteristics and floral color are not available for all taxa, but are reported whenever label data have provided them. In a few species, twigs have a particularly gracile or sturdy appearance that could be a useful taxonomic character. The difference among species is more prominent in twig segments below the terminal branches (which in almost all species are slender early in their growth period) but if this is to be described quantitatively, since all twigs ultimately arise from large branches, some consistent means of deciding which twigs to measure was necessary. The choice was made to measure highest and lowest leafing internodes, i.e., those that bore leaves at nodes both above and below the internode at the time of collection, except that if a single leaf were borne at the apex of a twig the internode below it was measured, and if a single leaf was borne on an older proximal twig segment the internode above it was measured.

In most species the sepal length greatly increases during the process of floral and fruit maturation, while petal size increases to a lesser extent. There are differences among species in initial and final perianth size that provide support for recognition of taxa. However, perianth size can be used to aid in specimen identification only with caution, because the ovary and calyx enlarge only slightly as fruit develops in *Homalium*, so the stage of development may not always be obvious.

There are few fruit characters of taxonomic utility within sections of *Homalium* because the capsules are so small. Specimens with apparently mature seeds are rare, in part because the entire flower is the unit of dispersal and is consistently lost as seeds mature, but possibly also because rates of fertilization and successful seed maturation may be low. In this paper, specimens are described as fruiting if many flowers appear to be post-anthesis due to visible ovary/calyx expansion, strong inward curving of petals over the ovary, and/or the loss of most anthers. There may be differences among species in whether the basal portion of the ovary and calyx cup or the upper free portion of the ovary expands most in fruit, but this is not emphasized here because, given the tendency of flowers with the most mature ovaries to be lost, floral characters are far more useful.

To save space, locality data are not provided for all specimens seen of the most common taxa, and those that are provided are edited for brevity, especially where more complete label data are available from TROPICOS (2020). “Fkt.” is used throughout as an abbreviation for “fokontany”. Madagascar



Fig. 1. – Flower of *Homalium confertum* Baker post-anthesis. [Buerki 106] [Photo: S. Buerki]

has traditionally been divided into six provinces, but these have recently been dissolved and the country divided into 22 regions. Because provincial names will still be more familiar to many readers, localities are organized by region, with the province of which each region was formerly a part given in brackets. A complete index of specimens seen is provided as an appendix. Maps of georeferenced specimens that have been databased in Tropicos may be viewed within the Missouri Botanical Garden's Catalogue of the Plants of Madagascar project (MADAGASCAR CATALOGUE, 2020), which is continually updated with new determinations and specimens.

A preliminary risk of extinction assessment 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) could affect the assessed status, GeoCAT (BACHMAN & MOAT, 2012) was used to estimate those values. Geographic coordinates were taken from label data or approximated from the Missouri Botanical Garden's gazetteers or coordinates estimated in prior georeferencing efforts (TROPICOS, 2020). If coordinates for a specified locality could not be obtained, coordinates for the closest locatable population center mentioned on the label were used.

Taxonomic treatment

Homalium sect. *Nisa* (Noronha ex Thouars) Baill. ex Warb. in Engl. & Prantl, Nat. Pflanzenfam. 98–99: 36. 1893.

= *Nisa* Noronha ex Thouars, Gen. Nov. Madagasc.: 24. 1806. = *Homalium* [unranked as §] *Nisa* (Noronha ex Thouars) Baill. in Bull. Mens. Soc. Linn. Paris 1: 575. 1886.

Typus (designated by SLEUMER, 1973: 295): *Homalium nudiflorum* (DC.) Baill. (= *Nisa nudiflora* DC.).

Stipules opposite the petiole base and fused (in *H. intercedens* Sleumer axillary, free), usually caducous. *Leaves* with venation more or less brochidodromous. *Inflorescences* spicate; bract and bracteoles large, usually broad, thick-textured, persistent. *Flowers* sessile (rarely subsessile); perianth 5–6(–8)-merous. *Sepals* obovate to oblanceolate (to nearly ligulate), oblanceolate-oblong or narrowly elliptic (in *H. louvelianum* H. Perrier oblong-ovate to ovate-deltoid), spreading, accrescent (only slightly so in *H. louvelianum*); calyx tube short, broadly funnelform to cup-shaped, or in fruit hemispherical. *Petals* ovate to oblong, usually smaller than sepals, modestly accrescent and curving over fruit (in *H. louvelianum* similar to sepals in size and spreading); sepals and petals not ciliate, or ciliolate in conjunction with overall surface pubescence. *Sepal glands* large, elliptic to elongated oblong-elliptic or roughly trapezoidal. *Stamens* 1 per petal, inserted between glands; anthers dorsifixed, broadly oblong-elliptic with oblong-elliptic locules and a large connective, the slits of dehiscence nearly parallel. Upper surface of *ovary* often nearly flat in flower, in fruit becoming hemispherical or broadly conical; styles 3–4, fused basally (rarely fused for most of length). *Locule of fruit* subglobose or vertically compressed, internally glabrous (short-pubescent); seeds sometimes 1 per fruit, subglobose, largely filling the locule (or several small immature seeds, possibly most never maturing).

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

1. Sepals about equal to petals at anthesis, broadly oblong-ovate (to ovate-deltoid), in fruit slightly accrescent, < 3.5 mm and only modestly longer than petals; petals not curving inward over fruit 5. *H. louvelianum*
- 1a. Sepals longer than petals at anthesis, oblanceolate to narrowly oblong-oblanceolate, spatulate, narrowly elliptic, or nearly ligulate (in flower obovate to elliptic), in fruit conspicuously accrescent, > 3.5 mm and much longer than petals; petals usually curving inward as fruit matures 2
2. Sepal glands densely pubescent on upper (inward-facing) surface 10. *H. stelliferum*
- 2a. Sepal glands glabrous or glabrate throughout 3

3. Leaves lanceolate; stipules free 4. *H. intercedens*
- 3a. Leaves elliptic, oblong-elliptic, obovate or oblanceolate (rarely to ovate, very rarely a few lanceolate); stipules fused, opposite petioles 4
4. Calyx densely pubescent to sericeous at least on cup, basal portion of abaxial sepal surface 5
- 4a. Calyx glabrous or sparsely pubescent, often more densely short-pubescent on cup, with trichomes confined to medial or marginal areas of one or both sepal surfaces 7
5. Leaves elliptic to narrowly elliptic, obovate, or oblanceolate, (2.5–)3–6(–9) × 1.3–2.5(–3) cm, without marginal glands; bracts and bracteoles often ciliate, pubescent only along midrib or glabrous; adaxial surface of sepals glabrous; petals 1.5–2.5 mm, densely pubescent abaxially (to sparsely at margins), densely to sparsely pubescent adaxially; filaments 0.9–1.1 mm, anthers 0.2–0.3 mm 11. *H. tenue*
- 5a. Leaves elliptic to broadly or narrowly elliptic or obovate, (3.3–)5–9.5 × (1.8–)2–4.5(–5.4) cm, usually with inconspicuous marginal glands; bracts and bracteoles ciliate and usually pubescent throughout (mostly along midrib); adaxial surface of sepals short-pubescent at least basally; petals 2–5 mm, velutinous on both surfaces; filaments (1.2–)1.9–2.8 mm, anthers 0.4–0.65 mm 6
6. Flowers mostly borne in pairs or closely clustered; bracts and bracteoles 3.5–5 mm; calyx cup long-sericeous, both sepal surfaces densely pubescent; southern Madagascar 2. *H. ciliolatum*
- 6a. Flowers usually borne singly; bracts and bracteoles 1.5–2.5(–3) mm; calyx cup densely pubescent, sepals densely pubescent towards base of both surfaces, becoming sparsely pubescent (to glabrous) near apical margins; northeastern Madagascar 1. *H. antilabimenae*
7. Petioles (10–)15–30 mm; inflorescences paniculate, pubescent; flowers mostly paired 9. *H. retusum*
- 7a. Petioles 3–15 mm; inflorescences racemose or paniculate, glabrous or seldom sparsely or patchily pubescent; flowers borne singly 8
8. Leaves oblanceolate, (2.7–)3.4–6.8 × (0.9–)1.1–2 cm, with revolute margins; inflorescences racemose, (0.5–)1–2.5(–3.3) cm; filaments 0.5–0.8 mm, anthers ca. 0.2 mm 6. *H. mandenense*
- 8a. Leaves elliptic to broadly or narrowly elliptic, oblong-elliptic, or obovate (to oblanceolate in *H. nudiflorum*), 4.9–16 × 1.5–9 cm, with entire (sometimes partly, not strongly revolute), crenate, or serrate to dentate margins; inflorescences racemose or paniculate, (2–)3–12 cm; filaments 1.6–3.1(–3.7) mm, anthers (0.3–)0.5–0.7(–0.8) mm 9
9. Leaves (5–)6–16 × (1.8–)3–6.2(–7) cm with petiole 3–7(–10) mm; leaf margins usually prominently toothed

- (subentire) with elongated glands in tooth apices; both surfaces of petals densely (to moderately) pubescent especially on apical half; humid forests to drier central forests, at elevations of 445–1860 m 3. *H. confertum*
- 9a. Leaves 4.9–14.5 × 1.5–7 cm with petiole (3–)4–13(–15) mm; leaf margins entire to repand (crenulate, partly somewhat revolute), with glands small and round or absent; petals usually moderately (to densely) pubescent only at apex of one or both surfaces (rarely on entire apical portion), otherwise sparsely pubescent with often ciliate margins, or glabrous; humid (to littoral) forests, at elevations of 12–1220 m 10
10. Leafing internodes (1.7–)2–4(–5.5) mm diam.; leaves 8.5–14.5 × 5–7 cm; inflorescences paniculate; petals in fruit 3–5.6 mm 8. *H. pachycladum*
- 10a. Leafing internodes (0.9–)1.1–2.4(–3.2) mm diam.; leaves 4.9–9(–10.5) × 1.5–4.2(–5.4) cm; inflorescences racemose (paniculate); petals 1.5–4 mm 7. *H. nudiflorum*

Taxonomy

1. *Homalium antilabimenae* Wassel & Appleg., **sp. nov.** (Fig. 2).

Holotypus: MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Fiv. Maroantsetra, comm. Ambinan-itelo, fkt. Marovovonana, 15°19'41"S 49°31'29"E, 199 m, 29.VIII.2004, fl., *Antilabimena* 2621 (MO [MO-6755052]); iso-: G!, K!, P!, TAN, USMS).

Homalium antilabimenae Wassel & Appleg. differs from *H. ciliolatum* (Sleumer) Wassel & Appleg. in having shorter inflorescences with most flowers borne singly, smaller bracts and bracteoles, and less densely pubescent calyces with indument shorter on cup and sparser towards apical margins of sepals.

Tree 10 to 15 m tall, 60 cm dbh; twigs dark to reddish brown when young, becoming gray to medium brown, glabrous, leafing internodes (0.9–)1.3–2.4(–4) mm diam.; stipules fused, caducous. *Leaves* elliptic to broadly or narrowly elliptic or obovate, (3.3–)5–8(–10.7) × (1.8–)2–4.5(–5.4) cm; base cuneate to convex, often short-attenuate at extreme base; apex rounded to cuspidate (acute to slightly acuminate, retuse); margin entire, glands small or absent; secondary veins 7–11 per side; both surfaces glabrous, drying medium-brown on adaxial surface, darker on abaxial surface; petiole glabrous, 4–14 mm. *Inflorescences* paniculate to racemose, axillary, 2.5–8(–11.8) cm; rachis pubescent, often densely on apical portion; bracts and bracteoles 1–2.5(–3) mm, densely to sparsely short-pubescent throughout or mostly along midrib, often ciliate; flowers usually borne singly, rarely opposite or subopposite. *Flowers* 6–7(–8)-merous, pale yellow, yellow-green, or whitish; sepals

oblanceolate to narrowly oblong-oblanceolate, narrowly elliptic, or in flower obovate to elliptic, 3–6 mm in flower, 5–8 mm in fruit, both surfaces densely to moderately pubescent at base, always densely so on outer surface of calyx cup, short-pubescent on basal portion or along midrib, more sparsely pubescent (to glabrous) towards apical margins; sepal glands glabrous; petals ovate (to broadly ovate when young), 2–3.5 mm in flower, to 5 mm in fruit, both surfaces velutinous; filaments glabrous, (1.2–)1.9–2.4 mm; anthers 0.4–0.6 mm; styles 1–2 mm.

Etymology. – *Homalium antilabimenae* is named for botanist Patrice Antilahimena, one of the most experienced living field botanists in Madagascar, who has made over 9500 collections, including the type, and additionally made valuable contributions to ecological and floristic studies (e.g., ANDREWS et al., 1998; PHILLIPSON et al., 2010).

Vernacular names and use. – “Jaborahoditra” (*Rakotonirina et al. 180*); “Mafaikoditra” (*Antilahimena et al. 1213*); “Maroam-pototsa” (*Antilahimena 2621*); “Tanampotsy” (*Service Forestier 15944*).

Wood is used to construct houses (*Rakotonirina et al. 180*).

Distribution, ecology and conservation status. – *Homalium antilabimenae* is native to the northeastern regions of SAVA and Analanjirofo, where it usually occurs in low- to mid-elevation humid forests (with one specimen labeled at a range of 740–1200 m). It appears to be uncommon. As few as six distinct locations may be known; the Extent of Occurrence (EOO) is calculated as c. 11,190 km² (which includes a significant area of open water) and the Area of Occupancy (AOO) as 32 km². Its habitat includes the protected area of Masoala, but other portions of the known habitat are more subject to ongoing anthropogenic degradation. A preliminary assessment of its conservation status is therefore “Vulnerable” [VU B1ab(iii)+2ab(iii)].

Notes. – *Homalium antilabimenae* is part of a group of three species, including *H. ciliolatum* (Sleumer) Wassel & Appleq. and *H. tenue* Wassel & Appleq., that are separated from *H. nudiflorum* s.str. by more pubescent flowers and inflorescences. *Homalium ciliolatum* has often longer inflorescences, 3.5–11.5(–20) cm, larger bracts and bracteoles, 3.5–5(–7) mm long, and sepal indument that covers the entirety of both surfaces, with a markedly longer sericeous indument on the calyx cup. *Homalium tenue* is distinguished by smaller sepals, 3.5–5(–6) mm in fruit with a glabrous adaxial surface, less pubescent petals, usually smaller leaves, and slender-graceful twigs and rachises.

Paratypes. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Maroantsetra, Anjahana, Amodivangy, 15°25'47"S 49°50'07"E, 200 m, 19.VII.2002, fl., *Antilahimena et al. 1213* (G, MO); Maroantsetra, Ambanizana, NP Masoala, 15°37'48"S 49°59'03"E, 473 m, IX.2002, fl., *Antilahimena 2911* (MO); Anefitrakely private forest, 15°50'04"S 49°40'05"E, 128 m, 28.VII.2007,

fl., *Antilahimena 5763* (G, K, MO); Ambodimangavolo, Mahaso, Ambato-haranana, 17°33'57"S 48°53'45"E, 740–1200 m, 25.X.2000, fl., *Ratovoson et al. 327* (G, MO); Farankaraina, Maroantsetra, 24.VII.1956, fl., *Service Forestier 15944* (P); env. de la Baie d'Antongil, forêt de Fahampanambo, dans la basse vallée de l'Antanambalana, 25–26.IX.1957, fl., *Service Forestier 18278* (P [2 sheets]). Reg. SAVA [Prov. Antsiranana]: Sambava, Marogaona, Ambo-divapaza, 14°08'20"S 49°55'27"E, 378 m, 27.VIII.2013, *Rakotonirina et al. 180* (MO).

2. *Homalium ciliolatum* (Sleumer) Wassel & Appleq., **comb. & stat. nov.**

≡ *Homalium nudiflorum* var. *ciliolatum* Sleumer in Bull. Jard. Bot. Belg. 43: 299. 1973.

Lectotypus (designated here): MADAGASCAR. Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]: Ifanadiana, forêt d'Ambohimiera [Tsaratanana], 20.VIII.1954, fl., fr., *Service Forestier 14566* (P [P00375093]); isolecto-: L [L0010977] image seen, P [P04734282]!.

Tree to 25 m tall, 1 m dbh; bark gray-green; twigs gray to light brown, sometimes minutely pubescent on new growth, otherwise glabrous, leafing internodes (0.8–)1.2–2.4(–3.2) mm diam.; stipules fused, caducous. **Leaves** elliptic to broadly elliptic or obovate, (3.6–)4.5–9.5(–11.6) × (1.6–)2.3–4.9 cm; base convex to broadly cuneate; apex rounded to cuspidate or obtuse (retuse, short-acuminate); margin entire, glands inconspicuous; secondary veins (5–)7–10 per side, sometimes with intersecondary veins almost equally large; both surfaces glabrous, drying pale to medium or olive-brown; petiole glabrous, 4–10 mm. **Inflorescences** mostly pseudoterminal, confined to twig apices, racemose to paniculate, 3.5–11.5(–20) cm; rachis pubescent, especially towards apex; bracts and bracteoles 3.5–5(–7) mm long, short-pubescent and ciliate; flowers mostly borne in pairs or gathered in widely-spaced clusters. **Flowers** 6–7(–8)-merous, white; sepals elliptic when young to narrowly elliptic or oblong-elliptic, becoming oblanceolate, 4.8–9 mm in flower, (7–)8.5–10 mm in early fruit, entire adaxial and abaxial surfaces of sepals short-pubescent, base of calyx cup sericeous; sepal glands glabrous; petals lanceolate to narrowly ovate or narrowly oblong-ovate, 3–4 mm in flower, 4–5.5 mm in early fruit, both surfaces velutinous; filaments glabrous (rarely sparsely pilose), (1.5–)2.2–2.8 mm; anthers 0.5–0.6 mm; styles (2–)2.4–3 mm.

Vernacular names and use. – “Fotsiakara” (*Service Forestier 21504*); “Fotsiankara” (*Service Forestier 13984, 21504* [Antsaka-général dialect]); “Fotsivony” (*Service Forestier 6390*); “Hazo-fotsy à grandes feuilles” (*Service Forestier 3796*); “Hazombato” (*Service Forestier 14719*); “Kamirisa” (*Antilahimena et al. 4863*); “Ramanerika” (*Service Forestier 14566*).

Wood is used for construction and firewood (*Service Forestier 21504*).

Distribution, ecology and conservation status. – *Homalium ciliolatum* is confined to the southeastern regions of Atsimo-Atsinanana, Vatovavy-Fitovinany, and Anosy. It is usually found near the coast at low elevations, but the type was probably from a mid-elevation forest. Reported substrates include basalt and rocky soil; habitats include forest and savoka (disturbed grassland). As many as ten subpopulations have been collected in the past (older locality data are imprecise). However, it has only been collected twice in the past 54 years, though much of its habitat is relatively accessible, so it is evidently rare. From all historical localities, the Extent of Occurrence is calculated as c. 15,980 km² and the Area of Occupancy as 40 km². Most historical populations were from land that has been subject to serious anthropogenic damage in the intervening decades and is still not protected. Therefore a preliminary assessment of its conservation status is “Vulnerable” [VU B1ab(iii) + 2ab(iii)], but this is likely to underestimate the degree of threat it faces.

Notes. – *Homalium ciliolatum* was described by SLEUMER (1973) as a variety of *H. nudiflorum*, from which it is most obviously separated by its densely pubescent flowers. The petals are velutinous on both surfaces; the basal part of the calyx externally is densely sericeous, and the remainder of the sepals are short-pubescent and ciliate. Also, the upper portions of the inflorescence rachis and the bracts and bracteoles are pubescent, and the bracts and bracteoles short-ciliate. The petals appear often to remain curved over the ovary before fruit develops. It is likely that no fully mature perianths have been seen and the final size is larger than the range reported here. The distribution of *H. ciliolatum* is more southerly than that of *H. nudiflorum* and it is confined to lower altitudes. Two other species herein excluded from the *H. nudiflorum* complex, the newly described *H. antilabimena* Wassel & Appleg. and *H. tenue* Wassel & Appleg., also have calyces much more pubescent than those of *H. nudiflorum*. *Homalium ciliolatum* is distinguished from these by the distinctive long-sericeous indument of the calyx cup, which is not seen in any other species, and by having most flowers borne in pairs.

Service Forestier 14566 at P was stated (SLEUMER, 1973: 299) to be the “holotype” of *H. nudiflorum* var. *ciliolatum*. There are in fact two duplicates of this collection at P, which are therefore syntypes. The duplicate designated herein as lectotype is in better condition and has better original label data.

Additional materials examined. – **MADAGASCAR. Reg. Anosy [Prov. Toliara]:** Iabakoho, Antsontso, Ivohibe forest, 24°34'10"S 47°12'37"E, 41 m, 24.V.2006, fr., *Antilabimena* et al. 4863 (MO, P); forêt d'Androkabe, Fort-Dauphin, 15.VIII.1951, fr., *Service Forestier 3796* (P). **Reg. Atsimo-Atsinanana [Prov. Fianarantsoa]:** Vangaindrano, Vohipaho, 23°31'40"S 47°29'46"E, 73 m, 17.IX.2009, fl., *Andriamihajarivo* et al. 1701 (MO); Farafangana, Ihorombe, Mahatsinjoriaka, 23.X.1952, fr., *Service Forestier 6390* (P); Farafangana, Amporofo, 26.VII.1955, fr., *Service Forestier 13984* (P); Farafangana, Beka-raoka, 8.X.1963, fl., *Service Forestier 21504* (MO, P); S de Farafangana, rte de

Manombo, aux P.K. 20–21, 14–17.X.1964, fr., *Service Forestier 23613* (P). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Mananjary, Ambohiniaonana, 2.VI.1954, fl., *Service Forestier 14476* (P); Mananjary, Vohilaba, Ambodono-noka, 20.VI.1954, fl., *Service Forestier 14719* (P).

3. *Homalium confertum* Baker in J. Linn. Soc., Bot. 21: 341. 1884 (Fig. 1).

Lectotypus (designated by SLEUMER, 1973: 298): **MADAGASCAR:** “Central Madagascar”, s.d., fr., *Baron 3185* (K [K000231489] image seen; isolecto-: BM, L [L0010973] image seen, P [P00418088]!). **Syntypus:** **MADAGASCAR:** “Central Madagascar”, s.d., fr., *Baron 3256* (K [K000231490] image seen).

Tree to 22 m tall, 60 cm dbh; bark exfoliating in plaques; twigs gray to medium brown, glabrous, leafing internodes (1.2–)1.7–4(–5) mm diam.; stipules fused, sometimes persistent. *Leaves* elliptic to oblong-elliptic, narrowly or broadly elliptic, or obovate, (5–)6–16 × (1.8–)3–6.2(–7) cm; base convex to cuneate; apex cuspidate, obtuse, acute, or rounded (short-acuminate); margin serrate to dentate or slightly crenate, rarely nearly entire, glands in tooth apices elongated and relatively conspicuous; secondary veins 8–14(–16) per side, sometimes with similar intersecondary veins; both surfaces glabrous (aberrantly bearing patches of short trichomes, possibly pathogenic), or abaxial surface moderately glaucous, drying medium to dark brown on both surfaces (rarely light green); petiole 3–7(–10) mm, glabrous. *Inflorescences* racemose, axillary (often paired), (2–)4–8.5(–11) cm; rachis glabrous (sparsely short-pubescent or more densely so in irregular patches); bracts and bracteoles (1.5–)2–4 mm, glabrous except margins of bracts usually ciliate; flowers borne singly. *Flowers* 5–6-merous, white to green or yellow-green; sepals 3–7 mm in flower, 8–12.5 mm in fruit, oblanceolate to spatulate or narrowly oblanceolate-oblong, adaxial surface usually glabrous (midrib sometimes sparsely short-pubescent), abaxial surface usually glabrous (sparsely short-pubescent at base); sepal glands yellow, glabrous; petals ovate, 2–4 mm, both surfaces densely (to moderately) pubescent especially on apical half; filaments glabrous (sparsely pubescent on the basal portion), 1.7–3.1 mm; anthers (0.45–)0.5–0.6 mm; styles 1.5–2.5 mm.

Vernacular names and use. – “Hazombato” (*Razafindramora 1*, *Service Forestier 1776*, 25277); “Hazombatofotsy” (*Razanatsima et al. 1136*, *Service Forestier 7362*, 16801, 25277); “Lalondalitra” (*Service Forestier 15406*); “Longotra-fotsy” (*Service Forestier 1249*); “Marankoditra” (*Réserves Naturelles 6043*, *Service Forestier 25277*); “Tsianhiposa” (*Service Forestier 10148*).

Wood is used to make unspecified products (*Service Forestier 25277*).



Fig. 2. – Holotype of *Homalium antilahimeneae* Wassel & Appleg.
[*Antilahimena* 2621, MO] [© Missouri Botanical Garden, Saint Louis]

Distribution, ecology and conservation status. – *Homalium confertum* is widespread in eastern and central regions of Madagascar. It usually occurs in humid forests at mid- to high elevations (range 445–1860 m), but also extends into relatively dry western forests (Ankarafantsika). Reported substrates include gneiss. It is sometimes common and locally dominant (*Randrianaivo et al.* 526). It has been collected in several protected areas, including Ambohitantely, Anjanaharibe-Sud, Ankarafantsika, Montagne d'Ambre, and Zahamena. Its conservation status is estimated as “Least Concern” [LC].

Notes. – *Homalium confertum* was lumped into *H. nudiflorum* by SLEUMER (1973). It differs from *H. nudiflorum* s.s. in its larger, often strongly toothed leaves with many marginal glands and its more densely pubescent petals; the final perianth size may also be larger. The two overlap in range, but *H. confertum* is more tolerant of dry climate and high altitude, with much of its habitat on the central plateau. It is similar to *H. pachycladum* and *H. retusum*, which also overlap in range, in maximum leaf size, but *H. pachycladum* and *retusum* are distinguished by entire leaf margins, fewer leaf glands, and petals glabrous on the abaxial surface.

Several possible hybrids between *H. confertum* and *H. nudiflorum* are seen in two regions where both are known, and gene flow is suspected to be responsible for some of the range of variation in *H. nudiflorum*; these are discussed under the latter species. Hybridization is seen in most sections of *Homalium*, even rarely among species of different sections (APPLEQUIST, 2018b), so the ability of these species to hybridize does not suggest that they should not be recognized as distinct, given their significant morphological and ecological differences.

Additional material examined. – MADAGASCAR. **Reg. Alaotra-Mangoro [Prov. Toamasina]:** PN Zahamena, 17°38'25"S 48°38'34"E, 989 m, 30.III.2000, buds, *Ratovoson et al.* 184 (MO, P); Manaka, Ambatondrazaka, 20.II.[?].1953, fl., *Reserves Naturelles 6043* (MO); P.K. 39 route d'Anosibe, canton and sous-préfecture Anosibe, 4.V.1965, fr., *Service Forestier 25277* (P). **Reg. Amoron'i Mania [Prov. Fianarantsoa]:** commune d'Ambalamanakana, 20°44'01"S 47°11'42"E, 1860 m, 27.III.1996, fl., *Rakotomalaza et al.* 681A (MO, P). **Reg. Analamanga [Prov. Antananarivo]:** Tampoketsa-Ankazobe, RS Ambohitantely, 18°11'52.5"S 47°17'3"E, 1620 m, 7.III.2004, fl., *Almeda et al.* 8636 (MO); Anjozorobe, commune d'Ambongamarina, Andreba, 18°16'55"S 47°54'24"E, 1400 m, 11.III.2000, fl., *Randrianaivo et al.* 526 (MO); Ambohitantely RS, 18°11'46"S 47°17'24"E, 1620 m, 12.III.1997, *Ravololonanabary et al.* 69 (MO). **Reg. Analanjirofo [Prov. Toamasina]:** Beanana, 700 m, 22.II.1954, fl., *Service Forestier 9058* (MO, P [2 sheets]). **Reg. Anosy [Prov. Toliara]:** Antsotso Avatrata, forêt Tsitongambarika, 24°34'S 47°12'E, 2.IV.2008, fr., *Razakamalala et al.* 4148 (MO, P). **Reg. Atsinanana [Prov. Toamasina]:** Ambodilendemy, Ankerana, 18°25'49"S 48°47'14"E, 890 m, 24.III.2011, fl., *Antilabimena* 7778 (MO); Ambodilendemy, vers le sommet d'Ankerana, 18°25'49"S 48°47'14"E, 900m, 14.III.2011, fl., *Ravelonarivo & Felix* 3663 (MO); Vatomandry, Ambalabe, 19°09'27"S 48°34'57"E, 596 m, 11.III.2013, fl., *Razanatsima et al.* 1136 (BR, G, K, MO, USMS). **Reg. Boeny [Prov. Mahajanga]:** Réserve Naturelle Intégrale d'Ankarafantsika, 16°18'00"S 46°49'00"E, 22.IV.1994, fl., *Rajemisa* 24 (MO). **Reg. Bongolava [Prov. Antananarivo]:** Tsiroanomandidy, Ambara-

varanala, 18°25'S 45°40'E, 1190–1200 m, 25.VI.1997, fl., *Rakotomalaza et al.* 1353 (G, MO). **Reg. DIANA [Prov. Antsiranana]:** Montagne d'Ambre (partie N.O.), 1000–1800 m, 23.XII.1967, fr., *Bernardi* 12003 (MO, P); contreforts occidentaux du Massif de Marojejy (NE) près du col de Doanyanala (limite des bassins de la Lokoho et de l'Andraronga), 800–1200 m, 25.I–25.II.1949, fl., *Humbert* 23040 (P [3 sheets]); montagnes au N de Mangindrano (haute Maevarano) jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Andraronga), 1500 m, 19.I–12.II.1951, fr., *Humbert & Capuron* 24888 (P); flanc S du M. Tsaratanana, 1700 m, XII.1912, fl., *Perrier de la Bâthie* 6705 (P). **Reg. Haute Matsiatra [Prov. Fianarantsoa]:** Ampamaherana, Fianarantsoa, 13.XII.1949, fl., *Service Forestier 1249* (P). **Reg. SAVA [Prov. Antsiranana]:** Daraina, forêt d'Antsahabe, 13°13'03"S 49°32'46"E, 780 m, 2.XII.2004, fr., *Gautier* 4806 (MO, P); Ampasindava, forêt de Bongomihirahavavy, 13°46'11"S 48°04'58"E, 445 m, 4.XII.2013, fr., *Gautier et al.* 6092 (G, P); massif de l'Anjanaharibe (pentes et sommet N) à l'W d'Andapa (haute Andramonta, bassin de la Lokoho: NE), 1600–1800 m, 10.XII.1950–3.I.1951, fl., *Humbert et al.* 24704 (P); Doany, Anjialavahely, 14°17'41"S 49°32'50"E, 949 m, 15.III.2006, fl., *Rakotoavao et al.* 2986 (MO, P); Anjialavabe, Ankiakabe, 14°10'47"S 49°22'01"E, 1567 m, 23.II.2007, fl., *Ravelonarivo et al.* 2238 (MO, P); Antalaha, Bealampona, village de Befingotra, 14°45'11"S 049°28'49"E, 762 m, 21.IV.1997, fl., *Razafindramora* 1 (MO). **Reg. Sofia [Prov. Mahajanga]:** Marsoandakana, 14°55'39"S 49°25'52"E, 1176 m, 23.II.2008, fl., *Bernard et al.* 876 (MO); NW du campement Bemafo, 14°13'17"S 49°03'55"E, 1830 m, 26.X.2005, fl., *Buerki et al.* 106 (MO, P). **Reg. Vakinankaratra [Prov. Antananarivo]:** Angodona, Tsinjoarivo, 6.VI.1950, fl., *Service Forestier 1766* (P [2 sheets]). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Ampasinambo, Nosy-Varika, 21.IV.1954, fl., fr., *Service Forestier 10148* (MO, P).

4. *Homalium intercedens* Sleumer in Bull. Jard. Bot. Belg. 43: 300. 1973.

Holotypus: MADAGASCAR. **Reg. DIANA [Prov. Antsiranana]:** plateau calcaire de l'Ankarana, à l'E d'Ambondromifehy, 8.III.1951, fr., *Service Forestier 3047* (P [P00375092]!; iso-: P [P04677610, P04677611]!).

Tree to 25 m tall, 30 cm dbh; bark gray-white, exfoliating, platanoid; twigs dark brown, glabrous, leafing internodes ca. 0.7–1.3 mm diam.; stipules free, caducous. *Leaves* lanceolate, 3.4–6.7 × 1.2–2.4 cm; base convex; apex acuminate; margin serrulate with round to elongated glands in tooth apices; secondary veins 10–12(–14) per side; both surfaces glabrous, drying dark brown with paler veins on adaxial surface, lighter to greenish on abaxial surface; petiole glabrous, 7–16 mm. *Inflorescences* racemose, axillary, 2.1–2.8 cm; rachis glabrous; bracts and bracteoles glabrous, ca. 1.5–2.5 mm; flowers borne singly. *Flowers* (5–)6-merous, yellowish-green; sepals narrowly oblanceolate to nearly ligulate, 6–8 mm in fruit, adaxial surface with appressed pubescence on calyx cup and sparsely pubescent on sepal bases, adaxial surface glabrous; sepal glands glabrous; petals deltoid-ovate, 2.5–3 mm in fruit, abaxial surface short-pubescent, adaxial surface glabrous; filaments glabrous, ca. 2 mm; anthers not seen; styles ca. 1.5–1.8 mm.

Distribution, ecology and conservation status. – *Homalium intercedens* is known only from Ankarana in the DIANA region in the extreme north of Madagascar. It is reported on

limestone and at a relatively low altitude. It is known from only one subpopulation (or perhaps two subpopulations close together) and rarely collected. Ankarana has been visited by many collectors over the years. TROPICOS (2020) has databased over 2100 historical and recent specimens from the area so the small number of collections is likely to indicate that the taxon is either narrowly endemic or uncommon within its range. However, the population is in a protected area that is known for inaccessible terrain, so it is at little risk of loss due to human activity. Therefore, its conservation status is tentatively assessed as “Least Concern” [LC].

Notes. – *Homalium intercedens* is easily distinguished from other species of sect. *Nisa* by its free stipules (caducous, but leaving two stipule scars rather than a single fused scar) and small lanceolate leaves with serrulate margins.

Additional material examined. – MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: Ambilobe, Mahamasina, RS d'Ankarana, chemin du canyon forestier, 12°55'22"S 049°06'27"E, 130 m, 16.I.2003, fr., Bardot-Vaucoulon et al. 1207 (P).

5. *Homalium louvelianum* H. Perrier in Mém. Mus. Natl. Hist. Nat. 13: 292. 1940.

Lectotypus (designated by SLEUMER, 1973: 296): MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Tampina, s.d., fl. & fr., Louvel 87 (P [P04704068]!). **Syntypi:** MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Ambila au S de Tamatave, 4.V.1928, fl., Decary 6381 (P [P04704069]!, PRE [PRE0602227-0] image seen, S [S10-10168] image seen, US [US00603578] image seen); forêts côtières [Tampina?], s.d., fl., Louvel 109 (P [P04704067]!). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Mananjary, zone côtière, III–IV.1909, fl., Geay 7425 (P [P04704065]!); *ibid. loco*, fl., Geay 7426 (P [P04704066]!); *ibid. loco*, fl., Geay 8069 (P [P04704064]!).

Tree to 16 m tall, 40 cm dbh; bark orange or yellowish, exfoliating in plaques; twigs reddish brown when young, becoming grayish brown, glaucous to glabrous (minutely papillate), leafing internodes 1–2.5(–4.2) mm diam.; stipules fused, caducous. *Leaves* narrowly elliptical to oblanceolate or elliptical (obovate), (3.5–)5.5–12(–14) × (1.5–)2–3.9(–4.5) cm; base cuneate to narrowly convex (slightly attenuate); apex acute to rounded, sometimes partly rounded-cuspidate, short-acuminate, or retuse; margin subentire, usually somewhat revolute at least at base, with glands in inconspicuous concavities or projections; secondary veins (6–)8–12(–14) per side, sometimes with very similar intersecondary veins; both surfaces glabrous, drying brown to dark (or greenish) brown on adaxial surface, usually somewhat paler brown on abaxial surface; petiole glabrous, (2–)3–11(–15) mm. *Inflorescences*

racemose, axillary, 0.7–3.7(–5.6) cm; rachis glabrous; bracts and bracteoles glabrous except for sometimes ciliate margins, 0.5–1.5 mm; flowers borne singly (but usually clustered close together) or paired. *Flowers* 5–6-merous (aberrantly 4-merous), pale yellow to pale green or green sometimes with pinkish margins, or abaxial surface of calyx reddish; sepals broadly oblong-ovate (to ovate-deltoid), (1–)1.2–1.8 mm in flower, (1–)1.5–2.6(–3.5) mm in fruit, adaxial and abaxial surfaces glabrous (calyx cup seldom sparsely pubescent); sepal glands yellow, glabrous; petals oblong-elliptic (broadly oblong-ovate), not curving inwards in fruit, 1.3–1.8 mm in flower, (1–)1.5–2(–2.5) mm in fruit, abaxial surface densely short-pubescent (to glabrous at margins toward base), adaxial surface densely to moderately short-pubescent towards apex, ciliate on most of margin; filaments glabrous, (0.8–)0.9–1.2(–1.3) mm; anthers 0.3–0.4(–0.45) mm; styles (0.4–)0.5–0.5(–1) mm.

Vernacular names and use. – “Fotsiakara” (Ludovic & Ratiana 666, Ludovic 703, 735, Service Forestier 15375); “Fotsiakarjay fotsy” (Ludovic 391), “Gavoala” (Service Forestier 1562, 4702, 5690, 9531, 16869, 19188, 19502 [Betsimaraka dialect]); “Goaviala” (Service Forestier 4916); “Goviala” (Louvel 87, 109); “Hafeala” (Service Forestier 2936); “Hazombato” (Birkinshaw et al. 355, Rabevohitra et al. 4985, Randrianaivo et al. 1875); “Hazombatovavy” (Service Forestier 14837); “Langipasina” (Service Forestier 9514); “Ramirisa” (Service Forestier 2851, 3361); “Ramirisy” (Service Forestier 6975 [Tanosy dialect]); “Rotra” (Cours 2952); “Zahandambo” (Service Forestier 2110).

Wood is used for construction (Ludovic & Ratiana 666, Ludovic 703, Service Forestier 19188, 19502).

Distribution, ecology and conservation status. – *Homalium louvelianum* is widely distributed along most of the eastern coast of Madagascar. It is found in littoral forests, or less often low-altitude humid forests near the coast, on sand and ferrallitic soil. Although littoral forests are highly fragmented and threatened, *H. louvelianum* is still frequently collected over a wide range. Its conservation status is assessed as “Least Concern” [LC].

Notes. – *Homalium louvelianum* displays less perianth accrescence than any other species of *Homalium* sect. *Nisa*. It has the smallest flowers within the section, and is unique in having sepals similar in size to the petals and broadest towards the base. The flowers often appear crowded on short racemes, though occasionally the rachis is relatively elongated and flowers more widely spaced. In these characters and the unusually short styles and filaments, the species bears a strong resemblance to those species of *Homalium* sect. *Odontolobus* Warb. s.l. (APPLEQUIST, 2018a) that display less extreme floral reduction. While no molecular data adequate to resolve relationships within Malagasy *Homalium* are available, this species

suggests an intermediate or transitional form between those two sections which may provide a clue as to their relationships.

Razakamalala et al. 3796 is identified as a hybrid between *H. louvelianum* and *H. tenue*. The leaves are consistent with *H. louvelianum*, narrowly elliptical with acute to acuminate apices. The sepals are only slightly longer than the petals, but resemble those of most species of *Homalium* sect. *Nisa* in shape and texture and are slightly reflexed, while the petals are densely pubescent and slightly inward-curving. *Homalium tenue* is found at this locality and its leaf shape and dense petal indument make it the presumptive second parent.

Three specimens are from farther north than any population of typical *Homalium louvelianum* and occur at unusually high altitudes. *Birkinshaw et al.* 2015 has large, unusually shaped leaves and pubescent inflorescences and sepals. Two others from the forest of Ampondrabe have small leaves; their floral morphology is largely consistent with *H. louvelianum*. If typical *H. louvelianum* occurred in these regions, these specimens would be presumed to be hybrids, but since they are far from the known range of *H. louvelianum*, it is possible that they represent distinct species for which material is insufficient to allow recognition. Further investigation of these populations would be desirable.

Additional material examined. – MADAGASCAR. **Reg. Analanjirofo [Prov. Toamasina]:** 1 km S Mandrisy along road, 16°29'02"S 49°50'45"E, 10 m, 9.VII.1996, fr., *Birkinshaw et al.* 355 (MO, P); Ile Sainte-Marie, forêt d'Ambohidena, 16°51'11"S 49°57'10"E, 10 m, 13.V.2003, fr., *McPherson et al.* 18894 (MO, P); Soanierana-Ivongo, Antanambao-Ambodimanga, 16°46'19"S 49°43'52"E, 18.V.2003, fr., *Rabenantoandro et al.* 1481 (MO, P); fkt. Ambohidena, forêt d'Ambohidena, 16°51'11"S 49°57'18"E, 18.II.2004, fl., *Rabevohitra et al.* 4985 (MO, P); fkt. Manompana, forêt de Pointalare [Pointe à Larée], 16°47'18"S 49°41'08"E, 24 m, 14.VI.2011, fr., *Randrianaivo et al.* 1875 (P); Tampolo, 17°17'S 49°25'E, 0–5 m, 5–15.V.1997, fl., *Ravololonanabary et al.* 82 (MO, P); fkt. Ambohidena, forêt d'Ambohidena, 16°50'25"S 49°57'09"E, 10 m, 19.II.2004, fl., *Razakamalala et al.* 899 (MO, P); Mahambo, au S de Fénérive, 30.VIII.1957, fr., *Service Forestier* 18143 (P [2 sheets]); S de la Mandrisy, S d'Antanambe, Mananara, 13.XI.1964, fr., *Service Forestier* 23771 (P [2 sheets]). **Reg. Anosy [Prov. Toliara]:** Mandena, 24°57'S 47°00'E, 0–10 m, 19.IV.1989, fl., *Gereau et al.* 3388 (MO, P); Ste. Luce, 24°47'S 47°10'E, 20 m, 15.I.1990, fl., *McPherson et al.* 14796 (MO, P); Ft-Dauphin, fkt. Tsiharoa, forêt d'Etazo (S5), 24°49'36"S 47°06'44"E, 20 m, 8.VIII.2012, *Rakotonirina et al.* 870 (MO); Mandena, 24°57'S 47°00'E, 0 m, 22.VI.1996, fr., *Razafimandimbison* 211 (G, K, MO, P); Mandena, Ft-Dauphin, 7.III.1951, fl., *Service Forestier* 2851 (P); Mandena, 11 km au N de Ft. Dauphin, IV–V.1953, fl., *Service Forestier* 6975 (P). **Reg. Atsimo-Atsinanana [Prov. Fianarantsoa]:** fkt. Baboaka, 1.5 km SW d'Analomena, 23°09'37"S 47°44'41"E, 15 m, 6.VI.2003, fr., *Ludovic* 391 (MO); Vohimasy, Agnalazaha Ampokafo, 23°10'58"S, 47°42'27"E, 12 m, 13.VIII.2006, fr., *Razafitsalama* 961 (MO); Mahabo Mananivo, forêt de Manombo, 23°10'12"S 47°42'50"E, 21 m, fl., *Razakamalala & Rabehevitra* 701 (MO [2 sheets], P); Manombo RS, parcelle I, forêt d'Anaviavy, 22°59'16"S 47°42'26"E, 65 m, 14.IX.2005, fl., *Razakamalala et al.* 2127 (P); Analazaka, Efotsy, 30.VIII.1955, fl., *Service Forestier* 15375 (P); Vohimasy, Agnalazaha Ampokafo, 23°10'58"S 47°42'27"E, 12 m, 13.VIII.2006, fr., *Razafitsalama* 961 (MO). **Reg. Atsinanana [Prov. Toamasina]:** Ambila-Lemaitso, 18°49'28"S 49°09'19"E, 10 m, 25.IX.2000, fl., *Andrianjafy et al.* 108 (MO, P); Vohibola, N of Lac Ampitabe, 18°33'34"S 49°15'01"E, 5 m, 12.II.2003, fr., *Lowry et al.* 6074 (MO, P); fkt. Andranonkoditra, forêt de Vohibola, 18°35'32"S

49°14'02"E, 5 m, 11.II.2003, fr., *Rabenantoandro et al.* 1259 (MO, P); Akanin'ny Nofy, forêt de Vohibola, 18°33'46"S 49°15'06"E, 3.VIII.2003, fr., *Razakamalala & Rabehevitra* 649 (MO, P); Ambila-Lemaitso, 25.X.1950, fr., *Service Forestier* 1562 (P); Ambila-Lemaitso, 14.IV.1952, fr., *Service Forestier* 4702 (MO, P); *ibid. loco*, 25.IX.1952, fr., *Service Forestier* 5690 (P); *ibid. loco*, 16.III.1954, fr., *Service Forestier* 9531 (P); Tampina, JB20, 12.IX.1958, fr., *Service Forestier* 19188 (P); Ambila-Lemaitso, Jardin Botanique no. 2, 22.V.1959, fl., *Service Forestier* 19502 (P). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** fkt. Marohita, forêt d'Ambahisosotra, 21°29'12"S 48°16'20"E, 13 m, fr., *Ranaivojaona et al.* 541 (MO, P); fkt. Ambalavontaka, forêt d'Antaimby, 20°23'26"S 48°32'43"E, 10 m, 20.IV.2004, fr., *Ranaivojaona et al.* 651 (MO, P); Pangalane, sud[?] Mananjary, 24.2.1954, fl., *Service Forestier* 9514 (P); forêt de Manampano, Mananjary, 17.VI.1955, fr., *Service Forestier* 14837 (P). **Sine loco:** 3–5 m, 10.X.1946, fr., *Cours* 2952 (MO, P).

Hybrid specimen. – MADAGASCAR. **Reg. Anosy [Prov. Toliara]:** Iaboko, Antsotsa Avaratra, 24°34'16"S 47°12'06"E, 271 m, 8.XII.2007, fr., *Razakamalala et al.* 3796 (P).

Specimens incertae sedis. – MADAGASCAR. **Reg. SAVA [Prov. Antsiranana]:** Tsihomanaomby access from Antanambaoisokitra, 14°05'52"S 50°00'26"E, 331 m, 23.IV.2014, fl., *Birkinshaw et al.* 2015 (MO); Daraina, forêt d'Ampondrabe, 12°57'14"S, 49°42'13"E, 517 m, 9.IV.2004, fl., *Ranirison* 612 (P); Tsaratanana, Ambarilao, forêt d'Ampondrabe (Antsanjoana), 12°57'29"S 49°41'32"E, 600 m, 9.XI.2005, fr., *Ratovoson et al.* 1094 (MO, P).

6. *Homalium mandenense* Wassel & Appleg., **sp. nov.** (Fig. 3).

Holotypus: MADAGASCAR. **Reg. Anosy [Prov. Toliara]:** préfecture de Taolagnaro, forêt de Mandena, piste au N de l'intersection des piste-Camp, 24°57'S 47°00'E, 0–10 m, 8.III.1989, fr., *Dumetz* 537 (MO [MO-3662611]!; iso-: P [P04734305]!, TAN).

Homalium mandenense Wassel & Appleg. differs from *Homalium nudiflorum* (DC.) Baill. in having smaller, consistently oblanceolate leaves with revolute margins, shorter racemes, and flowers smaller at maturity.

Tree or shrub to 7 m tall, 6 cm dbh; twigs medium brown to grayish, usually glaucous when young, peeling (glabrous), leafing internodes 1.0–2.5(–3.2) mm diam.; stipules fused, caducous. *Leaves* oblanceolate, (2.7–)3.4–6.8 × (0.9–)1.1–2 cm; base cuneate; apex rounded to acute or cuspidate; margin more or less revolute, glands inconspicuous or absent; secondary veins 6–7(–8) per side; both surfaces glabrous, drying brown (seldom to green) on adaxial surface, brown or greenish on abaxial surface; petiole glabrous, (3–)6–12(–14) mm. *Inflorescences* racemose, axillary, (0.5–)1–2.5(–3.3) cm; rachis glabrous; bracts and bracteoles glabrous except for ciliate margins, 0.9–1.6 mm; flowers borne singly. *Flowers* 6–7(–8)-merous, white to yellowish; sepals elliptical (to obovate) in early flower, becoming oblanceolate to narrowly oblong-oblanceolate, 2.8–4 mm in flower, 3.5–4.7 mm in fruit, adaxial and abaxial surfaces glabrous or with sparse pubescence only at base of calyx cup; sepal glands yellow, glabrous;

petals elliptic, to oblong at maturity, 1.4–2.4 mm, moderately (densely) pubescent on apical portion of both surfaces, sometimes extending to most of adaxial surface, and margins ciliate; filaments glabrous, 0.5–0.8 mm; anthers 0.2 mm; styles ca. 0.5(–1?) mm.

Vernacular names and use. – “Zôra” (Ludovic 1649); “Zoramena” (Ratovoson 1719).

Wood is used for construction (Ludovic 1649, Ratovoson 1719).

Distribution, ecology and conservation status. – *Homalium mandenense* is or has been endemic to four littoral forests in a very small portion of the southeastern region of Anosy, near Toliara. The potential habitat has been declining in area and quality, but Mandena is now a protected area. The Extent of Occurrence is calculated as 72 km² and the Area of Occupancy as 20 km². While some subpopulations are in protected areas, others are not, and their habitat is threatened by mining and wood harvest for firewood and charcoal. Therefore, the preliminary assessment of this species' conservation status is “Endangered” [ENB1ab(iii)+2ab(iii)].

Notes. – *Homalium mandenense* is distinguishable from *H. nudiflorum* by its small leaves, racemes, and flowers. The calyx appears to increase in size less than in most species of the section, so that at maturity the flowers are markedly smaller than those of *H. nudiflorum*. Though the twigs are often strongly glaucous, the leaves are not; they are coriaceous in texture, with unusual strongly revolute margins. This species may also be confused with *H. tenue*, another small-leaved species newly described from southeastern Madagascar. *Homalium tenue* has frequently elliptical to obovate leaves with entire margins; its inflorescences are larger, and the outer surface of the calyx is densely pubescent. Both species have unusually short filaments and styles and small anthers, which in *H. mandenense* are also broader than usual. This suggests the possibility that they share a close relationship with *H. louvelianum*.

Paratypes. – MADAGASCAR. Reg. Anosy [Prov. Toliara]: fkt. Ebakika, forêt d'Ampagnorona, 24°43'46"S 47°09'26"E, 34 m, 6.IX.2012, fr., Ludovic 1649 (MO); Sainte Luce, près du segment forestier S8, 24°46'19"S 47°08'55"E, 17 m, 20.X.2012, fl., Ramananjana et al. 826 (MO); Sainte Luce S7, 2.5 km au S d'Ambandrika forêt, 24°48'22"S 47°08'17"E, 15 m, 22.XI.2011, fl., Ratovoson 1719 (MO); sables dunaires anciens à Mandromondromotra, au N de Fort-Dauphin, 9.XII.1968, fl., Service Forestier 28645 (MO, P [2 sheets]).

7. *Homalium nudiflorum* (DC.) Baill. (Fig. 4).

= *Nisa nudiflora* DC., Prodr. 2: 55. 1825.

Lectotypus (designated here): MADAGASCAR: *sine loco*, s.d., fr., Petit-Thouars s.n. (P [P00418087]!; isolecto-: P [P00418086]! pro parte).

Tree to 20 m tall, 50 cm dbh; bark gray, yellowish inside, sometimes platanoid; twigs light to medium gray or brown, glabrous, leafing internodes (0.9–)1.1–2.4(–3.2) mm diam.; stipules fused, caducous. *Leaves* obovate to elliptic, broadly or narrowly elliptic, or oblanceolate, 4–9(–10.5) × 1.5–4.2(–5.4) cm; base convex to cuneate, rounded, or attenuate; apex rounded to slightly acuminate or apiculate, rarely acute with a rounded tip or retuse; margin entire (seldom shallowly repand, rarely slightly crenate-denticulate or partly and not strongly revolute), glands if present small, round, usually inconspicuous, rarely prominent in young leaves; secondary veins (5–)6–9(–11) per side; adaxial surface glabrous (glaucous), abaxial surface glabrous or seldom weakly glaucous, both surfaces drying light to medium brown or green to olive, sometimes the adaxial surface brown, young leaves sometimes dark brown; petiole glabrous, (3–)4–13(–16) mm. *Inflorescences* racemose or occasionally paniculate (especially in Alaotra-Mangoro region), axillary (rarely paired), (3–)4–9(–11) cm; rachis glabrous to moderately (partially densely) minutely pubescent; bracts and bracteoles 1.5–3.5(–4) mm, glabrous or occasionally ciliate; flowers borne singly. *Flowers* 5–6(7)-merous, pale yellow, pale green to yellowish green, or white; sepals oblanceolate to narrowly oblong-oblanceolate or spatulate (in early flower obovate), 3–6 mm in flower, 5.6–9.5(–10) mm in fruit, adaxial surface glabrous, abaxial surface glabrous or glabrate (rarely with margin ciliate or calyx cup pubescent); sepal glands orange to bright yellow, glabrous; petals ovate (broadly ovate at anthesis) to elliptic, 1.5–4 mm, both surfaces glabrous or short-pubescent near apex (seldom moderately or rarely densely pubescent over much of surface), sometimes also on midrib abaxially, margins sometimes ciliate; filaments glabrous, 1.6–3(–3.7) mm; anthers (0.3–)0.5–0.7(–0.8) mm; styles (0.8–)1.5–3.4(–4) mm.

Distribution, ecology and conservation status. – *Homalium nudiflorum* as circumscribed herein is a very widespread, though scattered species in eastern forests. It usually occurs in mid-elevation humid forests up to 1220 m, but is occasionally found near sea level. Reported substrates are lateritic soils, including ferruginous crust and cuirasse, volcanic soil, and gneiss or granite. It occurs in several protected areas, including Galoko, Manombo, Mantadia, Midongy du Sud, Montagne d'Ambre, and Zahamena. Its conservation status is estimated as “Least Concern” [LC]. However, it should be noted that regional variants of the species may be genetically distinct and at greater risk.

Vernacular names and uses. – “Antevaratra” (Randriamanarivo et al. 10); “Fotsiakara” (Service Forestier 10150); “Hazofotsy à [petits] feuilles” (Service Forestier 3794); “Hazomalany” (Andriamahafarivo et al. 90); “Hazombato” (Service Forestier 11013, 13239); “Hazondroka” (Service Forestier

16192 [Antaisaka dialect]); “Hazoporofoka” (*Service Forestier* 2231); “Lamotiala” (*Service Forestier* 10435); “Lapivahatra” (*Razanatsima et al.* 1364); “Menavahatra” (*Antilahimena et al.* 3005); “Remirisa” (*Antilahimena et al.* 4826).

Wood is used for construction of houses (*Randriamanarivo et al.* 10, *Service Forestier* 16192) and for heating and charcoal production (*Service Forestier* 16192).

Notes. – *Homalium nudiflorum* as defined by SLEUMER (1973) was much too broadly circumscribed, including in a single species with one variety all of sect. *Nisa* that was not obviously excluded by having greatly different perianth morphology (*H. louvelianum*), stipule morphology (*H. intermedium*), or sepal gland and foliar indument (*H. stelliferum*). In this treatment, eight species are recognized within what was formerly the *H. nudiflorum* complex. *Homalium nudiflorum* as herein defined is much less heterogeneous, but remains a widespread and morphologically variable taxon. Variation in morphology is probably geographically correlated, but since most parts of the range are represented by few individuals, it is impossible to determine how consistently so.

Most conspicuously, most collections from the far north (DIANA and SAVA) have broadly elliptical leaves (providing the upper extreme of the size range) with usually rounded bases, a glaucous upper surface, and often shallowly repand rather than entire margins. Additionally, these collections have moderate (to dense) indument on the apical half of the petals, while material from other parts of the country usually has trichomes only at the extreme petal apices. These populations might merit recognition as a species. However, most of their distinctive characters may be found individually in specimens from other regions (e.g., there are southern collections with large, broad-based, broadly elliptical leaves or with heavy petal indument) and there are both typical northern collections and potential intermediates. Because hybridization between *H. nudiflorum* and *H. confertum* is suspected to occur primarily in the north (see below), it is also possible that some characters of these specimens are attributable to gene flow or incomplete separation from *H. confertum*.

SLEUMER (1973: 299) stated that *Petit Thouars s.n.* “P & P-Juss 14 411” was the “holotype” of *Homalium nudiflorum*, and that no duplicate was found at G-DC, where material possessed by De Candolle might have been expected to be located. Two sheets of *Petit Thouars s.n.* were located at P, both of which were labeled “holotype” by Sleumer; these should be considered syntypes. Both are of poor quality, but the sheet barcoded [P00418086] includes a fragment packet containing flowers of *H. nudiflorum* along with mounted material that appears to be *H. louvelianum*. Therefore, [P00418087] is chosen as lectotype. The type collection has narrowly elliptic to obovate or narrowly obovate leaves (some fairly large, though

not broad for their size), a glabrous rachis, bracts (except for cilia) and calyx, and sparsely pubescent petals. Without locality data, it is not possible to identify this as pertaining to any specific geographic variant of *H. nudiflorum*, which favors the maintenance of a relatively broad species concept for pragmatic reasons, while excluding several segregate taxa that are clearly not conspecific with the type.

Several specimens (see below) are observed that have the fairly small leaves and most other features of *Homalium nudiflorum* s.str. combined with features of *H. confertum*, in particular dense indument on most, or sometimes all, of both petal surfaces. A few have variable leaf morphology with some leaves being crenulate or dentate-crenulate, with some elongated glands. A few other specimens with atypical morphology are herein treated as *H. nudiflorum*. All of the putative intermediates come from regions where both *H. nudiflorum* and *H. confertum* are found. Hybridization is observed in other sections of *Homalium* (APPLEQUIST 2016a, 2018b). Hybridization or gene flow between these species, which are probably closely related, is suggested to be responsible for the features of these specimens. One or two specimens, e.g., *Service Forestier* 23750 with very small anthers and short filaments and styles, might be suspected of other hybrid ancestry, but their morphology is otherwise consistent with *H. nudiflorum*.

Service Forestier 18334 has leaves similar to those of one form of *H. nudiflorum* (except that the adaxial surface is glaucous) but relatively gigantic flowers, with sepals reaching 20 mm in fruit. No other material of this section has flowers of similar size. As three characters to distinguish it from *H. nudiflorum*, as herein circumscribed, are not seen, it is tentatively placed in that species. However, further collections of this population would be highly desirable.

Baron 6251 is a specimen in poor condition with a few small flowers and a few elliptical to ovate leaves, one of them very large. Though leaf shape is quite variable in this species complex, ovate leaves are normally not seen. This may represent a hybrid with a larger-leaved species, possibly of another section, or a distinct species. *Baron* 6270 bears a fragment with short inflorescences and very small (2.2–3.3 × 1.5–2.2 cm), closely spaced, broadly elliptical leaves with entire margins, which are not glaucous. As the inflorescence is well past anthesis, the small size of the leaves and internodes is not due to immaturity. The specimen might be an aberrant individual of *H. nudiflorum* or an otherwise unknown related taxon. No locality data are available for Baron’s collections, so it is not possible to attempt to relocate the collected populations, and the available material is not adequate to recognize new species.

Additional material examined. – MADAGASCAR. Reg. Alaotra-Mangoro [Prov. Toamasina]: Menalamba, Ambatovy forest, 18°48'29"S 48°18'50"E, 1060 m, 16.XII.2004, fl., *Antilahimena et al.* 3005 (MO, P); Ampanantovana, Ambatovy forest, 18°51'35"S 48°19'12"E, 1116 m, 6.XII.2008, fl., *Antilahimena et al.* 6959 (G, K, MO); Ambatondrazaka, *Cours* 1095 (P);



Fig. 3. – *Homalium mandenense* Wassel & Appleg. **A.** Flowering branch; **B.** Inflorescence; **C.** Flower; **D.** Fruit. [Dumetz 537, TAN] [Drawings: R.L. Andriamiarisoa]



Fig. 4. – Inflorescences of *Homalium nudiflorum* (DC.) Baill. [Nusbaumer 1261] [Photo: L. Nusbaumer]

near Andasibe, forest of Mantadia, 18°55'S 48°25'E, 950–1150 m, 7.XI.1994, fl., *McPherson & van der Werff* 16535 (MO); Ampitambe, forêt d'Analamay, 18°48'39"S 48°20'35"W, 1077 m, 3.X.2008, fr., *Rakotonirina* 609 (MO); forêt de Berano, Ampitambe, Ambatovy, 18°51'21"S 48°20'04"E, 1048 m, 12.I.2005, fr., *Ranaivojaona et al.* 1043 (MO, P). **Reg. Analanjirifo** [Prov. Toamasina]: Maroantsetra, Anjahana, Ambanizana, 15°37'30"S 49°58'35"E, 190 m, 20.IX.2002, fl., *Antilabimena & Daiky* 1423 (MO, P); Marovovonana, Andampy forest, 15°19'03"S 49°24'06"E, 800 m, 3.IX.2004, fl., *Antilabimena* 2719 (G, MO); Parc National de Zahamena, 17°33'49"S 48°54'01"E, 794 m, fl., *Randriamanarivo et al.* 10 (MO); Antanambe, au S de Mananara, 10–14. XI.1964, fl., *Service Forestier* 23750 (P [2 sheets]). **Reg. Anosy** [Prov. Toliara]: fkt. Antsontso, Ivohibe forest, 24°34'13"S 47°12'01"E, 286 m, 23.V.2006, fr., *Antilabimena et al.* 4826 (P); forêt d'Analalava, 24°13'S 47°21'E, 40 m, 29.X.1989, fr., *McPherson* 14289 (MO, P); Antsotso, Vohimena, forêt d'Ivohibe, 24°33'45"S 47°12'19"E, 421 m, 28.I.2015, fr., *Razanatsima et al.* 1364 (G, MO); forêt de Vohibe-Manantenina, 14.VIII.1951, fl., *Service Forestier* 3794 (P). **Reg. Atsimo-Atsinanana** [Prov. Fianarantsoa]: Farafangana, forêt classée de Manombo, 23°04'00"S 47°40'33"E, 42 m, 27.IX.2002, fl., *Rabevohitra et al.* 4128 (MO, P); Farafangana, Ankarana, village le plus proche Manombo, 23°00'39"S 47°44'08"E, 12 m, 16.IX.2005, fl., *Rakotonirina et al.* 300 (MO, P); Midongy du Sud, Anaviavy, Kelilahy, 16.IV.1956, fr., *Service Forestier* 16192 (P). **Reg. DIANA** [Prov. Antsiranana]: Ampasindava, forêt d'Andranomatavy, 13°40'04"S 47°58'53"E, 410 m, 1.XII.2009, fr., *Madiomanana et al.* 282 (P); forêt sèche dégradée d'Andavakoera, à 3 km à l'Est de Marivorahona, 13°05'56"S 49°08'33"E, 54 m, 2.IX.2005, fl., fr., *Randrianaivo et al.* 1221 (MO, P); Marivorahona, W du mont Andavakoera, 13°05'14"S 49°10'29"E, 100 m, 4.II.2005, fl.,

Ratovoson et al. 881 (MO); 9 km SE d'Anketrabe, forêt de Kalabenono, chaîne de Galoko, 13°38'30"S 48°40'53"E, 976 m, 23.XI.2006, fr., *Razafitsalama & Torze* 1105 (MO, P); Ambilobe, Andampy, 14.V.1954, fl., *Service Forestier* 10435 (P); Ambilobe, comm. rurale Beramanja, Chaîne Galoka [Galoko], Mont Galoka [Galoko], fkt. Anketrabe-Belinta, révélé 2, 13°35'12"S 48°43'37"E, 22.II.2005, fr., *Wohlhauser et al.* 767 (MO). **Reg. Haute Matsiatra** [Prov. Fianarantsoa]: forêt d'Andrambovato à l'E de Fianarantsoa, 24.I.1955, fr., *Service Forestier* 11593 (P). **Reg. Ihorombe** [Prov. Fianarantsoa]: Farafangana, Ankarenambe, 24.II.1950, fr., *Service Forestier* 2231 (P). **Reg. SAVA** [Prov. Antsiranana]: fkt. d'Ankijabe, forêt de Binara, camp I (13°15'S, 049°37'E), 1.6 km au SW du camp, 900 m, 9.XI.2001, fl., *Gautier & Ravelonarivo* 4142 (MO, P); Montagne d'Ambre near Grand Cascade, 12°31'S, 049°10'E, 900 m, 22.I.1994, fr., *Leeuwenberg et al.* 14292 (P); Montagne d'Ambre, 12°32'S 49°09'E, 1000–1100 m, 20.XI.1989, fr., *McPherson* 14484 (MO, P); Daraina, forêt d'Antsahabe, 13°13'S 49°33'E, 896 m, 21.XI.2004, fl., *Nusbaumer & Ranirison* 1261 (MO, P). **Reg. Sofia** [Prov. Mahajanga]: Mandritsara, commune de Makira, 15°31'S 49°05'E, 1169 m, 26.IV.2007, fl., *Lehavana et al.* 481 (MO, P).

Selected hybrid or intermediate specimens. – **MADAGASCAR. Reg. Atsinanana** [Prov. Toamasina]: fkt. Ambatolampy, forêt d'Ankerana, 18°23'34"S 48°48'37"E, 952 m, 23.I.2012, fr., *Ravelonarivo et al.* 4149 (MO). **Reg. SAVA** [Prov. Antsiranana]: Montagne d'Ambre, 12°32'35"S 49°08'46"E, 1300 m, fl., 6.XII.2007, *Ramandimbimanana et al.* 9 (MO, P); J.B. 19 Roussettes, Diego-Suarez, 11.XI.1954, fl., *Service Forestier* 11013 (P); Montagne d'Ambre, 12°30'30"S 49°10'09"E, 1000 m, fr., 1.VI.2008, *Trigui et al.* 485 (MO).

Specimens incertae sedis. – **MADAGASCAR. Reg. Analanjirifo** [Prov. Toamasina]: Baie d'Antongil, massif de Farankaraina entre Navana et Andranofotsy, 0–150 m, 19.IX.1957, fr., *Service Forestier* 18334 (P). **Sine loco**: s.d., fr., *Baron* 6251 (P); s.d., fr., *Baron* 6270 (P).

8. *Homalium pachycladum* Wassel & Appleg., **sp. nov.** (Fig. 5).

Holotypus: **MADAGASCAR. Reg. Analanjirifo** [Prov. Toamasina]: fiv. Maroantsetra, comm. Antsirabesahatany, fkt. Anjahely, 15°23'06"S 49°26'58"E, 809 m, 20.XII.2002, fl., fr., *Antilabimena, Pascal & Sassidy* 1540 (MO [MO-6144913]); iso-, P!, TAN).

Homalium pachycladum Wassel & Appleg. differs from *H. retusum* (Blume) Wassel & Appleg. in having thicker twigs, shorter petioles, glabrous (to sparsely pubescent) inflorescences with flowers borne singly, and larger petals.

Shrub or tree to 10 m tall, 30 cm dbh; twigs medium brown or pale gray, glabrous, leafing internodes (1.7–)2–4(–5.5) mm diam.; stipules fused, caducous. *Leaves* broadly elliptic to elliptic or obovate (somewhat ovate), (3–)5.8–14.5 × (1.8–)3.5–7 cm; base rounded to cuneate; apex rounded to obtuse, apiculate, or emarginate; margin entire to subentire, with small, inconspicuous glands; secondary veins 8–11 per side; both surfaces glabrous, drying yellowish brown to greenish on adaxial surface, darker to pale brown on abaxial surface; petiole glabrous, 6–15 mm. *Inflorescences* paniculate, axillary, 4.5–11 cm; rachis glabrous to sparsely short-pubescent; bracts and bracteoles glabrous, (1–)1.8–3.5 mm; flowers borne singly.

Flowers 5–6(–7)-merous; sepals yellow to green, oblanceolate or oblong-oblanceolate to broadly spatulate in flower, 5.1–7.8 mm in flower, 7–10 mm in fruit, adaxial and abaxial surfaces glabrous; sepal glands glabrous; petals yellow to yellow-green, broadly ovate-elliptic to broadly ovate, 2.6–3.3 mm in flower, 3–5.6 mm in fruit, both surfaces sparsely to moderately pubescent only at apex and margins minutely ciliate; filaments glabrous, 2–3 mm; anthers 0.5–0.7 mm; styles ca. 2.5–4 mm.

Distribution, ecology and conservation status. – *Homalium pachycladum* is endemic to mid-elevation humid forest west of Maroantsetra. The Area of Occupancy is 12 km²; the Extent of Occurrence (EOO) would be calculated as c. 6 km², but following the IUCN (2017) guidelines for application of Red List Criteria, the EOO must be at least equal to the AOO and is therefore considered to be 12 km². All three collections were made inside the eastern edge of the recently delineated protected area of Makira. A preliminary assessment of this species' conservation status is therefore "Least Concern" [LC].

Notes. – *Homalium pachycladum* often has a particularly robust appearance, especially during fruiting, with thick twigs and sturdy inflorescences. Though twig diameter is too variable within species to serve as a primary taxonomic character, it may be of use in recognizing this species. It most closely resembles *H. retusum*, which has obovate to broadly elliptic leaves with a long petiole, (10–)15–30 mm, a cuneate to convex base, and more marginal glands; its flowers are smaller and mostly borne in pairs. That species favors low altitudes. Another species of moderate elevations with large, sometimes broad leaves, *H. confertum*, usually has a toothed leaf margin with conspicuous, elongated glands. The inflorescences of that species are racemose and its petals are densely pubescent.

Paratypes. – **MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]:** Maroantsetra, Marovovonana, Ankirindro forest, 15°17'35"S 49°23'59"E, 664 m, 15.I.2003, fr., *Antilabimena* 1734 (MO, P); Maroantsetra, Abinanitelo, fkt. Ambalahahogo, Maimborondro summit, 15°19'03"S 49°24'06"E, 800 m, 8.IX.2004, fl., *Antilabimena* 2861 (G, MO, P).

9. *Homalium retusum* (Blume) Wassel & Appleq., **comb. nov.**

≡ *Nisa retusa* Blume, Mus. Bot. Lugd.-Bat. 2: 28. 1856.

Lectotypus (designated here): **MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]:** Ile Ste. Marie, VIII–IX, fl., *Bernier* 173 (L [L0010974]; isolecto-: K [K000231491, K000231492] images seen, L [L0010975, L0010976] images seen, P [P00418083, P00418084, P00418085]!, TAN [TAN000593] image seen).

≡ *Homalium scleroxylon* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 575. 1886. ≡ *Nisa scleroxylon* Tul. in Ann.

Sci. Nat., Bot. sér. 4, 8: 69–70. 1857. **Lectotypus** (first step designated by SLEUMER, 1973: 299; second step designated here): **MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]:** Ile Ste. Marie, VIII–IX, fl., *Bernier* 173 (P [P00418085]!; isolecto-: K [K000231491, K000231492] images seen, L [L0010974, L0010975, L0010976] images seen, P [P00418083, P00418084]!, TAN [TAN000593] image seen). **Syntypus:** *Gaudich.* [Gaudichaud] 296 [in phytotheca Jalbertiana] (not located).

Tree 6–7 m tall, 10 cm dbh; twigs gray to medium brown, glabrous, leafing internodes 1.6–3.5(–4.5) mm diam.; stipules 2–6 mm, sparsely ciliate. *Leaves* obovate to broadly elliptic, (5–)7–16 × 3.5–9 cm (unusually small leaves sometimes subtending inflorescences); base cuneate to convex; apex rounded to retuse or cuspidate; margin entire, rarely slightly crenulate, glands small; secondary veins (5–)6–9(–14) per side; both surfaces glabrous, drying light to medium brown on adaxial surface and darker on abaxial surface; petiole glabrous, (10–)15–30 mm. *Inflorescences* paniculate, axillary, 8–12 cm; rachis short-pubescent; bracts and bracteoles 1–3 mm, usually ciliate, otherwise glabrous to sparsely pubescent; flowers mostly paired with 2 per bract. *Flowers* 5–6-merous, white or yellow; sepals obovate at anthesis becoming oblanceolate, 4–8(–9) mm, adaxial and abaxial surfaces glabrous; sepal glands glabrous; petals oblong-ovate, 1.5–3 mm, adaxial surface usually pubescent apically, basally glabrous, abaxial surface glabrous except often pubescent at extreme apex, margin usually ciliate; filaments glabrous, 1.2–1.9 mm; anthers (0.3–)0.35–0.45 mm; styles (0.7–)1.2–1.7(–2) mm.

Distribution, ecology and conservation status. – *Homalium retusum* is found near the eastern coast in the northern part of Madagascar at low elevations. Few specimens are known, suggesting that this is an uncommon to rare species. Only five clearly distinct subpopulations have been recorded (Ile Ste.-Marie in Analanjirofo, Foulpointe and Ambila-Lemaitso in Atsinanana, and Anjana and Andempona in SAVA). The Extent of Occurrence (EOO) is calculated as c. 9847 km² and the Area of Occupancy (AOO) as 28 km². Much of the habitat is subject to ongoing anthropogenic damage, especially in view of its relative accessibility. Therefore, a preliminary assessment of its conservation status is Endangered [EN B1ab(iii)+2ab(iii)].

Vernacular names and use. – "Hazombato" (*Service Forestier* 2587); "Longotra" (*Service Forestier* 9646); "Marangue Touditch" (*Bernier* 173, *Chapelier* s.n.); "Voapak" (*Humblot* 63); "Zana" (*Service Forestier* 4918); "Zanakanivato" (*Service Forestier* 2597).

Wood is good for construction (*Bernier* 173).

Notes. – *Homalium retusum* has previously been lumped into *H. nudiflorum* s.l. (SLEUMER, 1973), which as herein circumscribed, differs in having smaller, narrower, shorter-petioled leaves; its inflorescences are usually racemose, not over 9 cm, glabrous or sparsely pubescent, with flowers borne singly. *Homalium retusum* most closely resembles *H. pachycladum*: both have relatively large leaves, paniculate inflorescences, and flowers with glabrous sepals and near-glabrous petals. *Homalium retusum* is known only from low-altitude and littoral forests, while *H. pachycladum* occurs farther inland and at much higher elevations. *Homalium pachycladum* has elliptic to obovate (or rarely ovate) leaves with shorter petioles (6–15 mm) and flowers all borne singly; its twigs seem usually to be thick, giving a robust appearance. Another inland species with large leaves, *H. confertum*, is distinguished by having usually elliptic to oblong-elliptic leaves with a serrate to crenate margin, racemose inflorescences with flowers borne singly, and petals densely pubescent on most of both surfaces.

The history of the names applying to this species resembles that of *Homalium planiflorum* (Boivin ex Tul.) Baill. (*Blackwellia planiflora* Boivin ex Tul.) versus *Blackwellia gracilis* Blume (see APPLEQUIST, 2017, 2018b), but without disruptive nomenclatural consequences. Blume published *Nisa retusa* based on material of Bernier 173 a year before Tulasne published *N. scleroxylon* based mostly on the same collection. Blume specified that his name was based only on material sent from P to L. That material was described in the protologue (BLUME, 1856–1857: 28) as “*Nomine Asteropeia et Mourangia Touditsch ex Herb. Mus. Paris. mecum benevole communicata.*” Three sheets at L bore labels initially marked “*Asteropeia* [or *Asteropeja*] *multiflora*” then “*Mourangia* [or *Morangia*] *touditch*” (a vernacular name, though not identified as such on those sheets); Blume later added “*Nisa retusa*” in the top margins. Much more recent pink typed labels identify these sheets as being type material of *N. scleroxylon*, “leg. Bernier 173”.

One year later, Tulasne published *N. scleroxylon*, citing “Bernierii herb., n. 173; Galdich. herb., n. 296, in phytotheca Jalbertiana” (TULASNE, 1857: 70). These are Latinizations for Bernier and Gaudichaud-Beaupré respectively. Although Tulasne presumably used only those duplicates of Bernier 173 to be found in France, he did not say so. The protologue (TULASNE, 1857: 70) further states: “*Marangue-Touditch* (1), auctore Bernerio, vernaculare audit...”, explaining the labeling seen, and apparently misinterpreted, by Blume. Three duplicates of Bernier 173 exist at P; two were labeled as having the vernacular name “*Maranguá touditch*” and one had initially been labeled “*Asteropeia*”. Though the sheets sent to L were not initially labeled as Bernier 173, they can be confidently assigned to that collection.

SLEUMER (1973: 299) referred to Bernier 173 (L) as the “holotype” of *Nisa retusa* and to Bernier 173 (P) as the

“holotype” of *Nisa scleroxylon*. For *N. retusa*, the original material was already restricted to the three sheets at L, which are syntypes, and Sleumer made no choice between them. The sheet that appears most complete is here chosen as a lectotype. For *N. scleroxylon*, Sleumer’s statement constitutes a first-step lectotypification (Art. 9.17 of ICN; TURLAND et al., 2018). This action means that *N. retusa* and *N. scleroxylon* are not nomenclatural synonyms, since their types are different specimens, even though they are from the same gathering. The best of the sheets at P is here chosen as a second-step lectotypification.

Additional material examined. – MADAGASCAR. **Reg. Atsinanana** [**Prov. Toamasina**]: Foulpointe?, s.d., fl., *Chapelier* [*Herb. Boivin*] s.n. (P [2 sheets]); Foulpointe, Morarano, Andohanakoho, 17°41'52"S 49°27'28"E, 34 m, 9.III.2005, fl., *Lebavana et al.* 304 (MO, P); Foulpointe, forêt d'Analava, 17°42'00"S 49°26'00"E, 35 m, 19.V.2004, fl., *Randrianarivelo et al.* 2 (MO, P); Sahapanpana, Foulpointe, 20.VI.1950, fl., *Service Forestier* 2587 (P); Ambila-Lemaitso, 1.II.1952, fr., *Service Forestier* 4918 (P); Ambila-Lemaitso, 27.IV.1954, fl., *Service Forestier* 9646 (P). **Reg. SAVA** [**Prov. Antsiranana**]: W de Nosiarina, sommet d'Anjana, 14°12'23"S 50°04'26"E, 190 m, 29.VIII.2007, fr., *Andriamihajarivo et al.* 1341 (MO); Antalaha, Andempona, 13.VI.1950, fl., *Service Forestier* 2597 (MO, P). **Sine loco**: Madag. bor., Andahoul, s.d., fr., *Humblot* 63 (P).

10. *Homalium stelliferum* H. Perrier in Mém. Mus. Natl. Hist. Nat. 13: 293. 1940.

Holotypus: MADAGASCAR. **Prov. Toamasina:** “Tananampotsy, forêt littorale orientale”, s.d., fr., *Perrier de la Bâthie* 14920 (leg. Louvel) (P [P04734366]!).

Tree to 30 m tall, 80 cm dbh; twigs pale to grayish or dark brown, glabrous to short-pubescent or pilose, leafing internodes 1–4.2 mm diam.; stipules fused, caducous. *Leaves* narrowly oblong-elliptic to oblong-oblancheolate, oblanceolate, elliptic, or obovate, 3.6–13.7 × 1.3–6.6 cm, coriaceous; base convex to rounded or cuneate; apex cuspidate to rounded, obtuse or acute, or emarginate (short-acuminate); margin subentire to inconspicuously toothed (dentate, somewhat revolute), usually with some glands in marginal convexities; secondary veins 7–11 per side; adaxial surface glabrous or bearing few trichomes on midrib, abaxial surface sparsely pilose to sparsely pubescent or glabrous, drying brown (to grayish green) or greenish brown to blackened on adaxial surface, lighter or medium brown (to green) on abaxial surface; petiole pilose, short-pubescent or glabrous, (2–)3–13 mm. *Inflorescences* racemose, axillary, (2.5–)4.5–9.5 cm; rachis densely to moderately (sparsely) pubescent or pilose; bracts and bracteoles usually with ciliate margin, densely to moderately pubescent (pilose, glabrate) or sparsely pubescent to glabrous, 2.3–4.5 mm; flowers borne singly. *Flowers* 5–6(7)-merous, greenish; sepals narrowly elliptic to narrowly oblong-elliptic, oblanceolate or oblanceolate-oblong, 6.6–8.4 mm after anthesis, 9.4–12 mm in fruit, glabrous or with dense appressed pubescence on calyx cup, dense to sparse pubescence in medial portion of one or both sepal surfaces; sepal glands pubescent on



Fig. 5. – *Homalium pachycladum* Wassel & Appleq. **A.** Flowering branch; **B.** Inflorescence; **C.** Flower post-anthesis. [Antilahimena et al. 1540, TAN] [Drawings: R.L. Andriamiarisoa]

upper (inward-facing) surface; petals oblong-ovate to elliptic, 3.5–4 mm after anthesis to in fruit, both surfaces densely (to moderately) pubescent at least on apical half; filaments sparsely pubescent to sparsely pilose, 1.6–2.5 mm; anthers 0.6–0.8 mm; styles ca. 2.4–3.4(–4?) mm.

Notes. – *Homalium stelliferum* is distinguished from all other species of sect. *Nisa* by having dense pubescence on the upper surface of the sepal glands, which is typically turned to face inward as the outer edge of the gland is elevated. In addition, the leaves are often sparsely pilose or pubescent, and sometimes the twigs and petioles are as well. Trichomes are also seen on the filaments, which is rare but not unknown in other species. Although limited material of *H. stelliferum* is known, it is quite variable in characters including leaf size and shape and the indument of several parts. A population from the northern extreme of the range with relatively large, broad, and long-petiolate leaves is herein segregated as *H. stelliferum* subsp. *andapense* Wassel & Appleq. This population's range of variation for key characters overlaps with that of subsp. *stelliferum*, which is not unusual in infraspecific taxa, but its typical appearance is sufficiently different from normal *H. stelliferum* that it is very likely to be genetically distinct to some degree.

Key to the subspecies of *Homalium stelliferum*

1. Leaves narrowly oblong-elliptic to oblong-ob lanceolate or oblanceolate (rarely obovate), 3.6–11.5 × 1.3–4.5(–5.5) cm; leafing internodes of twigs 1–2.7 mm diam.; petiole (2–)3–5(–10) mm; bracts densely to moderately pubescent (rarely to glabrate or pilose); calyx densely pubescent basally to glabrous 10a. *H. stelliferum* subsp. *stelliferum*
- 1a. Leaves elliptic to obovate, 6.3–13.7 × 3.1–6.6 cm; leafing internodes of twigs 2–4.2 mm diam.; petiole 6–13 mm; bracts sparsely pubescent to glabrous; calyx glabrous 10b. *H. stelliferum* subsp. *andapense*

10a. *Homalium stelliferum* H. Perrier subsp. *stelliferum*

Tree to 15 m tall, 80 cm dbh; twigs with leafing internodes 1–2.7 mm diam. **Leaves** narrowly oblong-elliptic to oblong-ob lanceolate or oblanceolate (rarely obovate), 3.6–11.5 × 1.3–4.5(–5.5) cm; apex cuspidate to rounded, obtuse or acute (short-acuminate); margin subentire to inconspicuously toothed (dentate), with glands usually present in marginal convexities; drying brown (to grayish green) on adaxial surface, lighter brown (to green) on abaxial surface; petiole pilose, short-pubescent or glabrous, (2–)3–5(–10) mm. **Inflorescences:** bracts and bracteoles usually with ciliate margin, densely to moderately pubescent (pilose, glabrate), 2.3–3.5(–4) mm. **Flowers** 5–6-merous; sepals narrowly elliptic to narrowly

oblong-elliptic or oblanceolate, (4–)6–8.4 mm after anthesis, 9.5–11 mm in fruit, glabrous or with dense appressed pubescence on calyx cup, dense to sparse pubescence in medial portion of one or both sepal surfaces.

Vernacular names and use. – “Fotsiakara” (*Service Forestier* 12394); “Tanatampotsy” (*Service Forestier* 5798); “Tanatana-potsy” (*Service Forestier* 12631); “Tsianihomposa” (*Réserves Naturelles s.n.*); “Tsitongamposa” (*Réserves Naturelles s.n.*); “Vavarony” ou “Voavarony” (*Service Forestier* 13709).

Wood is used for construction of houses (*Service Forestier* 19809).

Distribution, ecology and conservation status. – *Homalium stelliferum* subsp. *stelliferum* has been widely distributed in the past but is seldom collected; only two recent collections are known. It is usually found near the eastern coast in low-altitude forests, extending to coastal or mid-elevation forests. Nine widely separated locations have been collected. The historical habitat is mostly unprotected, but includes the protected area of Zahamena. The Extent of Occurrence (EOO) is calculated as c. 51,200 km² but the Area of Occupancy as 36 km², which is heavily dependent upon historical subpopulations. Low-elevation eastern humid forest has been subject to considerable anthropogenic damage from wood cutting and forest clearing for agriculture, and this continues to occur in unprotected areas. The preliminary conservation status of this subspecies is assessed as “Vulnerable” [VU B2ab(iii)], which may underestimate the level of threat it faces.

Additional material examined. – MADAGASCAR. **Reg. Alaotra-Mangoro [Prov. Toamasina]:** Ambatondrazaka [Zahamena], au bord de la riv. Ranomainty, 17°45'12"S 48°44'07"E, 5.III.2001, fr., *Ratovooson et al.* 460 (G, MO, P, K, TEF not seen). **Reg. Analanjirofo [Prov. Toamasina]:** Ambatomilona, Mananara, 15.XII.1951, fr., *Service Forestier* 5798 (P). **Reg. Anosy [Prov. Toliara]:** col Sakatelo (Ambazaha), canton Mahatalaky, distr. Ft-Dauphin, 12.XI.1949, fl., *Réserves Naturelles s.n.* (P). **Reg. Atsimo-Atsinanana [Prov. Fianarantsoa]:** Boma, distr. de Farafangana, 13.IX.1954, fr., *Service Forestier* 12394 (P). **Reg. Atsinanana [Prov. Toamasina]:** Vatondry, comm. Ambalabe, 19°09'43"S 48°36'05"E, 423 m, 26.XI.2004, fr., *Randrianasolo et al.* 953 (MO, P); Andriantantely, Brickaville, 22.X.1950, fl., *Service Forestier* 12631 (P). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Iaranina[?], Ampasinambo, Nosy-Varika, 24.XI.1954, fl., *Service Forestier* 13709 (MO, P); Antsampanandalana, Ambahaka, Ankarimbelo, Fort-Carnot, 23.X.1960, fl., fr., *Service Forestier* 19809 (P [2 sheets]); crête de Tsangatsanga, à l'E de Kianjavato (entre Ifanadiana et Anosivola), 550 m, 6.XII.1964, fl., *Service Forestier* 23918 (MO).

10b. *Homalium stelliferum* subsp. *andapense* Wassel & Appleq., subsp. nov. (Fig. 6).

Holotypus: MADAGASCAR. **Reg. Analanjirofo [Prov. Toamasina]:** Maroantsetra, Anjahana-Ambatoledama (à env. 7 km au NW d'Ankovana), massif de Bean-jada, 15°16'34"S 49°58'52"E, 1075 m, 26.XI.1997, fl. & fr., *Ralimanana & Ranaivojoana* 142 (MO [MO-6883982]); iso-: G!, K!, P!, TAN).



Fig. 6. – Holotype of *Homalium stelliferum* subsp. *andapense* Wassel & Appleq.
[Ralimanana & Ranaivojaona 142, MO] [© Missouri Botanical Garden, Saint Louis]

Homalium stelliferum subsp. *andapense* Wassel & Appleg. differs from *Homalium stelliferum* H. Perrier subsp. *stelliferum* in having broader and usually larger leaves.

Tree to 30 m tall, 55 cm dbh; bark whitish; twigs with leafing internodes 2–4.2 mm diam. *Leaves* elliptic to obovate, (5.2–)6.3–14.5 × (2–)3.1–6.6 cm; apex rounded to cuspidate or emarginate (retuse); margin subentire, sometimes somewhat revolute, to crenulate, with few small glands; drying greenish brown to blackened on adaxial surface, medium brown on abaxial surface; petiole glabrous, 6–13 mm. *Inflorescences*: bracts and bracteoles sparsely pubescent or glabrous with ciliate margins, (3–)3.5–4.5 mm. *Flowers* 6(7)–merous; sepals narrowly oblanceolate-oblong, 9.4–12 mm in fruit, adaxial and abaxial surfaces glabrous (calyx cup sometimes sparsely pubescent).

Vernacular names. – “Hazombato” (*Service Forestier* 916); “Longotra” (*Ralimanana* & *Ranaivojaona* 142); “Naroankoditra” (*Antilabimena* 1585).

Distribution, ecology and conservation status. – *Homalium stelliferum* subsp. *andapense* has been collected from three northern mid-elevation humid forests. The Extent of Occurrence is calculated as c. 2676 km² and the Area of Occupancy as 12 km². The subpopulation from Anjahely appears to have been within the boundaries of the Makira Natural Park, and the type collection might have been from the peripheral zone of Masoala National Park; the third, more northern locality was collected in 1950 and no recent collections are known from the area. Label data from *Ralimanana* & *Ranaivojaona* 142 describes the plant as “rare au bord d’une rivière”. Any accessible habitat outside protected areas in this region would be threatened by human activity such as cutting of trees for wood and fuel. It is unclear what the current range is or whether only a minority, most, or perhaps all of the habitat is within protected areas. It is suggested that the subspecies’ status might therefore best be considered “Data Deficient” [DD].

Notes. – The oldest collection of *Homalium stelliferum* subsp. *andapense* was included by SLEUMER (1973) in *H. stelliferum* without comment. The leaves are larger, at the upper end of their range, than those of *H. stelliferum* subsp. *stelliferum* and of different shape, being proportionately broader. There are several other apparent average differences between the two, e.g., *H. stelliferum* subsp. *stelliferum* has thinner young twigs, usually more pubescent bracts, bracteoles and calyces, and possibly slightly smaller flowers. However, the consistency of those characters is uncertain. *Homalium stelliferum* subsp. *andapense* has a distinct geographic range and perhaps habitat preferences. Because of the limited amount of material of both taxa and the variability seen within *H. stelliferum* subsp.

stelliferum, the new taxon is conservatively treated at subspecific level. Attempts to relocate it and document its range of variation would be highly desirable.

Paratypes. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Maroantsetra, Antsirabesahatana, fkt. Anjahely, 15°25'01"S 49°30'39"E, 420 m, 23.XII.2002, fl., fr., *Antilabimena* 1585 (MO, P). Reg. SAVA [Prov. Antsiranana]: vallée de l’Andramonta, W du distr. d’Andapa, 680–700 m, 14.XII.1950, fr., *Service Forestier* 916 (P [2 sheets]).

11. *Homalium tenue* Wassel & Appleg., sp. nov. (Fig. 7).

Holotypus: MADAGASCAR. Reg. Anosy [Prov. Toliara]: Comm. Iabokoho, fkt. Antsontso, Ivohibe forest, 24°34'10"S 47°12'37"E, 41 m, 24.V.2006, fl., *Antilabimena et al.* 4858 (MO [MO-6396271]!; iso-: P [P06161693]!, TAN, TEF).

Homalium tenue Wassel & Appleg. differs from *H. antilabimena* Wassel & Appleg. in having usually narrower leaves with shorter petioles, racemose (to racemiform) inflorescences with rachis not densely pubescent and bracts not pubescent on most of surface, and smaller flowers with sepals adaxially glabrous.

Tree to 16 m tall, 8 cm dbh; twigs gray to light brown, glabrous, leafing internodes 0.8–1.6(–2.3) mm diam.; stipules fused, caducous. *Leaves* elliptic to narrowly elliptic, obovate, or oblanceolate (very rarely a few lanceolate), (2.5–)3–6(–10) × 1.3–2.5(–3) cm; base cuneate to slightly attenuate; apex cuspidate to short-acuminate, acute, or rounded; margin entire, glands absent or very few; secondary veins 7–10(–12) per side, intersecondary veins sometimes similar; both surfaces glabrous, drying brown, adaxial surface usually paler; petiole glabrous, 3–7(–9) mm. *Inflorescences* racemose (racemiform panicles), axillary, (2–)3–7(–8) cm; rachis minutely pubescent (to glabrous), markedly thin; bracts and bracteoles pubescent on midrib, ciliate at margins or glabrous, 1–3 mm; flowers borne singly (or partly paired, the second flower probably being borne on a highly reduced branch). *Flowers* 5–7–merous, yellowish green, greenish white, or white; sepals in fruit narrowly oblong to oblanceolate-oblong, 3.5–5(–6) mm, abaxial surface densely pubescent on calyx cup and sepal bases with indument sometimes extending up the medial portion, elsewhere glabrous, adaxial surface glabrous; sepal glands glabrous; petals oblong-ovate to elliptic or lanceolate, 1.5–2.5 mm, abaxial surface densely pubescent (to moderately pubescent, sparsely pubescent near margins), adaxial surface densely to sparsely pubescent; filaments glabrous, 0.9–1.1 mm; anthers 0.2–0.3 mm; styles 0.5–1 mm.

Vernacular names and use. – “Fotsiakaraminty” (*Ludovic* 1074); “Fostiakora mena” (*Ludovic* 1061); “Hazofotsy” (*Service Forestier* 9742); “Hazomby” (*Ludovic* 1074); “Zora” (*Service Forestier* 9742).

Wood is used for construction (*Ludovic* 1074).



Fig. 7. – Holotype of *Homalium tenue* Wassel & Appleq.
[Antilahimena 4858, MO] [© Missouri Botanical Garden, Saint Louis]

Distribution, ecology and conservation status. – *Homalium tenue* is found in low-elevation forests in the southeastern regions of Anosy and Atsimo-Atsinanana; it is reported on sand and laterite. Although the localities in Anosy are variously described, all come from a single small region, so that not more than five distinct subpopulations are known. The Extent of Occurrence and Area of Occupancy are calculated including an unusual collection that may be of hybrid origin (*Service Forestier* 23622, discussed below) on the grounds that if it is a hybrid, the parental species is likely also to be present in the forest in question. The Extent of Occurrence (EOO) is calculated as c. 908 km² and the Area of Occupancy as 28 km². Habitat is largely unprotected and because low-elevation forest is easily accessed, it is very vulnerable to anthropogenic damage from wood harvest and forest clearing. A preliminary assessment of its conservation status is therefore “Endangered” [EN B1ab(iii)+2ab(iii)].

Notes. – *Homalium tenue* overlaps in distribution with *H. nudiflorum*, which has sometimes similar leaves. *Homalium tenue* differs in the denser indument on the petals and calyx cup, usually extending to the basal medial portion of the sepals, and its flowers are smaller; its slender twigs and inflorescences give it a more delicate appearance than *H. nudiflorum*, though it is reportedly a sometimes large tree. The leaves are usually quite small (the inclusion of *Service Forestier* 23622, which in most other features is consistent with the species, significantly increases the leaf size range). Collections from Atsimo-Atsinanana have more prominently acuminate and often larger leaves than those from Toliara.

Two other species, *H. antilahimenae* and *H. ciliolatum*, have dense pubescence on both petals and portions of the calyx; these two and *H. tenue* are suspected to be a natural group. Those two species have at least some indument on both sepal surfaces, with longer indument on the calyx cup, and their flowers are larger at maturity; they lack the gracile appearance of *H. tenue*. *Homalium ciliolatum*, which overlaps in geographic range, has usually larger and broader leaves, flowers usually borne in pairs, and large pubescent bracts and bracteoles; the calyx cup is long-sericeous and the sepals pubescent throughout on both surfaces. *Homalium antilahimenae* is native to northern Madagascar and has often larger leaves with some marginal glands, often densely pubescent rachises, and bracts and bracteoles often pubescent throughout.

Hybridization between *Homalium tenue* and *H. louvelianum* has been observed (see under the latter species above).

Paratypes. – MADAGASCAR. **Reg. Anosy** [Prov. Toliara]: Bemangidy Forest, 65 km N of Ft. Dauphin, 24°34'05"S 47°12'38"E, 100 m, 10.II.2006, fr., Lowry et al. 6718 (MO); Fort-Dauphin, Iabakoho, 24°35'33"S 47°12'52"E, 22.V.2006, fr., Rajobarison et al. 166 (MO); Anosy, Taolagnaro, Iaboko, 24°34'16"S 47°12'05"E, 271 m, 1.IV.2008, fr., Razakamalala et al. 4065 (MO); forêt Andrazato, Ft. Dauphin, 5.IV.1954, fr., *Service Forestier* 9742 (P); forêt

de Bemangidy, au N de Mahatalaky (Ft. Dauphin), 100 m, II.1995, fr., *Service Forestier* 11797 (MO, P). **Reg. Atsimo-Atsinanana** [Prov. Fianarantsoa]: Vangaindrano, Matanga, 23°30'57"S 47°29'33"E, 96 m, 18.IV.2008, fr., *Ludovic* 1061 (MO); *ibid. loco*, fr., *Ludovic* 1074 (MO); Mananivo, 40 km SW Farafangana, forêt Iabomary, 23°03'34"S 47°40'23"E, 0–50 m, 6.II.2001, buds, Rabenantoandro et al. 430 (G, K, MO, P); S de Farafangana rte de Manombo, aux P.K. 20–21, 14–17.X.1964, fl., fr., *Service Forestier* 23622 (P [2 sheets]).

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References

- ANDREWS, J., P. ANTILAHIMENA & C.R. BIRKINSHAW (1998). Use of a day resting box by a wild sportive lemur, *Lepilemur dorsalis*, on Nosy Be, north-western Madagascar. *Folia Primatol.* 69(Suppl. 1): 18–21.
- APPLEQUIST, W.L. (2013). A nomenclator for *Homalium* (Salicaceae). *Skvortsovia* 1: 12–74.
- APPLEQUIST, W.L. (2016a). A reconsideration of the infrageneric classification of *Homalium* Jacq. (Salicaceae). *Candollea* 71: 231–256.
- APPLEQUIST, W.L. (2016b). A revision of the Malagasy species of *Homalium* sect. *Eumyriantheia* Warb. (Salicaceae). *Candollea* 71: 33–60.
- APPLEQUIST, W.L. (2017). Proposal to conserve the name *Blackwellia* ('Blackwellia') paniculata (*Homalium paniculatum*) (Salicaceae). *Taxon* 66: 206–207.
- APPLEQUIST, W.L. (2018a). A revision of *Homalium* sect. *Odontolobus* (Salicaceae) endemic to Madagascar. *Candollea* 73: 27–48.
- APPLEQUIST, W.L. (2018b). A revision of the Malagasy species of *Homalium* sect. *Blackwellia* (Salicaceae). *Candollea* 73: 221–244.
- BACHMAN, S. & J. MOAT (2012). GeoCAT – an open source tool for rapid Red List assessments. *Bot. Gard. Conservation Int.* 9. [http://geocat.kew.org]

- BLUME, C.L. (1856–1857). *Museum Botanicum Lugduno-Batavum*. Vol. 2. E. J. Brill, Lugduni-Batavorum.
- CHASE, M.W., S. ZMARZTY, M.D. LLEDÓ, K.J. WURDACK, S.M. SWENSEN & M.F. FAY (2002). When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid rbcL DNA Sequences. *Kew Bull.* 57: 141–181.
- IUCN (2012). *IUCN Red List Categories and Criteria: Version 3.1*. Ed. 2. IUCN Species Survival Commission, Gland & Cambridge.
- IUCN (2017). *Guidelines for Using the IUCN Red List Categories and Criteria: Version 13*. Prepared by the IUCN Standards and Petitions Subcommittee. IUCN Species Survival Commission, Gland & Cambridge.
- MADAGASCAR CATALOGUE (2020). *Catalogue of the Plants of Madagascar*. Missouri Botanical Garden, St. Louis & Antananarivo. [http://www.tropicos.org/project/mada]
- PHILLIPSON, P.B., P.P. LOWRY II, L. ANDRIAMAHEFARIVO, P. ANTILAHIMENA & C. BIRKINSHAW (2010). Floristic inventory of the Ambatovy-Analamay mine site and comparison to other sites in Madagascar. *Malagasy Nat.* 3: 44–76.
- SLEUMER, H. (1973). Révision du genre *Homalium* Jacq. (Flacourtiacées) en Afrique (y compris Madagascar et les Mascareignes). *Bull. Jard. Bot. Natl. Belg.* 43: 239–328.
- SONNERAT (2020). *Base de données des collections du Muséum national d'Histoire naturelle*. MNHN, Paris. [http://science.mnhn.fr/institution/mnhn/collection/p/item/search/form]
- TROPICOS (2020). Missouri Botanical Garden, Saint Louis. [http://www.tropicos.org]
- TULASNE, L.-R. (1857). Florae Madagascariensis fragmenta. *Ann. Sci. Nat., Bot.* ser. 4, 8: 44–163.
- TURLAND, N.J., J.H. WIERSEMA, F.R. BARRIE, W. GREUTER, D.L. HAWKSWORTH, P.S. HERENDEN, S. KNAPP, W.-H. KUSBER, D.-Z. LI, K. MARHOLD, T.W. MAY, J. MCNEILL, A.M. MONRO, J. PRADO, M.J. PRICE & G.F. SMITH (2018). International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Veg.* 159.
- 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.
- Almeda 8636 (3); Andriamahefarivo 50 (7); Andriamihajarivo 1341 (9), 1701 (2); Andrianjafy 108 (5); Antilahimena 1213 (1), 1423 (7), 1540 (8), 1585 (10b), 1734 (8), 2621 (1), 2719 (7), 2861 (8), 2911 (1), 3005 (7), 3135 (7), 3188 (7), 4826 (7), 4858 (11), 4863 (2), 5763 (1), 6959 (7), 7778 (3).
- Bardot-Vaucoulon 1207 (4); Baron 3185 (3), 3256 (3), 6251 (aff. 7), 6270 (aff. 7); Barnett 275 (3); Bernard 876 (3); Bernardi 11944 (7), 12003 (3); Bernier 173 (9); Birkinshaw 355 (5), 2015 (5 vel aff.); Buerki 106 (3).
- Chapelier [Herb. Boivin] s.n. (9); Cours 1095 (7), 2952 (5), 3867 (3).
- Decary 6381 (5); Dorr 2723 (3); Dumetz 537 (6).
- Gautier 4142 (7), 4806 (3), 6092 (3); Geay 7425 (5), 7426 (5), 8069 (5); Gereau 3388 (5).
- Homolle 199 (7); Humbert 23040 (3), 24704 (3), 24888 (3), 31810 (7); Humblot 63 (9).
- Leeuwenberg 14292 (7); Lehavana 304 (9), 481 (7); Leopold 108 (7); Louvel 87 (5), 109 (5); Lowry 6074 (5), 6718 (11); Ludovic 391 (5), 1061 (11), 1074 (11), 1649 (6).
- Madiomanana 282 (7); McPherson 14289 (7), 14484 (7), 14796 (5), 16535 (7), 18894 (5); Miandrimanana 381 (7).
- Nusbaumer 1261 (7).
- Perrier de la Bathie 2307 (7), 6697 (3?), 6705 (3), 14920 (10a); Petit-Thouars s.n. (7).
- Rabenantoandro 430 (11), 1259 (5), 1481 (5); Rabevohitra 4128 (7), 4985 (5); Rajemisa 24 (3); Rajoharison 166 (11); Rakotondrajaona 609 (7); Rakotomalaza 681A (3), 1353 (3); Rakotonirina 180 (1), 300 (7), 870 (5); Rakotovao 2986 (3); Ralimanana 142 (10b); Ramananjana 826 (6); Ramandimbimanana 9 (3×7); Ranaivojaona 541 (5), 651 (5), 1014 (7), 1043 (7); Randriamanarivo 10 (7); Randrianaivo 526 (3), 1221 (7), 1875 (5), 2361 (5); Randrianarivelo 2 (9); Randrianasolo 953 (10a); Randriatafika 147 (3); Ranirison 612 (5 vel aff.); Ratovoson 184 (3), 327 (1), 460 (10a), 881 (7), 1094 (5 vel aff.), 1719 (6); Ravelonarivo 2238 (3), 3663 (3), 4149 (3×7); Ravololonanahary 69 (3), 82 (5); Razafimandimbison 211 (5); Razafindraibe 11 (7); Razafindramora 1 (3); Razafitsalama 961 (5), 1105 (7); Razakamalala 649 (5), 701 (5), 889 (5), 2127 (5), 3796 (5×11), 4065 (11), 4148 (3); Razanatsima 1136 (3), 1364 (7); Reserves Naturelles s.n. (10a), 6043 (3).
- Service Forestier 687 (7), 916 (10b), 938 (3), 991 (3), 1249 (3), 1562 (5), 1766 (3), 1776 (3), 2231 (7), 2587 (9), 2597 (9), 2851 (5), 3047 (4), 3794 (7), 3796 (2), 4702 (5), 4918 (9), 5798 (10a), 5960 (5), 6390 (2), 6975 (5), 7362 (3), 8414 (3), 9058 (3), 9514 (5), 9531 (5), 9646 (9), 9742 (11), 10148 (3), 10435 (7), 11013 (3×7), 11450 (3×7?), 11593 (7), 11797 (11), 12394 (10a), 12631 (10a), 13239 (7), 13709 (10a), 13984 (2), 14476 (2), 14566 (2), 14719 (2), 14837 (5), 15375 (5), 15406 (3), 15944 (1), 16192 (7), 16801 (3), 18143 (5), 18278 (1), 18334 (aff. 7), 18754 (3), 19188 (5), 19502 (5), 19809 (10a), 21504 (2), 23613 (2), 23622 (11), 23750 (7), 23771 (5), 23918 (10a), 25211 (3), 25277 (3), 28645 (6).
- Tabinarivony 180 (3×7?); Trigui 485 (3×7).
- Ursch 239 (7).
- van der Werff 13498 (7).
- Wohlhauser 767 (7).