

# A revision of the *Dombeya rigida* complex (Malvaceae)

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## ABSTRACT

A revision of *Dombeya* subsect. *Rigidae*, which comprises two Malagasy species (*D. linearifolia* and *D. rigida*), is presented. The classification of these species within *Dombeya* is preferred to an alternate placement within *Helmiopsis*. Three subspecies of *D. rigida* are recognized: subsp. *parvifolia*, characterized by small leaves, is newly described, and subsp. *guazumifolia* is newly recognized at that rank. Arènes' two subspecies of *D. linearifolia* are synonymized, and a new subsp. *muricata*, characterized by fruit similar to that of *D. rigida*, is described. Both species display considerable variation in leaf and fruit morphology in the north, but variation is discontinuous, indicating that the species are usually reproductively isolated.

## KEY WORDS

Malvaceae,  
*Dombeya*,  
*Helmiopsis*,  
Madagascar,  
new subspecies.

## RÉSUMÉ

*Une révision du complexe Dombeya rigida (Malvaceae).*

Une révision de *Dombeya* subsect. *Rigidae*, qui comprend deux espèces malgaches (*D. linearifolia* et *D. rigida*), est présentée. L'attribution de ces espèces au genre *Dombeya* est préférée à l'attribution alternative au genre *Helmiopsis*. Trois nouvelles sous-espèces de *D. rigida* sont reconnues : subsp. *parvifolia*, qui se caractérise par des feuilles petites, est nouvellement décrite, et subsp. *guazumifolia* est nouvellement reconnue à ce niveau. Deux sous-espèces de *D. linearifolia* proposées par Arènes sont mises en synonymie, mais une nouvelle subsp. *muricata*, qui se caractérise par un fruit semblable à celui de *D. rigida*, est décrite. Les deux espèces présentent une variabilité considérable de la morphologie des feuilles et des fruits dans le nord, mais la variation est discontinue, ce qui indique que les espèces sont normalement isolées génétiquement.

## MOTS CLÉS

Malvaceae,  
*Dombeya*,  
*Helmiopsis*,  
Madagascar,  
sous-espèces nouvelles.

## INTRODUCTION

*Dombeya rigida* Baill. and *D. linearifolia* Hochr. are two of nine species of *Dombeya* Cav. (Malvaceae s.l.; cf. Bayer *et al.* 1999) that Hochreutiner's (1926) treatment placed in sect. *Capricornua* Hochr., which is characterized by two- to several-branched, cymose inflorescences with scorpioid branches. Hochreutiner (1926) noted that *D. rigida* was "remarquable à cause de ses pétales glanduleux à la base". In the next and most recent complete treatment of Malagasy *Dombeya*, Arènes (1958, 1959) divided sect. *Capricornua* into subsect. *Rigidae* Arènes, limited to *D. rigida* and *D. linearifolia* and characterized by papillose glands on the basal portion of the adaxial petal surface, and subsect. *Greveanae* Arènes, comprising seven species without petal glands, including five previously recognized in sect. *Capricornua* by Hochreutiner. The two species of subsect. *Rigidae* have numerous characters in common, being distinguished largely by leaf size and shape and traditionally by the degree of ovary lobing, and are undoubtedly closely related.

Dorr (2001) transferred *Dombeya rigida* to *Helmiopsis* H.Perrier, as he felt that the species was improperly placed in *Dombeya*. He observed that the seeds of *D. rigida* were laterally flattened with a narrow curved dorsal wing. According to Arènes' (1959) treatment of Malagasy Sterculiaceae, winged seeds, combined with a coronate rather than fasciculate androecium, oppositipetalous staminodes and oppositisepalous stamens, and glabrous locules, would place this species in the genus *Helmiopsis* H.Perrier, a Malagasy endemic with previously nine species recognized. Most species of *Helmiopsis* have elongated apical seed wings, and four species, those placed within *Helmiopsis* sect. *Glandulipetalae* Arènes, have similar glandular petals and stamens shorter than the staminodes (the latter being a very common state in *Dombeya* as well).

Dorr's (2001) placement of *Dombeya rigida* within *Helmiopsis* seems no less awkward than its placement within *Dombeya*. The species does not possess other features characteristic of *Helmiopsis*, such as lepidote indument, small and rapidly ca-

duous bracteoles, or small patches of glandular tissue inside the sepal bases (also observable in many *Dombeya* species [Vogel 2000; pers. obs.]). Its scorpioid inflorescences and dense stellate pubescence throughout, though not seen elsewhere in *Helmiopsis*, are shared by other species of *Dombeya* sect. *Capricornua*. Stamen position appears to be more variable within both genera than has been previously recognized; some variation within *D. rigida* itself and in other *Dombeya* species can be observed, whereas members of *Helmiopsis* sect. *Glandulipetalae* usually have more or less oppositipetalous stamens, in contrast to most of sect. *Helmiopsis*. Finally, it is not clear that the very narrow curved marginal wing observed by Dorr (2001) is homologous with the greatly elongated apical wing of *Helmiopsis*; *Dombeya linearifolia*, whose placement he did not address but which is almost certainly the sister species of *D. rigida*, has unwinged seeds. *Dombeya rigida* has therefore been excluded from a recent treatment of *Helmiopsis* (Applequist 2009). The systematics of *Dombeya* and related genera are messy, and *Dombeya* may be paraphyletic with respect to several smaller genera, including *Helmiopsis* (Le Péchon *et al.* 2009, 2010). Until the relationships within this group are resolved by molecular analyses including more taxa (now in progress; C. Skema, pers. comm.), it seems most conservative to leave species of uncertain affinities in a broadly circumscribed *Dombeya*. However, examination of material of both *D. rigida* and *D. linearifolia* indicated that the range and distribution of morphological variation in these species was not adequately represented by the specimens available to Arènes (1959), who published the last complete treatment. An updated treatment of these species is therefore made available here.

## GEOGRAPHY AND CONSERVATION

Geographic distribution ranges from northern to western and southwestern Madagascar. *Dombeya linearifolia* is confined to the extreme north; *D. rigida* is widespread and found on a variety of substrates, although two of the subspecies herein recognized have narrower ranges and perhaps more selective habitat requirements. Specimen locality data were analyzed to provide preliminary

estimates of conservation status according to the IUCN Red List Categories and Criteria (IUCN 2001). For most included taxa, at least five separate localities have been recorded and the preliminary estimate of conservation status is Least Concern (LC). However, *Dombeya linearifolia* subsp. *linearifolia* is known from only three localities in relatively close proximity to one another (two of which possibly represent the same population); it is therefore provisionally assessed as Vulnerable (VU D2).

#### MORPHOLOGY

*Dombeya rigida* and *D. linearifolia* resemble one another in most characters, including distinctive features such as scorpioid-branched inflorescences and the presence of petal glands, the latter of which is otherwise unknown in *Dombeya*. The two are distinguished primarily by leaf morphology (size, shape, and relative petiole length). *Dombeya rigida* has ovate to narrowly ovate, oblong-ovate, or oblong-lanceolate leaves, often with relatively long petioles, whereas *D. linearifolia* has much narrower, oblong to lanceolate, short-petioled leaves. Most specimens of both species, including all subspecies herein recognized, have domatia, which within a taxon may be roofed or cleft with clusters of straight hairs, in axils of the lower lateral veins of large leaves. Domatia are uncommon in most subgroups of *Dombeya*, though they have previously been reported in a few species of subg. *Xeropetalum* (Del.) K. Schum., sect. *Xeropetalum* (Arènes 1958; Seyani 1991) and are frequent in one subgroup of sect. *Decastemon* Planch. (unpubl. data); they do not occur in *Helmiopsis*. Inflorescences of *D. rigida* have been repeatedly described as being in part terminal, but on some specimens the apparently terminal inflorescences are identifiable as pseudoterminal. Although the inflorescences of *D. linearifolia* are more strongly clustered at the ends of branches than are those of *D. rigida*, they are all visibly lateral rather than terminal or pseudoterminal.

Floral morphology is quite consistent throughout subsect. *Rigidae*, with variation in size of floral parts within taxa exceeding variation among taxa; *D. linearifolia* subsp. *linearifolia* has basally dilated

filaments. While Malagasy species of *Dombeya* have generally been described as hermaphroditic, some species native to the Mascarene Islands have been reported to display both cryptic and leaky, or inconsistent, dioecy (Humeau *et al.* 1999a, b), raising the possibility that a similar condition might also be present, overlooked, in Malagasy species. While material of subsect. *Rigidae* is too limited to rule out the possibility of leaky dioecy, a number of flowering specimens are observed to produce both pollen and ovules within the same flower.

Fruit morphology is a critical yet confusing character in subsect. *Rigidae*. Dorr (2001) discovered that *D. rigida* at maturity has unusual ribbed, strongly muricate capsules with marginally winged seeds (the wing is shallow or, in some fruiting specimens, reduced to an inconspicuous dorsal ridge). While one subspecies of *D. linearifolia* also has fruits of this type, the other has a smaller, deeply lobed, smooth-surfaced fruit; seeds have shallow or no marginal ridges. The northern subspecies of *D. rigida* whose leaves appear most similar to those of *D. linearifolia*, rather than having an intermediate fruit type, usually has an extreme version of the muricate fruit type with elongated, acute papillae. However, one specimen has fruits that, while not fully mature, are not muricate.

#### MATERIAL AND METHODS

Morphological, distributional, and phenological data were recorded from specimens of *Dombeya rigida* and *D. linearifolia* from P, MO and TAN. A taxonomic species concept is used according to which morphologically distinct groups of populations are recognized at the species level if they are distinguished by three consistent characters; forms distinguished by one or two characters or by overlapping quantitative characters are recognized at the subspecies level. Specimens were recorded as flowering if they were in full flower or very near anthesis, but not if only small buds were present. Estimated geographic coordinates added post facto are placed in brackets.

## SYSTEMATICS

Family MALVACEAE Juss.

Genus *Dombeya* Cav.*Dombeya* subsect. *Rigidae* Arènes*Candollea* 16: 296 (1958).TYPUS. — *Dombeya rigida* Baill.

## DESCRIPTION

Woody plants, usually trees; young twigs often scurfy or somewhat stellate-pubescent. Leaves alternate, simple, stipulate, sparsely pubescent; stipules small, lanceolate, caducous; petiole stellate; margins toothed; basal veins (3-)5(-7); small roofed domatia or clefts with clusters of unbranched hairs usually present in axils of lateral veins on larger leaves. Inflorescences lateral and sometimes pseudoterminal, cymose, with branches scorpioid when young, stellate throughout; bracts lanceolate, caducous; bracteoles 3, borne immediately beneath buds, caducous. Sepals 5, stellate, often irregularly connate; petals 5, broadly obovate, usually somewhat asymmetrical, the lower portion of the adaxial surface densely glandular; staminodes usually more or less opposite petals, papillate; fertile stamens 10 (very rarely to 20); filaments basally connate into a short corona; anthers linear-oblong with acute apex; ovary 5-locular, stellate-pubescent; style lobes 5. Fruit a loculicidal capsule, subglobose, longitudinally compressed, (3-)5-ribbed or lobed; seeds (1-)2 per locule, glabrous.

## REMARKS

In the present treatment, as in Arènes (1958, 1959), two species of subsect. *Rigidae* are recognized, *D. rigida* and *D. linearifolia*; the two are distinguished by vegetative morphology. To address considerable infraspecific variation, especially in northern Madagascar, three subspecies are recognized

within *D. rigida* and two within *D. linearifolia*. The northern tip of Madagascar represents the northern extreme of the range of *D. rigida* subsp. *rigida* and the entire range of *D. linearifolia*. In that region, populations of *D. rigida* with relatively narrow, often oblong leaves are recognized as subsp. *guazumifolia*, while populations of *D. linearifolia* with fruits similar to those of *D. rigida* are recognized as subsp. *muricata*. These populations, which seem to share characters of the sister species, are treated as distinct subspecies rather than as a hybrid zone because there is not a continuous range of intermediates between *D. rigida* subsp. *guazumifolia* and *D. linearifolia* subsp. *muricata*. Instead, all specimens can be comfortably assigned to one species or the other based on leaf morphology. This author therefore favors the view that the distribution of morphological variation in this group represents recent, perhaps still ongoing speciation of lineages derived from a variable ancestral taxon, combined with the evolution of novel fruit morphology in one lineage. However, genetic data and crossing studies would be required to clearly elucidate the ancestry of these populations.

The requirement of the ICBN Art. 37.1 (McNeill *et al.* 2006), that infrageneric names published after Jan. 1, 1958 must indicate a type to be validly published, was in force at the time of publication of this subsection by Arènes (1958). The name *Rigidae* may be taken as an indirect reference to *Dombeya rigida*, as permitted under Arts. 37.3 and 10.3 (McNeill *et al.* 2006). Likewise, the other subsection within sect. *Capricornua*, subsect. *Greveanae*, is validly published through indirect reference to *D. greveana* Baill. However, it should be noted that some of Arènes' (1958) novel infrageneric groups apparently are not validly published (e.g., subsect. *Cymoso-umbellatae*, comprising seven species with no similar epithets, or sect. *Paricapricornua*, comprising *D. borraginea* Hochr. and *D. glaberrima* Arènes).

KEY TO THE SPECIES OF *DOMBEYA* SUBSECT. *RIGIDAE* ARÈNES

1. Leaves narrowly oblong to lanceolate, almost always < 3 cm broad; petioles 0.5-2.3 cm long; inflorescences (2.5-)3.5-6.5(-8.0) cm long, usually 2-branched; ovary 5-ribbed or deeply 5-lobed; fruit variable; seeds laterally compressed, with at most shallow dorsal ridge ..... 1. *D. linearifolia* Hochr.

- Leaves ovate to narrowly ovate, oblong-ovate or oblong-lanceolate, if oblong usually > 3 cm broad; petioles 1-7 cm long; inflorescences (3-)6-12(-15) cm long, with (1 to) 2 to several branches; ovary 5-ribbed; fruit usually 5-ribbed and muricate; seeds laterally flattened, with shallow marginal wing ..... 2. *D. rigida* Baill.

1. *Dombeya linearifolia* Hochr.

DESCRIPTION

Tree to 6(-10) m or large shrub; twigs dark to dark reddish brown, often with irregular whitish coat. Leaves narrowly oblong to oblong-elliptical or lanceolate, 4.5-11.5(-13.0) cm long, (0.8-)1.2-3.2 cm broad; petioles 5-23 mm long; base rounded to shallowly cordate or rounded-truncate; apex acute to rounded, occasionally emarginate; margins serrulate to crenate-serrate; basal veins (3-)5(-7); lower surface sparsely pubescent, mostly stellate, especially on midrib and in axils of secondary veins, with small roofed domatia or hair clusters usually present; upper surface glabrous or rarely sparsely pubescent around midrib. Inflorescences lateral, clustered near twig ends, usually 2-branched; peduncle (1.2-)2.5-4.5(-5.0) cm long, entire inflorescence (2.5-)3.5-6.5(-8.0) cm long;

bracts rare, 2.5-3.5 mm long; bracteoles (1.5-)2.5-4.0 mm long, broadly ovate to lanceolate. Sepals 4.0-6.5(-7.2) mm long, lanceolate to ovate; petals white, 7-11 mm long, (4.5-)6.0-7.0(-7.5) mm broad; androecial corona 0.5-1.0 mm long; staminodes spatulate, 3.5-5.5(-7.5) mm long; fertile stamens 10; filaments (0.5-)0.8-1.5 mm long, sometimes dilated basally; anthers (1.3-)1.6-2.0(-2.8) mm long; ovary 5-ribbed to deeply 5-lobed; style (2.0-)3.0-4.0(-5.2) mm long with lobes 0.5-1.0 mm long. Fruit *c.* 8-12 mm in diameter, (3-)5-lobed, sparsely stellate-pubescent; fruit either shallowly lobed and becoming muricate during maturation or very deeply lobed and smooth-surfaced, frequently 3-4-lobed with unfertilized locules not developed; seeds broadly elliptical to rounded-oblong, 3.3-4.6 mm long, somewhat laterally compressed, dark brown, glossy, with irregular surface, sometimes with a shallow dorsal ridge.

KEY TO SUBSPECIES OF *DOMBEYA LINEARIFOLIA* HOCHR.

- 1. Young inflorescence variably stellate-pubescent; filaments more or less basally dilated; ovary deeply lobed; fruit deeply lobed, smooth-surfaced ..... 1a. subsp. *linearifolia*
- Young inflorescence and often other parts densely stellate-pubescent, with large multi-branched hairs; filaments broadening gradually towards base; ovary ribbed or shallowly lobed; fruit shallowly lobed, becoming muricate ..... 1b. subsp. *muricata* Appleq., subsp. nov.

1a. *Dombeya linearifolia* Hochr.  
subsp. *linearifolia*

*Annuaire du Conservatoire et du Jardin Botaniques de Genève* 11-12: 1 (1907). — Type: Madagascar, Prov. Antsiranana (bords de la baie de Lingvatou [12°26'S, 049°30'E]), fl., 1835, *Bernier 340* (2<sup>e</sup> envoi) pro min. parte (holo-, G [photo!]).

*Dombeya linearifolia* Hochr. subsp. *sely* Arènes, *Candollea* 16: 297 (1958). — Type: Madagascar, Prov. Antsiranana, Montagne des Français [12°22'S, 049°21'E], fl., 4.IV.1954, *Service Forestier 9734* (holo-, P!; iso-, P!).

ADDITIONAL MATERIAL EXAMINED. — **Madagascar.** Prov. Antsiranana, Montagne des Français (12°22'S,

049°21'E), fl., 16.III.1950, *Service Forestier 1285* (P, TAN). — Montagne des Français (12°22'S, 049°21'E), fl., 4.IV.1954, *Service Forestier 9734*, (P, 2 sheets). — Massif calcaire de la Montagne des Français, vallée de l'Andavakoera, fl., 24.II.1962, *Service Forestier 20920* (P, TAN). — Butte calcaire au P. K. 8 de la route de Diégo-Suarez-Orangea (12°15'S, 049°23'E), fr., 12.XII.1963, *Service Forestier 22943* (P). — Same loc., fl., 24.II.1964, *Service Forestier 23237* (P, TAN). — Same loc., fr., 10.V.1966, *Service Forestier 24629* (P, TAN).

DESCRIPTION

Tree to 6 m or large shrub. Young inflorescences stellate-pubescent, sometimes doubly stellate with some large erect hairs. Filaments abruptly dilated

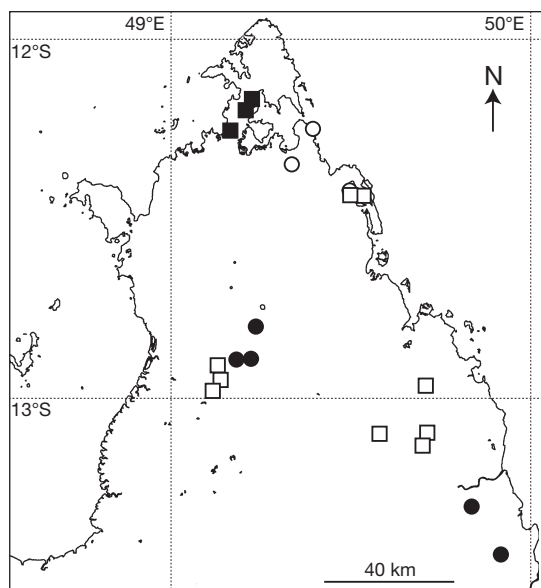


FIG. 1. — Distribution in extreme northern Madagascar of *Dombeya linearifolia* Hochr. subsp. *linearifolia* (○), *D. linearifolia* subsp. *muricata* Appleq., subsp. nov. (●), *D. rigida* Baill. subsp. *guazumifolia* (Baill.) Appleq., comb. nov., stat. nov. (□), and *D. rigida* subsp. *rigida* (■).

at the base, sometimes with paler wings. Ovary longitudinally compressed, deeply lobed. Fruit deeply 3-5-lobed, with unfertilized locules not developed, smooth-surfaced, light to dark brown; seeds lacking dorsal ridges.

REMARKS

Arènes (1958) recognized two subspecies of *D. linearifolia*: subsp. *linearifolia*, with narrowly oblong leaves and filaments with dilated bases, was known from the type and a specimen from Montagne des Français, whereas subsp. *sely*, described from the type alone, had lanceolate leaves to 3 cm broad and filaments not strongly dilated at the base. The two subspecies also were said to have moderate differences in the size of floral parts; more recent specimens display a range of variation encompassing that in Arènes' original descriptions. *Dombeya linearifolia* does encompass two morphologically distinct, possibly allopatric taxa, which are distinguished by ovary and fruit morphology and filament dilation. The populations around Antsiranana and Montagne des Français, herein

recognized as subsp. *linearifolia*, have longitudinally compressed, deeply lobed ovaries; deeply lobed, smooth-surfaced fruits; and filaments with dilated bases. Populations collected near Ankarana and Vohémar, herein recognized as subsp. *muricata*, have ribbed or shallowly lobed ovaries, strongly muricate fruits, and filaments not dilated at the base. No specimens from these areas were available to Arènes (1958). The unusually broad-leaved type of subsp. *sely* does have at least slightly dilated filaments and is referable to subsp. *linearifolia*. Leaf shape in *D. linearifolia* is not consistently correlated with other morphological characters or with geographic origin.

DISTRIBUTION

Extreme north of Madagascar, endemic to the areas around Antsiranana and Montagne des Français, usually on calcareous substrates (Fig. 1).

VERNACULAR NAMES

Sely (*Service Forestier* 9734), Dingadingana (*Service Forestier* 1285).

1b. *Dombeya linearifolia* Hochr.

subsp. *muricata* Appleq., subsp. nov.  
(Fig. 2)

*Haec subspecies a Dombeya linearifolia subsp. linearifolia filamentis non fortiter dilatatis ovario costato vel non profunde lobato fructu muricato differt.*

TYPUS. — Madagascar. Prov. Antsiranana, forêt d'Analafiana (13°26'S, 049°55'E), au N de la basse Manambery (au SW de Vohémar), fl., 11.III.1967, *Service Forestier* 27502, (holo-, P!; iso-, TAN!).

PARATYPES. — Madagascar. Prov. Antsiranana, plateau calcaire de l'Ankarana, à l'W d'Ambondromifehy (12°53'S, 049°12'E) (J.B. 8), fl., 24.IV.1963, *Service Forestier* 22697 (P, TAN). — Butte calcaire au S de Marotaolana (12°48'S, 049°14'E) (Anivorano-Nord), fl., 27.IV.1966, *Service Forestier* 24719 (P, TAN). — Same loc., fl., 27.IV.1966, *Service Forestier* 24719bis (P, TAN). — Versant E du massif de l'Ankarana (partie S du massif de Mafofoko [13°18'S, 049°50'E]), au N de Vohémar, 50-450 m, fr., 17.XII.1966, *Service Forestier* 27377 (P). — Same loc., fl., 12.III.1967, *Service Forestier* 27422. — Massif calcaire de l'Ankarana, aux environs d'Ambondromifehy (12°53'S, 049°12'E) (Anivorano-Nord), fl., fr., 7.VI.1970, *Service Forestier* 29211 (P).



FIG. 2. — *Dombeya linearifolia* subsp. *muricata* Appleq. subsp. nov.: **A**, flowering branch; **B**, flower; **C**, petal glands; **D**, old fruit; **E**, immature fruit; **F**, fruit of *Dombeya linearifolia* subsp. *linearifolia* for purposes of comparison. **A-C**, *Service Forestier* 27502; **D**, *Service Forestier* 27377; **E**, *Service Forestier* 29211; **F**, *Service Forestier* 24629. Scale bars: A, 2 cm; B, D, F, 5 mm; C, 1 mm; E, 2 mm. Drawing Barbara Alongi.

## DESCRIPTION

Tree to 8(-10) m. Young inflorescences densely stellate-pubescent, with some large erect hairs. Filaments wider at the base, tapering, not abruptly dilated. Ovary 5-ribbed or shallowly lobed. Fruit 5-lobed, becoming woody and muricate at maturity, dark brown; seeds sometimes have a shallow dorsal ridge.

## REMARKS

*Dombeya linearifolia* subsp. *muricata* may be distinguished from subsp. *linearifolia* primarily by its shallowly lobed ovary and muricate fruit, similar to those of *D. rigida*. Unlike *D. rigida*, discussed below, the seeds have at most a slight dorsal ridge and are not strongly flattened, although the ovules of one young fruit may have a shallow dorsal wing. The filaments of subsp. *muricata* are not conspicuously dilated. The inflorescences at flowering are always densely stellate-pubescent with very large erect multibranching hairs as well as smaller, flatter stellate hairs, a pubescence type that frequently extends to other parts such as young twigs and petioles, whereas the inflorescences of subsp. *linearifolia* are sometimes more sparsely pubescent, with few or no large erect hairs. Leaf veins of subsp. *muricata* seem to be more frequently darkened in herbarium specimens, although this could be an artifact of processing.

Vegetative features do not reliably distinguish the two subspecies. The full range of leaf shapes, from extreme *linearifolia* morphology (very narrow with parallel sides for almost all of the length) to larger, broader, and lanceolate, can be seen in each subspecies. By contrast, although the extremes of leaf size and shape and petiole length of *D. linearifolia* subsp. *muricata* and *D. rigida* subsp. *guazumifolia* (discussed below) appear to overlap, there is not in fact a continuum of variation encompassing those two taxa; they are easily distinguished in practice. The possibility that populations of subsp. *muricata* are conspecific with *D. rigida*, rather than *D. linearifolia*, is therefore rejected. For the same reason, these populations seem unlikely to represent recent interspecific hybrids, although they could potentially be of hybrid ancestry. Muricate fruits may well be the plesiomorphic condition in this

group, with small deeply lobed fruits arising as an autapomorphy only in subsp. *linearifolia*. Similarly conspicuous variation in fruit morphology among subspecies of a single species has been previously recognized (e.g., Aronson 1992), although it is unusual. A population genetic study of these taxa would be of interest.

## DISTRIBUTION

Northern Madagascar, with disjunct populations in the regions of Ankarana and Vohémar; usually on calcareous substrate (Fig. 1).

2. *Dombeya rigida* Baill.

## DESCRIPTION

Tree to 10(-12) m or rarely a shrub, to *c.* 20 cm dbh; bark gray-beige or gray; twigs dark brown. Leaves ovate to narrowly ovate or oblong-ovate, often somewhat asymmetrical; petioles 1-7 cm long; base shallowly cordate or occasionally shallowly oblique or rounded; apex acute to short-acuminate or rarely rounded-emarginate; margins crenate-serrate to crenulate; basal veins (very rarely 3-5(-7)); surfaces sparsely pubescent, mostly stellate, especially around large veins beneath, with hair clusters or small roofed domatia often present especially on larger leaves. Inflorescences lateral and sometimes pseudoterminal with usually 2 to several branches, rarely 1-branched, sparsely to densely stellate; peduncle (1.5-)3.0-7.5(-11.0) cm long, entire inflorescence (3-)6-12(-17) cm long; bracts lanceolate, occasionally subulate, 1.5-4.0 mm long; bracteoles (2.5-)3.0-4.0(-4.5) mm long, lanceolate to broadly elliptic or elliptic-obovate; pedicels 0.5-2.0(-2.5) mm long. Sepals (4.0-)4.5-6.5 mm long, lanceolate; petals white, creamy, or yellowish, sometimes yellow at the base, (6.5-)7-10(-10.5) mm long, (4.5-)6.0-8.0(-10.5) mm broad; androecial corona 0.3-0.6 mm long; staminodes usually opposite petals, sometimes in intermediate position or apparently opposite sepals, narrowly spatulate to elliptical, (3.5-)4.0-5.5(-6.5) mm long; fertile stamens 10(-20); filaments 0.5-2.0 mm long; anthers (1.0-)1.5-2.5 mm long, orange to light brown; ovary 5-ribbed, sometimes flattened; style



2.0-3.5(-4.3) mm long, often basally pubescent, with lobes 0.4-1.0 mm long; ovules bearing shallow marginal wing. Fruit (9-)11-15 mm in diameter, 5-ribbed to shallowly 5-lobed, becoming strongly

muricate during maturation, stellate-pubescent often becoming glabrous in old fruit; seeds broadly oblong-elliptical to orbicular, 3.0-5.1 mm long, laterally flattened, with shallow marginal wing.

KEY TO SUBSPECIES OF *DOMBEYA RIGIDA* BAILL.

1. Leaves oblong to oblong-lanceolate or oblong-ovate; endemic to extreme northern Madagascar ..... 2b. subsp. *guazumifolia* (Baill.) Appleq., comb. nov., stat. nov.  
— Leaves more or less ovate; range from extreme northern to southwestern Madagascar .....
2. Leaves (4.5-)7.0-13.0(-16.0) cm long, (2.0-)4.0-7.5(-9.0) cm broad; leaf apex acute to short-acuminate; peduncles usually > 4 cm long; inflorescences always with 2 or more branches ..... 2a. subsp. *rigida*  
— Leaves 3.5-8.5(-10.5) cm long, (1.2-)1.5-3.5(-4.5) cm broad; leaf apex acuminate to acute; peduncles usually <4 cm long; inflorescences (1-)2-branched .....  
..... 2c. subsp. *parvifolia* Appleq., subsp. nov.

2a. *Dombeya rigida* Baill. subsp. *rigida*

*Bulletin mensuel de la Société linnéenne de Paris* 1: 487 (1885).

TYPUS. — Madagascar. Prov. Mahajanga, Trabonji (15°49'S, 048°38'E), fl., V.1880, *Hildebrandt 3442* (holo-, P!; iso-, G [photo!]).

ADDITIONAL MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana, Andranovondronina, Antsisikala, Ambatoara (Analamangidy), 12°10'02"S, 049°13'06"E, 110 m, fl., fr., 15.V.2005, *Guittou et al. 111* (MO, P). — Andranovondronina, Antsisikala, Analamangidy, 12°10'04"S, 049°13'06"E, 112 m, fl., 17.V.2005, *Guittou et al. 113* (MO, P). — Andranovondronina, Antsisikala, à l'W d'Ampasikely, 12°11'35"S, 049°12'45"E, 197 m, fl., 13.V.2005, *Ramananjahary et al. 272* (MO, P). — Massif de l'Ambongoabo, entre la baie de Diégo et celle du Courrier (12°15'S, 049°10'E), fl., 21.IV.1966, *Service Forestier 24655* (P). — Prov. Mahajanga, rives de l'Anjobony (= Anjombony), Boisy, fr., VIII.1905, *Perrier de la Bâthie 5535* (P). — Boïna, haute Bemarivo, fl., fr., IV.1907, *Perrier de la Bâthie 12163* (P). — RN 8 (Namoroka, 16°26'S, 045°21'E), canton Anomavo, district Soalala, fl., 13.VII.1954, *Réserves Naturelles 6282* (P). — Canton Andromomano, district Soalala, fl., 12.V.1958, *Réserves Naturelles 10173* (P). — Ambalono, district Antsalova, Bemaraha Réserve (18°41'S, 044°46'E), 20.XII.1958, *Réserves Naturelles 10324* (MO, 2 sheets, P). — Tsingy de Namoroka (8° Réserve), fl., 1933?, *Service Forestier 31* (P). — Bord route vers Soalala, vallée Ambatofotaka, village Vilanandro-Andranomavo (16°30'S, 045°26'E), fl., 12.V.1958, *Service Forestier 48-RN VIII* (P). — Au bord de la rivière Harofototra, sur la route de Befandriana-Nord-Ambararatra, district

de Befandriana-Nord, 300 m, fl., fr., 4.VI.1951, *Service Forestier 3570* (P). — Environs de Morafinobe (= Morafenobe, 17°48'S, 044°55'E), fl., 26.V.1955, *Service Forestier 14121* (P). — Ambatolampikely (17°14'S, 047°30'E?), canton d'Ambalanjanakomby, district de Maevatanana, 20.IV.1955, *Service Forestier 14937* (MO, 2 sheets, P). — Analahafina, Analava (= Analava), fl., 15.VI.1955, *Service Forestier 15086* (MO, P, 3 sheets). — Forêt d'Andranomazava (14°22'S, 48°19'E), près d'Antsiamala, canton Ambararata, district Befandriana-Nord, fl., 12.VI.1956, *Service Forestier 15772* (MO, 2 sheets, P). — 12 km E Ankiliromotsy, 24 km SE Antsalova (18°51'S, 044°42'E), fl., 26.III.1993, *Villiers et al. 4887* (MO, P). — Prov. Toliara, environs d'Ankilivalo (Mahabo) (20°17'S, 044°38'E), 2.IV.1970, *Service Forestier 29149* (P).

DESCRIPTION

Leaves ovate, (4.5-)7.0-13.0(-16.0) cm long, (2.0-)4.0-7.5(-9.0) cm broad; petioles 1.5-5.0(-7.0) cm long, pubescent; leaf apices usually acute to short-acuminate, occasionally emarginate as an aberration; basal veins 5(-7). Inflorescences with at least two branches, 6-17 cm long at maturity, densely pubescent; peduncles (2.5-)3.5-7.5(-11.0) cm long. Fruit strongly ribbed to shallowly lobed, strongly muricate with rounded papillae, old fruit becoming glabrous.

REMARKS

As for most species of *Dombeya*, no fruit was known for *D. rigida* at the time of its description. Dorr

(2001) discovered a fruiting specimen at K (*Perrier de la Bâthie* 5535), which he was able to identify by vegetative features as belonging to *D. rigida*, with an unusual, strongly muricate capsule. Upon publishing this fruit description, he expressed some concern over the fact that the ovaries of *D. rigida* in flower give no evidence of bearing papillae. However, examination of available fruiting specimens at P reconfirms the correctness of Dorr's (2001) identification. In a single specimen of *D. rigida* bearing all stages of development from flowers to nearly mature fruit (*Perrier de la Bâthie* 12163), the ovary at anthesis is stellate-pubescent but not at all papillate; the papillae begin to appear during fruit development, and grow to a very conspicuous size in larger fruits. A similar but more extreme fruit type, with grossly elongated papillae, is seen in subsp. *guazumifolia*.

Leaves are reported to be caducous (*Service Forestier* 15772).

#### DISTRIBUTION

Widely distributed from extreme northern Madagascar to the middle western portion of the country. Habitat is in dry forest, particularly along rivers; reported substrates include alluvial soil, lateritic soil, silica, rocks, and tsingy.

#### VERNACULAR NAMES

Hafobalo (*Réserves Naturelles* 10173, *Service Forestier* 48-RN VIII), Selibe (*Service Forestier* 14121), Sely (*Guittou et al.* 113), Valoamboka (*Réserves Naturelles* 6282), Valovembaka (*Service Forestier* 15086, 15772).

#### 2b. *Dombeya rigida* Baill.

subsp. *guazumifolia* (Baill.) Appleq.,  
comb. et stat. nov.

BASIONYM. — *Dombeya guazumifolia* Baill., as "*guazumaefolia*", *Bulletin mensuel de la Société linnéenne de Paris* 1: 495 (1885).

TYPUS. — Madagascar. Prov. Antsiranana, bords de la baie de Lingvatou (12°26'S, 049°30'E), fl., 1835, *Bernier* 340 (2<sup>e</sup> envoi) pro max. parte (holo-, P!; iso-, P, 2 sheets!).

ADDITIONAL MATERIAL EXAMINED. — Madagascar. Prov. Antsiranana, Ambilobe, Mahamasina, Réserve Spéciale d'Ankarana, chemin d'Ambohimalaza, 12°58'22"S, 049°06'59"E, fl., fr., 28.III.2007, *Bardot-Vaucoulon et al.* 1587 (MO,P). — Baie de Rigny (12°26'S, 049°32'E), fl., 1846?, *Bernier* 2601 (P). — Dist. d'Ambilobe, montagne d'Andavakafanihy, calcaires de l'Ankarana, km 105 de la route d'Ambilobe, vers 200 m, fl., 3.II.1960, *Cours & Humbert* 5612 (P). — Sous-préfecture de Vohémar, commune rurale de Daraina, forêt de Solaniampilana-Maroadabo, à 350 m du point coté 214, au 266°, 13°06.2'S, 049°34.62'E, 200 m, 6.III.2004, *Gautier et al.* LG 4469 (MO). — Sous-préfecture de Vohémar, commune rurale de Daraina, forêt de Solaniampilana-Maroadabo, à 500 m du point coté 109, au 283°, 13°05.67'S, 049°34.85'E, 100 m, fr., 9.III.2004, *Gautier et al.* LG 4512 (MO). — Collines et plateaux calcaires de l'Ankarana (12°54'S, 049°08'E) du N, vers la grotte du Fanihy, 30-350 m, fr., 24.I-29.II.1960, *Humbert* 32710 (MO, P). — Mantamena, part of Bekaraoka Range, 7 km NE Daraina (Vohémar), 13°08'S, 049°42'E, 112-330 m, fr., IV.1990, *Meyers & Boltz* 107 (MO). — Sous-préfecture de Vohémar, commune rurale de Daraina, forêt de Bekaraoka, partie N, à 380 m du point coté 96, au 329°, 13°06.11'S, 49°42.39'E, 120 m, fl., 14.II.2004, *Nusbaumer & Ranirison* LN 1178 (MO). — Sous-préfecture de Vohémar, commune rurale de Daraina, forêt de Bekaraoka, partie N, à 320 m du point coté 138, au 171°, 13°05.5'S, 049°42.34'E, 380 m, 14.II.2004, *Ranirison & Nusbaumer* PR 447 (MO). — Daraina, forêt d'Ampondrabe, à 990 m du point coté 594, au 121°, 12°57.71'S, 049°42.34'E, 285 m, fr., 8.IV.2004, *Ranirison* PR 582 (MO). — Plateau calcaire de l'Ankarana, à l'W de Mahamasina (Antanatsimanaja) 12°57'S 049°08'E), fl., 23.IV.1963, *Service Forestier* 22680 (MO, P, 3 sheets).

#### DESCRIPTION

Leaves oblong to oblong-lanceolate or narrowly ovate or rarely oblong-obovate, 5.5-16.5(-19) cm long, 2.5-5.8(-7) cm broad; petioles (1.0-)2.0-5.7 cm long, sometimes only weakly pubescent; leaf apices acute to short-acuminate; basal veins usually 5(-7), very rarely 3. Inflorescences variable, usually with 1-2, sometimes few-flowered branches, occasionally multibranching with numerous flowers, 4-8(-14) cm long, more or less pubescent; peduncles 1.5-3.5(-5.0) cm long. Fruits irregularly lobed, usually strongly muricate with often elongated acute papillae (to 4 mm long), rarely not muricate, remaining densely stellate at fruit maturity; old fruit not seen.

## REMARKS

*Dombeya rigida* subsp. *guazumifolia* is characterized by the usually more or less oblong shape of its leaves, whereas both of the other subspecies have ovate leaves. The leaves are as long as those in subsp. *rigida* or longer, but are proportionally narrower (with the length of the larger leaves being two to three times the width) and sometimes have fewer basal veins. This subspecies also has smaller inflorescences than subsp. *rigida* and sometimes less dense pubescence. The mature fruit morphology is sometimes more extreme, with prominently elongated, acute, irregularly curved papillae, and remains stellate at least to the time of dehiscence; however, one collection (*Bardot-Vaucoulon et al.* 1587) has immature fruits to 9 mm diameter, irregularly lobed and shallowly ridged, with at most small and inconspicuous papillae. This subspecies is confined to the extreme north of Madagascar, where it occurs in close proximity to the northernmost populations of typical subsp. *rigida*. Two collections, including, unfortunately, the type, as well as one collection from the Daraina region (*Gautier et al.* 4512), have variable leaf shape, which ranges from ovate to oblong (or, in one leaf of the latter collection, obovate-oblong); these may represent intermediates between the two morphotypes due to gene flow between subspecies.

*Dombeya rigida* subsp. *guazumifolia* is known to occur sympatrically with *D. linearifolia*; the types of the two taxa derive from a single collection. These taxa are presumed to be capable of hybridization, and *Bardot-Vaucoulon et al.* 1587, having non-muricate fruit and sometimes greatly elongated leaves, is potentially of hybrid origin.

Fruits of *Dombeya rigida* subsp. *guazumifolia* are eaten by *Propithecus tattersalli* (*Meyers & Boltz* 107). Following Art. 60.8 of the ICBN (*McNeill et al.* 2006), the original spelling of the epithet is treated as an orthographical error to be corrected.

## DISTRIBUTION

Confined to extreme northern Madagascar (Fig. 1). Common habitat is in dry forest, including gallery forest, often associated with mountains or massifs; it seems to occur most frequently on limestone substrates and probably near watercourses.

## VERNACULAR NAMES

Sely-bara (*Meyers & Boltz* 107).

2c. *Dombeya rigida* Baill. subsp. *parvifolia*  
Appleg., subsp. nov.  
(Fig. 3)

*Haec subspecies a Dombeya rigida subsp. rigida foliis minoribus apice saepius acuminato atque inflorescentiis minoribus differt.*

TYPUS. — Madagascar. Prov. Toliara, près d'Ankazoabo (22°17'S, 044°31'E), fl., II.1963, *Bosser* 17502 (holo-, P!).

PARATYPES. — Madagascar. Prov. Fianarantsoa, PK 40 route Ihoso-Ivohibe, 22.II.1964, *Peltier & Peltier* 4381 (MO). — Bassin de la Menarahaka, près du carrefour des routes d'Ihoso à Ivohibe et Iakora (22°35'S, 046°30'E), 650 m, fl., s.d., *Service Forestier* 22630 (MO 2 sheets, P 2 sheets). — 10 km NE d'Ihoso, entre Ihoso et Ambarara (22°20'S, 046°12'E), fl. 22.II.1970, *Service Forestier* 29070 (P). — Prov. Toliara, forêt d'Analavelona au N du Fiherenana (22°37'S, 044°12'E), 950-1250 m, fl., III.1934, *Humbert* 14201 (P). — Ambinda (23°40'S, 044°38'E), fl., 30.III.1966, *Peltier & Peltier* 5767 (P). — Ankazoabo-Betsako (22°21'S, 044°42'30"E), fl., 12.II.1952, *Service Forestier* 4526 (P). — Analavelona (22°37'S, 044°12'E), fr., 2.VI.1952, *Service Forestier* 5260 (MO, P).

## DESCRIPTION

Small tree or large (4-5 m) shrub. Leaves (3.5-)4.5-8.5(-10.5) cm long, (1.2-)2.2-3.5(-4.5) cm broad; petioles (1.5-)2.5-4.5 cm long, slender, moderately pubescent; leaf apices usually acuminate, sometimes acute; basal veins 5(-7). Inflorescences (1-)2-branched, 5-9(-13) cm long, more or less pubescent; peduncles 2.0-5.0(-6.5) cm long, slender; branches thickening and becoming glabrous in fruit. Fruit irregularly lobed, muricate with rounded papillae; seeds possibly unwinged.

## REMARKS

The ovate leaves of *Dombeya rigida* subsp. *parvifolia* are smaller and proportionally somewhat narrower than those of subsp. *rigida*, and are more often acuminate; the petioles are more slender than in subsp. *rigida* and the ratio of petiole length to leaf length is on average longer. The inflorescences also are on average smaller, fewer in number, and less

heavily pubescent, and the ovary is somewhat more longitudinally compressed. The two are virtually identical in other characters. There is a geographical separation between subsp. *parvifolia*, which is native to the southwest (with known latitudes between 22°17' and 23°40'S), and the more broadly distributed subsp. *rigida* (with known latitudes from 11°58' to 18°51'S, and one outlying population with leaves of relatively modest size, perhaps an intermediate or of questionable identity, at 20°17'S). *Dombeya rigida* subsp. *parvifolia* appears to have a shorter and earlier flowering period, in February through March, which is common in southwestern taxa due to the very limited rainy season; subsp. *rigida* flowers from February through July, with most flowering from April through June. The combination of morphological differentiation and geographical separation indicates that recognition of these populations as a subspecies is warranted, although this subspecies is less distinctive than is the northern subsp. *guazumifolia*.

#### DISTRIBUTION

Native to southwestern Madagascar, usually in dry forest, also in the semi-humid forest of Analavelona. Substrate is variable, reported to be basalt and sandstone at Analavelona; easternmost collections are probably on sand.

#### VERNACULAR NAMES

Selinala (*Service Forestier* 5260), Selyfamonty (*Service Forestier* 4526).

#### POSSIBLE INTERSPECIFIC HYBRIDS

Madagascar: Prov. Antsiranana: DIANA region, Ankarongana, forêt sur sable, Analafandro, 12°37'38"S, 049°31'37"E, 71 m, fl., 25.II.2006, *Andrianjafy et al.* 1632 (MO, 3 sheets); Montagne des Français, Diego-Suarez, fl., 25.V.1955, *Service Forestier* 14228 (MO, P).

#### DISCUSSION

Two putative hybrids having characters typical of subsect. *Rigidae*, such as glandular petals, are observed from the extreme north of Madagascar;

both are believed to be hybrids involving *D. rigida*, which occurs near both localities, and unidentified species of *Dombeya* (not *D. linearifolia*). *Service Forestier* 14228 has oblong to oblong-elliptical leaves, with rounded bases and short-cuspidate apices, and small inflorescences with large flowers and short, thickened pedicels, peduncles, and branches, all of which are densely stellate with unusually long reddish hairs. The second parent is presumed to belong to *Dombeya* subg. *Dombeya*. Alternatively, this specimen could be an unrecognized local endemic species of subsect. *Rigidae*, although the fact that no similar material has been found in the numerous collections since made from Montagne des Français makes this possibility less likely.

*Andrianjafy et al.* 1632 (of which other duplicates were sent to CNARP, P, and TAN) has inflorescences and flowers similar to those of *D. rigida*, but the leaves are very numerous and small (most under 4.5 cm), broadly ovate-acuminate and strongly cordate, with only a few lateral leaf veins, the domatia consisting of relatively prominent hairy clefts. This specimen's second parent is predicted to be a *Dombeya* species with small, strongly cordate leaves, probably lacking dense leaf indument (because the specimen's leaves are glabrate at maturity). Since closely related species known to occur in the north do not fit this description, the second parent is likely to be a more distantly related species, indicating that hybridization may occur between normally well-distinguished lineages.

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FIG. 3. — *Dombeya rigida* subsp. *parvifolia* Appleg., subsp. nov.: **A**, flowering branch; **B**, flower; **C**, section of androecium and gynoecium; **D**, inflorescence; **E**, fruit. **A-D**, Bosser 17502; **E**, Service Forestier 5260. Scale bars: A, 2 cm; B, C, 2 mm; D, 1 cm; E, 5 mm. Drawing Barbara Alongi.

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