

Classification of Boraginaceae subfam. Ehretioideae: Resurrection of the genus *Hilsenbergia* Tausch ex Meisn.

James S. MILLER

Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 U.S.A.
james.miller@mobot.org

ABSTRACT

The genus *Hilsenbergia* (Boraginaceae: Ehretioideae) is resurrected to accommodate a group of east African and west Indian Ocean species that have been included in *Ehretia* or *Bourreria* by other authors. These species differ from the pantropical *Ehretia* in having 4 winged to ridged pyrenes in the fruit, flowers with valvate calyx lobes, and fleshy, urceolate corollas. *Hilsenbergia* differs from the Neotropical *Bourreria* in having fruits that lack a fibrous connection between the apex of the pyrenes and the gynobase and having smaller flowers with urceolate corollas, as well as in its African/Indian Ocean distribution. As defined here, *Hilsenbergia* consists of 18 species, 13 of which are endemic to Madagascar and all of these are newly described. A key and nomenclatural notes for all species and full descriptions for the thirteen new species that are described are provided. Conservation analyses indicate that all of the *Hilsenbergia* species from Madagascar are threatened and five species are critically endangered and nine are endangered.

KEY WORDS

Hilsenbergia,
Ehretia,
Boraginaceae,
Madagascar,
Conservation.

RÉSUMÉ

Classification des Boraginaceae subfam. Ehretioideae : Réhabilitation du genre Hilsenbergia Tausch ex Meisn.

Le genre *Hilsenbergia* (Boraginaceae : Ehretioideae) est réhabilité pour un groupe d'espèces d'Afrique orientale et de l'ouest de l'Océan Indien qui ont été placées dans *Ehretia* ou *Bourreria* par divers auteurs. Ces espèces diffèrent du genre pantropical *Ehretia* par les pyrènes du fruit ornées de 4 côtes ailées, et les fleurs à lobes du calice valvaires et une corolle charnue urcéolée. *Hilsenbergia* se distingue du genre néotropical *Bourreria* par des fruits qui ne présentent pas une connection fibreuse entre les sommets des pyrènes et la gynobase, et par des fleurs plus petites à corolle urcéolée, ainsi que par sa répartition en Afrique et dans l'Océan Indien. Ainsi défini, *Hilsenbergia* comprend 18 espèces, dont 13 endémiques de Madagascar toutes décrites ici. Une clé des espèces et des notes nomenclaturales, sont présentées pour toutes les espèces ; une description complète est donnée pour chaque nouveau taxon. Des analyses pour la conservation indiquent que toutes les espèces malgaches de *Hilsenbergia* sont menacées, dont cinq en danger critique et neuf en danger.

MOTS CLÉS

Hilsenbergia,
Ehretia,
Boraginaceae,
Madagascar,
Conservation.

The nearly ubiquitous Boraginaceae have been thought of as a family with five subfamilies by most recent authors (e.g. MILLER 1989), including the largely tropical Ehretioideae, Cordioideae, and Heliotropioideae, the mostly temperate Boraginoideae, and the monogeneric Wellstedtioideae from Socotra, east, and southern Africa. However, recent molecular data (FERGUSON 1999) suggest that Boraginaceae are paraphyletic if Hydrophyllaceae and Lennoaceae are not included.

While four subfamilies of Boraginaceae are well defined by morphological synapomorphies, Ehretioideae are diverse morphologically and have included mostly woody genera, all with a bifid style and abundant endosperm, characters that are probably all ancestral within the family. Ehretioideae have been defined as consisting of eleven genera (MILLER 1989). Recent molecular evidence (OLMSTEAD pers. comm.) indicates that *Pteleocarpa* Oliv. is most closely related to *Gelsemium* Juss. and *Mostuea* Didr., two genera traditionally placed in Loganiaceae but segregated as Gelsemiaceae based on recently available molecular data (STRUWE et al. 1994). *Coldenia* L., a monospecific, anomalous annual, often allied with *Tiquilia* Pers. (RICHARDSON 1976), appears to be sister to Cordioideae and best placed with the genera of that subfamily. *Tiquilia*, traditionally considered sister to *Coldenia*, is a genus of new world desert plants with separate, dry nutlets and is quite distinct in the subfamily. *Cortesia* Cav. (Argentinian) and *Halganina* Gaudich. (Australian) are both sclerophyllous-leaved shrubs that appear distinct within Ehretioideae. Recently available data suggest *Halganina* is sister to *Tiquilia* and distinct from the woody genera. Furthermore, *Cortesia* appears to be nested within *Ehretia* P. Br. (GOTTSCHLING pers. comm.) and that its distinctive morphological features may be due to adaptation to an extreme, saline habitat.

The remaining six genera are a group of tropical trees and shrubs that form a confusing complex including *Ehretia*, *Bourreria* P. Br., *Rotula* Lour., *Carmona* Cav., *Lepidocordia* Ducke, and *Rochefortia* Sw. Their relationships are not at all clear and circumscription of genera in the group has been interpreted differently by various

authors. ITS1 data (GOTTSCHLING & HILGER 2001) for these genera indicate that *Carmona* and *Rotula* are nested in *Ehretia*. This prompted GOTTSCHLING & HILGER (2001) to include both of them within a broadly defined *Ehretia*. *Lepidocordia*, including *Antrophora* I.M. Johnst. (MILLER & NOWICKE 1990), and *Rochefortia* are sister to *Bourreria*. *Lepidocordia* is distinct from *Bourreria* in being dioecious and *Rochefortia* differs in being both dioecious and spiny.

Ehretia and *Bourreria* together comprise nearly 100 species and account for almost all of the species within this complex of genera, so the placement of their constituent species is critical to resolving generic limits within Ehretioideae. Early authors included most of the species in this group in a broadly defined *Ehretia* (e.g. BENTHAM & HOOKER 1876) but modern authors have frequently chosen to elevate these taxa to generic rank.

Patrick BROWNE published polynomial names in *Ehretia* and *Bourreria*, the former named in honor of George Dionysius EHRET, who illustrated of his treatise on the natural history of Jamaica (BROWNE 1756). *Ehretia* was later validated by LINNAEUS (1759), who created the binomial *Ehretia tinifolia* L. The history of *Bourreria* is more complex. EHRET published a plate in his *Plantae et Papiliones Rariores* (EHRET 1755) with the diagnosis for a new genus named in honor of his friend, J.A. BEURER, a noted pharmacist in Nuremberg. BROWNE (1756), describing another genus, published *Bourreria*, based on a misspelling, accredited to EHRET's friend "Mr. BOURER", which led to many orthographic variants as authors attempted to correct this in ensuing years (reviewed by STEARN 1971). BROWNE's original generic name *Bourreria* was conserved over all of these orthographic variants and also over *Beurrieria* Ehret, now considered to be *Calycanthus floridus* L. BROWNE's *Bourreria* was validated by RAFINESQUE (1838), who published *B. baccata* based on the Linnaean names *Cordia bourreria* (LINNAEUS 1759) and *Ehretia bourreria* (LINNAEUS 1762).

Ensuing authors struggled with generic delimitation, differed widely in their definition of *Ehretia* and *Bourreria*, and published geographic reviews that treated species from only portions of

the range of the genera, but DE CANDOLLE (1845) provided the first comprehensive taxonomic review of Ehretioideae. He defined the genus *Ehretia* in a very broad sense, including *Bourreria*, *Rochefortia*, *Carmona*, and *Rotula*. His section *Bourrerioides* consisted primarily of species later authors assigned to *Bourreria*, with a few other *Bourreria* species scattered among other sections. His other three sections do not correspond well with modern ideas of relationship within the group.

John MIERS (1869) reviewed all of the New World species of *Bourreria*, breaking the genus in two and recognizing the segregate *Crematomia* Miers. He provides a very detailed morphological review of the group, although his attention to detail resulted in the description of narrowly delimited species beyond what later authors have been willing to accept. SCHULZ (1911) provided a thorough review of the Caribbean species. Although BENTHAM & HOOKER (1876) followed DE CANDOLLE (1845) in including most of these genera in a broadly defined *Ehretia*, their assignment of species to sections *Euehretia*, *Carmona*, and *Bourrerioides* more closely resembles how these groups have been defined by subsequent authors.

The small genera that are closely related to *Ehretia* were mostly described in the late 1700s: *Rochefortia* (SWARTZ 1788), *Rotula* (LOUREIRO 1790), and *Carmona* (CAVANILLES 1799). DUCKE (1925) described *Lepidocordia* from Venezuela and JOHNSTON (1950) described *Antrophora* from Nicaragua, noting that the two were closely related; they were later combined by MILLER & NOWICKE (1990).

Ivan JOHNSTON, the great student of Boraginaceae whose publications dominate study of the family from the 1920s into the 1960s, provided no overview of the problem of delimiting woody genera of Ehretioideae. His assignment of species, however, indicates that he accepted *Bourreria* as distinct from *Ehretia* following SCHULZ (1911) and that he also accepted the segregates *Rochefortia*, *Carmona*, and *Rotula* (JOHNSTON 1949, 1951).

Bourreria has traditionally been defined as a group Neotropical species centered in the

Caribbean (SCHULZ 1911). THULIN (1987) recognized that *Ehretia petiolaris*, and four of its east African relatives, share valvate calyx lobes and ridged endocarps with *Bourreria* and transferred the five species from *Ehretia* to *Bourreria*. GOTTSCHLING & HILGER (2001) published ITS1 sequence data that supported THULIN's hypothesis that the five African species were more closely related to *Bourreria* than they were to *Ehretia*, but also demonstrated that the African and the New World species represented different clades. While the New and Old World members of this *Bourreria* clade share many features, and molecular data confirm their close relationship, they are quite different morphologically and the African species are separated here in the genus *Hilsenbergia* Tausch ex Meisn.

GOTTSCHLING & HILGER's (2001) data also demonstrated that *Ehretia*, excluding the species that THULIN (1987) transferred to *Bourreria*, consists of two distinct clades, one with endocarps that break into four pyrenes at maturity and the other in which endocarps break into two 2-seeded units or remain entire. In their analysis, *Carmona* was basal to one of these clades and *Rotula* was basal to the other, thus their recognition would result in a paraphyletic *Ehretia* or require segregate generic status for the clade characterized by having the endocarp break into four parts at maturity.

RESURRECTION OF THE GENUS *HILSENBERGIA*

The molecular data presently available are not comprehensive enough to resolve all of the problems of generic circumscription within Ehretioideae, but they do support several changes in generic delimitation and subfamilial placement that differ from what has recently been accepted (e.g. MILLER 1989). The analyses of GOTTSCHLING & HILGER (2001) and GOTTSCHLING (pers. comm.) distinguish four clades within Ehretioideae. *Tiquilia* and *Halgania* are each distinct from the arborescent genera. A broad *Ehretia* clade also contains *Carmona* and *Rotula* and a broad *Bourreria* clade has *Lepidocordia* and *Rochefortia* as sister taxa. The

broad *Ehretia* clade consists of three distinct lineages of *Ehretia* species and also includes *Carmona* and *Rotula*. The *Ehretia* I subclade includes African, Indian Ocean, and Asian species with endocarps that break into four single-seeded pyrenes at maturity. The *Ehretia* II subclade includes American and Asian species with endocarps that mature with two 2-seeded endocarps in each fruit and the third subclade consists of *Ehretia longiflora* (GOTTSCHLING pers. comm.), which has an endocarp that remains entire at maturity. *Rotula* is sister to the *Ehretia* I clade and *Carmona* may be as well, although its position is not entirely resolved. Based on these data, GOTTSCHLING & HILGER chose to accept a broadly defined *Ehretia* that included both *Carmona* and *Rotula*.

The *Bourreria* clade likewise contains three lineages. The first subclade includes *Lepidocordia* and *Rochefortia*, which are sister to one another and form a group that is in turn sister to the remaining species. These two genera are morphologically distinct as both are dioecious and

Rochefortia differs further in possessing spines. The second subclade consists of New World *Bourreria*, with leathery, rotate to funnellform corollas, and the third comprises the African and Indian Ocean island species and their relatives in Madagascar, with fleshy, urceolate to campanulate corollas. The third subclade contains the group of species that THULIN (1987) included in *Bourreria*. Because each subclade is both morphologically and geographically coherent, maintaining them in a single, broadly-defined genus would unnecessarily obscure meaningful groups. The alternative approach, in which each subclade is treated as a separate, easily recognized genus, is considered more informative, and is adopted here. Thus *Rochefortia* and *Lepidocordia* are maintained, and *Bourreria* is restricted to the New World, with the Old World species comprising the genus *Hilsenbergia*.

This circumscription of genera differs from previous classifications (e.g. JOHNSTON 1949, 1951; MILLER 1989) so the following key is provided as a synopsis of the subfamily.

Key to genera of Ehretioideae

- | | |
|-------------------------------------------------------------------------------------------|---------------------|
| 1. Fruits dry, of 4 separate nutlets; North and South American deserts | Tiquilia |
| 1'. Fruits fleshy, at least when young | 2 |
| 2. Leaves sclerophyllous; low shrubs | 3 |
| 2'. Leaves membranaceous to coriaceous; erect shrubs or trees | 4 |
| 3. Anthers free; Argentina | Cortesia |
| 3'. Anthers connate in a cone surrounding the style; Australia | Halgania |
| 4. Flowers unisexual, the plants dioecious; New World tropics | 5 |
| 4'. Flowers all bisexual; the plants hermaphroditic | 6 |
| 5. Plants without spines; endocarps remaining entire at maturity | Lepidocordia |
| 5'. Plants with spines; endocarps dividing into 4 single-seeded pyrenes at maturity | Rochefortia |
| 6. Calyx lobes imbricate; outer surface of endocarp smooth to ridged | Ehretia s.l. |
| 6'. Calyx lobes valvate; outer surface of endocarp ridged to winged | 7 |
| 7. Corollas urceolate to campanulate; Africa and Indian Ocean Islands | Hilsenbergia |
| 7'. Corollas rotate to funnellform; Neotropics | Bourreria |

MORPHOLOGY

Habit

All species of *Hilsenbergia* are trees or shrubs, ranging from densely branched shrubs of extreme dry habitats (e.g. *H. leslieae* J.S. Mill.) to trees, the largest of which (*H. labatii*) may reach 20 m

tall and 60 cm dbh. The Malagasy species of *Hilsenbergia* span the full range of variation in size and growth form. Notes on the characteristics of bark are seldom included on specimen labels, but the limited information available from specimens and supplemental field observations demonstrate that some species of *Hilsenbergia* have exfoliating bark (CAPURON was exceptional

in noting “écorce platanoïde” on numerous specimens). This character is shared with some species of *Bourreria* from Central America, but is unknown in *Ehretia* or in other genera of Ehretioideae.

Inflorescence

Species of *Hilsenbergia* have cymose inflorescences that vary from terminal to subterminal. In some species, such as *H. lesliae*, the cymes are reduced and flowers are borne in small clusters or are solitary. *Hilsenbergia apetala*, *H. labatii*, and *H. randrianasoloana* have inflorescences in which the lateral branches are absent or significantly reduced so that they appear racemose or nearly so. In general, inflorescences of *Hilsenbergia* lack bracts, but *H. moratiana* is characterized by having small leafy bracts scattered among the inflorescence branches.

Flowers

The flowers of *Hilsenbergia*, *Bourreria*, and *Ehretia*, are quite different in size and form. In general, all three genera have bisexual flowers except for two *Hilsenbergia* species that appear to have at least some dioecious populations, *H. capuronii* and the Madagascar populations of *H. lyciacea*. Illustrations of *Hilsenbergia* flowers are included here as Figs. 5B, 9B, 10B, 12B, 13B, and 15B; illustrations of flowers of *Ehretia* may be seen in MILLER (2002), and those of *Bourreria* may be seen in LOTT & MILLER (1986), MILLER & SIROT (1997), and MILLER (1999).

Calyx

One of the primary characters that THULIN (1987) used to support his transfer of five east African species from *Ehretia* to *Bourreria* was their valvate, triangular calyx lobes. *Bourreria* (restricted here to the Neotropical species) and *Hilsenbergia* are the only genera of Ehretioideae that have calyces that are valvate in bud, with lobes that are less than half the length of the calyx. The calyx lobes of *Ehretia*, and the other woody genera

of Ehretioideae, are imbricate and usually divided nearly to the base. The calyces of *Hilsenbergia* and *Bourreria* are unique among Ehretioideae in having a prominent sericeous indument on the interior surface, and they are more coriaceous than the calyces of other woody Ehretioideae. *Hilsenbergia* has almost uniformly campanulate calyces that are evenly 5-lobed while *Bourreria* differs in having calyces that are generally tubular and often with a reduced number of lobes.

Corolla

Hilsenbergia has small corollas (less than 7.5 mm long) that are urceolate, or less commonly campanulate, with short lobes that are wider than long, and not acute at the apex. The lobes vary from erect through reflexed and the texture of the corolla is usually fleshy. The corolla of *H. apetala* is unique among Boraginaceae in being reduced to a ring of tissue connecting the staminal filaments and completely lacking elongated corolla lobes. *Bourreria* has larger (mostly 10-90 mm long), usually rotate corollas with spreading lobes that are usually at least as long as wide and acute at the apex. The corollas of the larger-flowered species of *Bourreria*, in particular, may be almost leathery. The corolla of *Ehretia* is usually small (mostly less than 5 mm, although up to 10 mm in *E. longiflora* Champ. ex Benth. of China), tubular with spreading to reflexed lobes that are almost always longer than wide and variable at the apex. *Ehretia* has thin, often membranaceous corollas with a tube that dries white or nearly transparent in herbarium material.

Stamens

The stamens of both *Hilsenbergia* and *Bourreria* are generally included in the corolla tube or borne in the mouth. The filaments are adnate to the corolla tube for nearly their full length, with only a short portion of the apex free. They may be either pubescent or glabrous at the point of insertion. In contrast, the stamens of *Ehretia* are usually prominently exserted. The base of the filaments is adnate to the corolla in *Ehretia*, but a substantial portion

is generally free, holding the anthers well above the mouth of the corolla. The filaments of *Ehretia* are glabrous at the point of insertion.

Gynoecium

Hilsenbergia usually has an ovoid ovary with a short style that is divided only near the apex or is undivided with two stigmas that are borne laterally on the style apex. Two African species, *H. lyciacea* and *H. orbicularis*, have styles that are more deeply divided and are more distinctly two-branched (THULIN 1987). *Bourreria* and *Ehretia* have ovoid ovaries with styles that are more deeply divided, often about half of the length, with each branch ending in a small, capitate stigma.

Fruits

The structure of the fruits, particularly the sculpturing of the endocarps, varies considerably between *Hilsenbergia*, *Bourreria*, and *Ehretia*. All three genera share a more or less drupaceous fruit with a thin endocarp (leathery in some species of *Hilsenbergia* and *Bourreria*), a thin to mucilaginous mesocarp, and a bony endocarp that at maturity divides into 2 or 4 parts, or less frequently remains entire. *Hilsenbergia* and *Bourreria* have endocarps that always divide into four single-seeded pyrenes, whereas *Ehretia* has more variable endocarps and two distinct clades may be defined on the basis of how they break up at maturity (GOTTSCHLING & HILGER 2001). One clade, restricted to the Old World and including all of the Malagasy species, has an endocarp that divides into four single-seeded pyrenes at maturity, while the second clade, with species in both hemispheres, but absent from Africa, has endocarps that divide into two 2-seeded pyrenes at maturity or remain entire and 4-locular.

In *Hilsenbergia* and *Ehretia*, the pyrenes are attached to the gynobase dorsally, as they are in most other genera of Ehretioideae. In most species of *Bourreria*, however, the pyrenes are attached apically by a fiber than runs the length of the dorsal surface to a basal attachment with the gynobase, a unique feature in Ehretioideae.

Endocarps in *Ehretia* have a dorsal surface that is usually reticulate but occasionally smooth. The dorsal surface of endocarps in *Hilsenbergia* and *Bourreria* varies from having a series of thick, parallel ridges to possessing lamellae, with a series of parallel wings.

CONSERVATION STATUS OF *HILSENBERGIA* IN MADAGASCAR

All of the fourteen species of *Hilsenbergia* that occur in Madagascar are endemic, except *H. lyciacea*, which also occurs in Kenya, Ethiopia, and Somalia. None of the fourteen species that occur in Madagascar are common and widespread and none have been observed to be locally abundant or dominant in the habitats where they occur. Locality data from available herbarium specimens have been analyzed to generate a preliminary measure of the risk of extinction of each species following the IUCN Red List Categories and Criteria (IUCN 2001). The results of these analyses are presented in Table 1 and a detailed discussion follows the taxonomic treatment for each species.

The estimates of conservation status made here are based entirely on specimen data. Field studies to determine abundance and patterns of change over time have not yet been conducted and will be necessary to confirm the provisional assignments that are provided here. However, it is clear from fieldwork in the area surrounding Tuléar that the dry forests of the area are being seriously degraded by collection of firewood and wood to prepare charcoal. Even in areas that remain forested, it is clear that species with hard wood are being selectively removed to produce charcoal and this is seriously altering the floristic composition of these forests. *Hilsenbergia lowryana* was apparently common in forests east of Tuléar, having been collected multiple times near Route Nationale 7 in the 1950s and 1960s, but numerous recent efforts failed to locate plants near the road. Interviews with local people, however, revealed that they know the species by its vernacular name, *Lambotaha*, that they value it as a firewood, and they confirm that it used to occur near the road but now can be

TABLE 1. — Collection and conservation information for the species of *Hilsenbergia* in Madagascar. Extent of occurrence is indicated in km² and Area of occupancy in 10 km² grid cells occupied. Conservation status follows IUCN (2001).

Species	Number of collections	Most recent 2 collections	Extent of occurrence	Area of occupancy	IUCN Red List Category
<i>H. angustifolia</i>	1	1965	0	1	CR
<i>H. apetala</i>	5	1996; 1965	15100	5	EN
<i>H. bosseri</i>	30	2003; 2000	61246	22	EN
<i>H. capuronii</i>	9	2003; 1969	111159	7	EN
<i>H. comorensis</i>	2	1997; 1996	0	1	CR
<i>H. croatii</i>	15	1993; 1990	10977	9	EN
<i>H. darcyana</i>	10	1968; 1955	234965	6	EN
<i>H. labatii</i>	7	1996; 1992	43554	6	EN
<i>H. leslieae</i>	11	1990; 1988	22621	6	EN
<i>H. lowryana</i>	13	2003; 1969	18983	12	EN
<i>H. lyciacea</i>	21	2003; 1995	30432	14	EN
<i>H. moratiana</i>	6	1969; 1966	17307	4	CR
<i>H. randrianasoloana</i>	3	1966; 1956	7582	3	CR
<i>H. schatziana</i>	4	1967; 1954	89	2	CR

found only in remote forest patches. The forests of southern Madagascar are tremendously threatened (DU PUY & MOAT 1996), but this pattern of selective removal of useful plants suggests that the most valued species may face acute threat even in areas where vegetation appears to remain intact.

SYSTEMATIC TREATMENT

HILSENBERGIA Tausch ex Meisn.

Pl. Vasc. Gen. Comment.: 198 (1840); Reichenbach, Consp. Reg. Veg.: 117 (1828); De Candolle, Prodr. 13: 478 (1852).

Trees or shrubs, often multi-stemmed; glabrous or with an indument of simple hairs. Leaves alternate, or clustered near the apices of short lateral branches, the margin entire, sometimes revolute, the venation pinnate, brochidromous, petiolate, the petioles generally adaxially canaliculate.

Inflorescences terminal, cymose to paniculate, occasionally nearly racemose or reduced to 1-3 flowers. Flowers bisexual, or possible unisexual and the plants dioecious in *H. capuronii* and *H. lyciacea*; calyx 5-lobed, valvate in bud, pubescent inside; corolla white, urceolate with 5 spreading to reflexed lobes, these much shorter than the tube; stamens 5, included or slightly exerted, the filaments glabrous or pubescent at the point of insertion the anthers oblong to ellipsoid; ovary ovoid, 4-locular, the style 1, terminal, bifid, the stigmas 2, clavate to capitate.

Fruits drupaceous, ovoid to nearly spherical, the exocarp thin to leathery, mesocarp usually sparse, fleshy, the endocarp separating into 4, 1-seeded pyrenes, these winged or ridged on the exterior surface.

TYPE. — *Hilsenbergia ehretia* Tausch ex Meisn.

The genus *Hilsenbergia* consists of 18 species from east Africa, Madagascar, the Comores, and the Mascarenes.

Key to the species of *Hilsenbergia*

1. Leaf blades glabrous or nearly so on both surfaces 2
- 1'. Leaf blades evidently pubescent on one or both surfaces 11
2. Inflorescences paniculate, with a distinct central rachis, many-flowered (northern Madagascar) 8. *H. labatii*
- 2'. Inflorescences cymose or flowers in fascicles of 1-4 3

3. Densely branched shrubs or small trees, leaves less than 2(-3) cm long; fruits less than 5 mm in diam. (southern Madagascar) 4
- 3'. More laxly branched shrubs or trees, leaves greater than (2.4-)3 cm long; fruits greater than 6 mm in diam. 5
4. Petioles more or less equal to the blade in length; leaf blades more or less as broad as long 6. *H. croatii*
- 4'. Petioles about half as long as the leaf blade or less; leaf blades about twice as long as wide 9. *H. lesliae*
5. Leaf blades usually less than 5 cm long; shrubs or small trees of dry forests south of 22°S latitude in Madagascar 3. *H. bosseri*
- 5'. Leaf blades usually greater than 5 cm long; trees or occasionally shrubs of various habitats in east Africa, Mascarenes, or north of 22°S latitude in Madagascar 6
6. Leaf blades narrowly elliptic to lanceolate, length/width ratio 4-6:1; known only from near Lac Ihotry (21°50'S) in Madagascar 1. *H. angustifolia*
- 6'. Leaf blades lanceolate to elliptic or ovate, length/width ratio 2-3:1; plants of various habitats in east Africa, the Mascarenes, or north of 18°S latitude in Madagascar 7
7. Inflorescences with small leafy bracts (northern Madagascar) 12. *H. moratiana*
- 7'. Inflorescences ebracteate 8
8. Fruits less than 8 mm in diam. 9
- 8'. Fruits greater than 9 mm in diam.; leaf bases usually acute to obtuse 10
9. Leaf blades widest at the middle, the base obtuse to acute (east Africa, Mascarenes) 15. *H. petiolaris*
- 9'. Leaf blades widest below the middle, the base usually rounded (Mayotte) 5. *H. comorensis*
10. Fruits 9-12 mm in diam.; corollas greater than 7 mm long 17. *H. schatziana*
- 10'. Fruits 15-20 mm in diam.; corollas less than 6.5 mm long 7. *H. darciana*
11. Corolla reduced to a ring connecting the staminal filaments; plants of tsingy of western Madagascar 2. *H. apetala*
- 11'. Corolla urceolate, with 5 lobes; plants of SW Madagascar and east Africa 12
12. Leaves scabrous on the adaxial surface 13
- 12'. Leaves glabrous on the adaxial surface or essentially so 15
13. Styles completely undivided, the two stigmas borne on opposite one another on the style apex 18. *H. teitensis*
- 13'. Styles divided, the two stigmas each terminating a short branch 14
14. Leaves with glandular hairs 14. *H. orbicularis*
- 14'. Leaves with non-glandular hairs 11. *H. lyciacea*
15. Calyx visibly pubescent on the interior surface; leaves tomentose on the abaxial surface (southern Madagascar) 4. *H. capuronii*
- 15'. Calyx apparently glabrous on the interior surface; leaves scabrid to soft puberulent on the abaxial surface 16
16. Inflorescences nearly racemose, with a central axis; abaxial leaf surface evenly strigillose 16. *H. randrianasoloana*
- 16'. Inflorescences cymose, lacking a distinct central axis; abaxial leaf surface soft puberulent to glabrous 17
17. Abaxial leaf surface evenly soft puberulent (east Africa) 13. *H. nemoralis*
- 17'. Abaxial leaf surface sparsely puberulent to glabrous (southern Madagascar) 10. *H. lowryana*

1. *Hilsenbergia angustifolia* J.S. Mill., *sp. nov.*

Arbor usque ad 7 m alta, cortice in laminas tenues exfoliante, ramunculis glabris vel minute puberulis. Folia decidua, alterna; lamina anguste-elliptica usque lanceolata, 6.5-10 cm longa, 1-3 cm lata, apice basique attenuata, margine integra, adaxialiter glabra vel sparsim minuteque puberula, abaxialiter sparsim puberula; petiolo 8-18 mm longo. Inflorescentiae terminale, cymosae, c. 3 cm latae. Flores non visi. Fructus drupaceus, flavo-aurantiacus, depresso globosus, 20-23 mm longus, 23-28 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Service Forestier: SF24122 (Capuron)*, Madagascar, Prov. Toliara, forêt très dégradée, sur sable, près d'Andrenialamahitsy, au nord du Lac Ihotry, 21°50'S, 43°40'E, fr., 27 May 1965 (holo-, P!; iso-, G!, K!, MO!, P!, TEF!).

Tree 6-7 m tall, the bark exfoliating in plates, the twigs glabrous or minutely puberulent. Leaves deciduous, alternate; blades narrowly elliptic to lanceolate, the widest point near or below the middle, 6.5-10 cm long, 1-3 cm wide, the apex attenuate, the base attenuate, the margin entire, the adaxial surface glabrous to sparsely and minutely puberulent, the abaxial surface sparsely puberulent, the venation brochidodromous, the midrib impressed on the adaxial surface, raised on the abaxial surface, the secondary veins 8-13, the tertiary venation reticulate; petioles 8-18 mm long, sparsely puberulent, shallowly canaliculate on the adaxial surface.

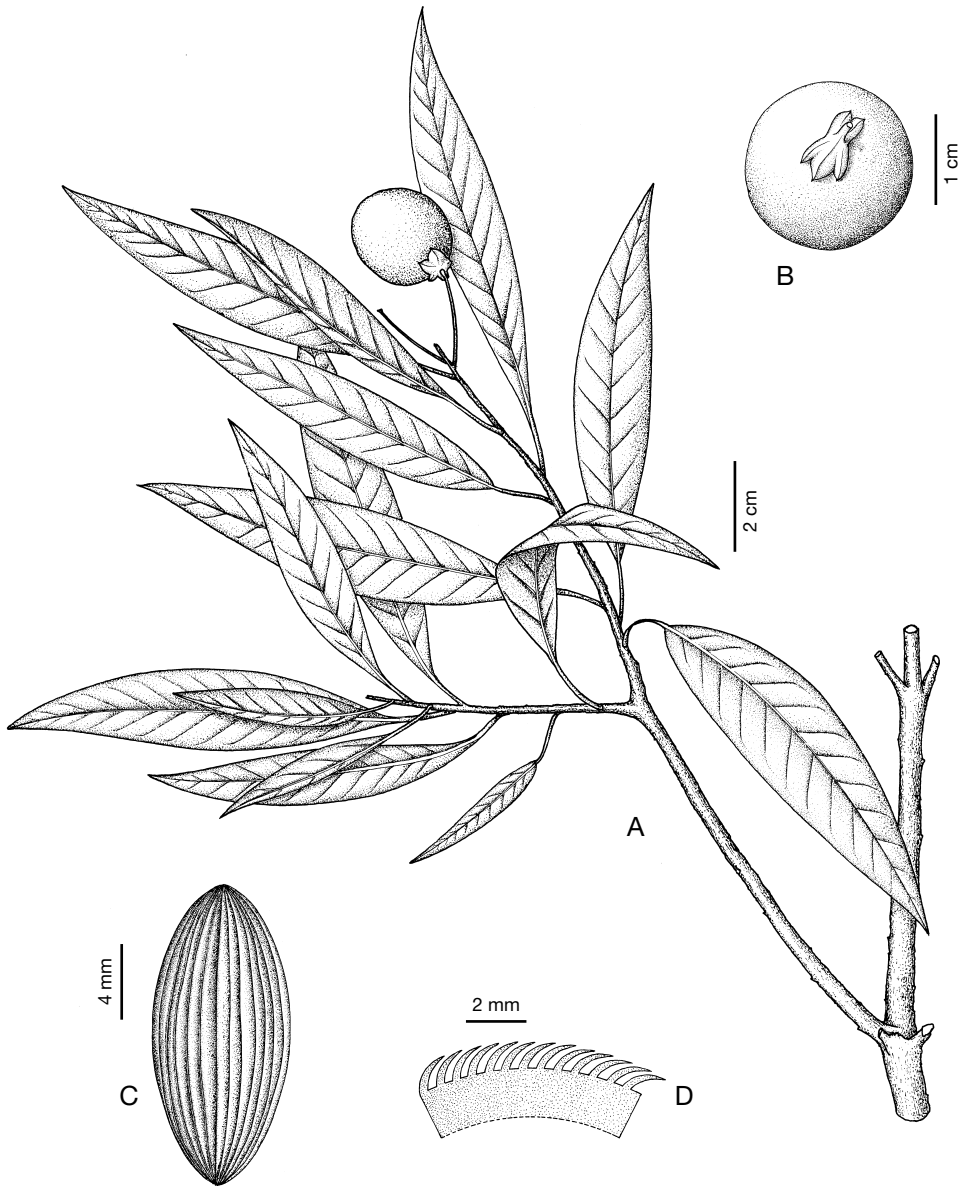


Fig. 1. — *Hilsenbergia angustifolia* J.S. Mill.: **A**, Fruiting branch; **B**, fruiting calyx showing uneven separation of the five lobes; **C**, dorsal view of pyrene; **D**, cross-section of dorsal surface of pyrene. Service Forestier: SF24122 (Capuron). Drawn by A. Jouy.

Inflorescences terminal, cymose, c. 3 cm broad, the branches glabrous. Flowers not seen.

Fruits drupaceous, yellow-orange at maturity, borne in the 7-11 mm broad persistent calyx, globose, 20-23 mm long, 23-28 mm in diameter, the endocarp bony, separating into 4 pyrenes at maturity, these c. 15 mm long, 8 mm wide,

with parallel papery wings on the exterior surface. — Fig. 1.

Hilsenbergia angustifolia is a very distinctive species easily recognized by its long, narrow leaves that are unlike any of the other large-fruited members of the genus.

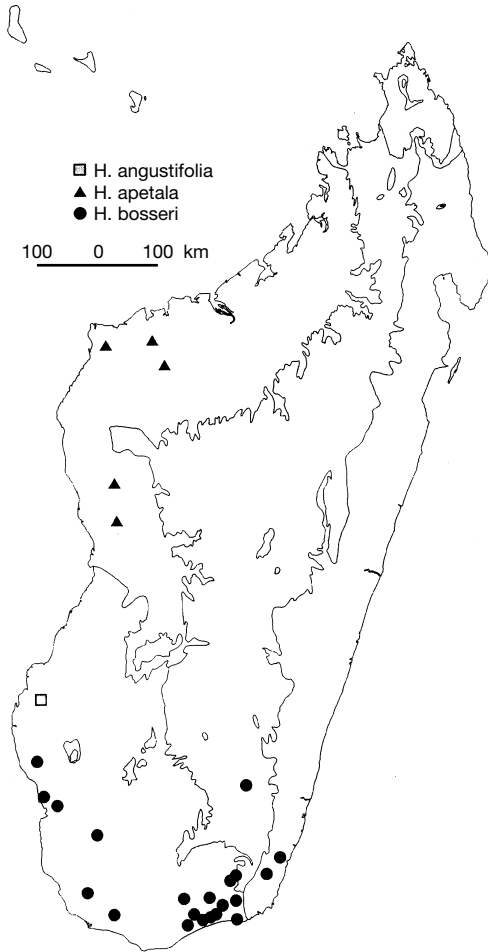


Fig. 2. — Distributions of *Hilsenbergia* species, mapped on the simplified bioclimate zones of Madagascar (after CORNET 1974; see SCHATZ 2000).

DISTRIBUTION. — *Hilsenbergia angustifolia* is known from only a single collection made on sand north of Lac Ihotry in southwestern Madagascar (Fig. 2).

CONSERVATION STATUS. — Provisional IUCN Red List Category: Critically Endangered (CR B1ab(I-iv) + 2ab(I-iv)). *Hilsenbergia angustifolia* has been collected only once from a locality that the specimen label described as very degraded in 1965. It is questionable whether this species still survives.

2. *Hilsenbergia apetala* J.S. Mill., sp. nov.

Frutex vel arbor parva, cortice subtiliter fissurata, ramunculis sparse puberulis vel glabris. Folia decidua, alterna vel sub-opposita, lamina ovata ad elliptica, 2.5-5.5 cm longa, 1.3-3 cm lata, apice acuminata usque acuta vel raro obtusa, basi acuta usque obtusa vel rotundata, margine integra, adaxialiter glabra vel trichomatibus secus costam vestita, abaxialiter puberula vel glabra; petiolo 5-17 mm longo. Inflorescentiae terminale, racemosae vel cymosae, 1.5-5.5 cm longae. Flores bisexuales; calyce campanulato usque urceolato, 3-3.5 mm longo, 5-lobato, glabro praeter trichomatium caespites ad apices lobulorum; corolla tubularis, lobis absentibus. Fructus non visi.

TYPUS. — *Service Forestier: SF24232 (Capuron)*, Madagascar, Prov. Mahajanga (Ambongo), calcaires, près d'un cours d'eau, au sud d'Antsakoamanera, baie de Marambitsy, 16°30'S, 44°40'E, fl., 20 Nov. 1965 (holo-, P!; iso-, G!, GH!, K!, MO!, P!, TEF!, WAG!).

Shrub or small tree, the bark finely fissured, the twigs sparsely puberulent to glabrous; leaves deciduous, borne only on the current season's growth, alternate to subopposite; blades ovate to elliptic, 2.5-5.5 cm long, 1.3-3 cm wide, the apex acuminate to acute or rarely obtuse, the base acute to obtuse or rounded, the margin entire, the adaxial surface glabrous or with hairs along the midrib, the abaxial surface evenly puberulent to glabrous, the venation brochidodromous, the midrib even with the adaxial surface or impressed near the base, raised on the abaxial surface, the secondary veins 3-5, the tertiary venation reticulate; petioles 5-17 mm long, narrowly canaliculate on the adaxial surface, glabrous but puberulent in the channel.

Inflorescences terminal, racemose or cymose, but branched only slightly toward the base if at all, 1.5-5.5 cm long, the branches glabrous to puberulent. Flowers bisexual; calyx campanulate to urceolate, 3-3.5 mm long, 2-3 mm long, 5-lobed, the lobes somewhat uneven, triangular, 1-1.5 mm long, glabrous on both surfaces but with minute tufts of hairs at the apex of the lobes; corolla tubular, included in the calyx or only shortly exerted, 2-3.5 mm long, lacking lobes; stamens 5, the filaments 2.5-5.5 mm long, adnate to the corolla for its full length, the upper 0.3-2.5 mm free, the free portion winged, the anthers ellipsoid, 1-2 mm long; ovary conical, 1-1.5 mm long, 1 mm wide, the style 2-3 mm long, the 2 stigmas capitate. Fruits unknown. — Fig. 3.

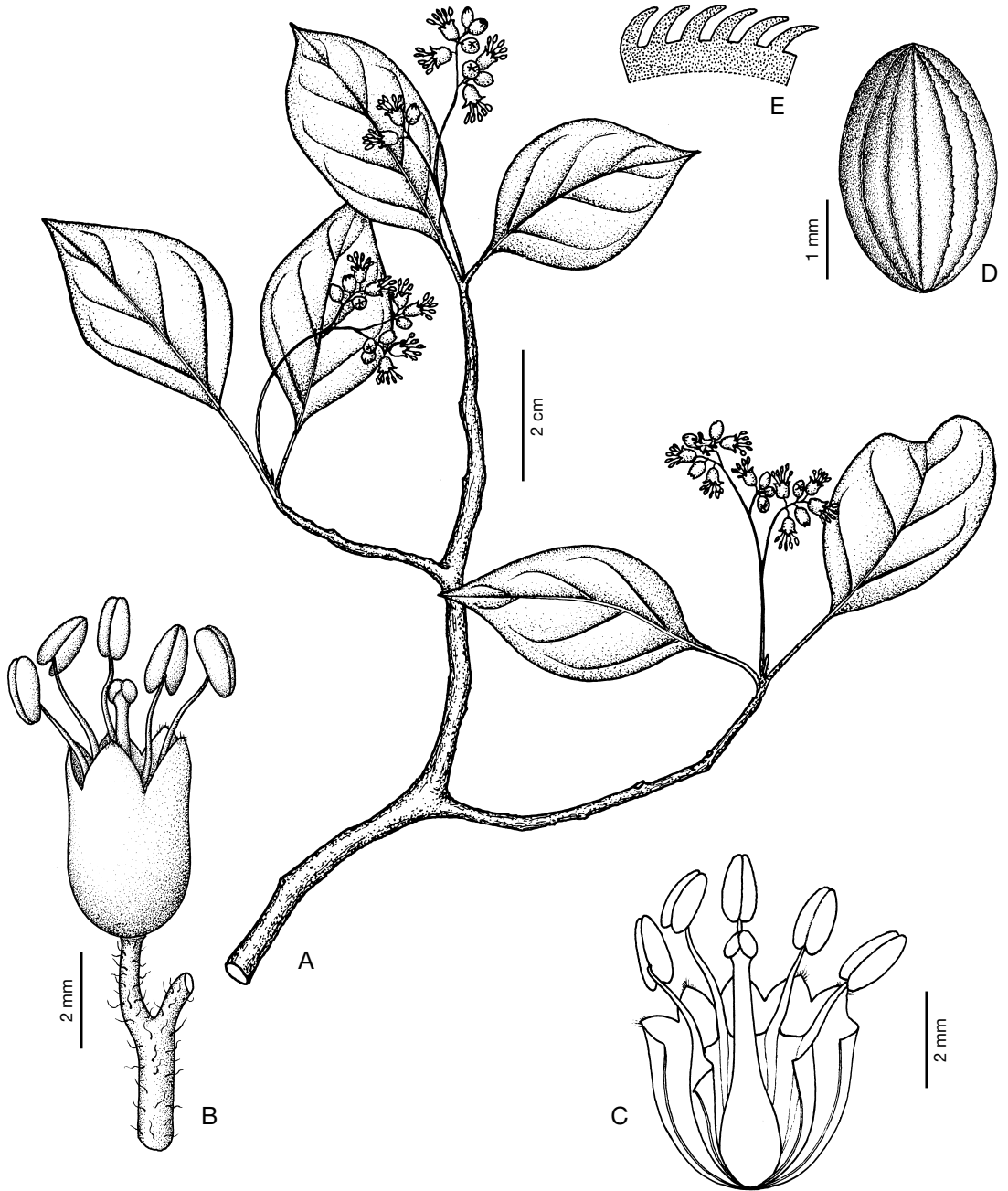


Fig. 3. — *Hilsenbergia apetala* J.S. Mill.: **A**, flowering branch with leaves; **B**, flower; **C**, open flower with calyx and corolla opened to show that the corolla is reduced and lacks lobes; **D**, dorsal view of pyrene; **E**, cross-section of dorsal surface of pyrene. *Service Forestier: SF24232 (Capuron)*. Drawn by A. Jouy.

Hilsenbergia apetala is a strikingly distinct species, easily recognized by its highly reduced corolla, which lacks lobes and has the staminal filaments adnate to it for its full length. It thus appears as though the staminal filaments are fused into a tube and no corolla is present. I am not aware of any other member of the Ehretioideae with this floral structure. It is also unusual in its nearly racemose inflorescence, which is usually reduced to a simple rachis, or occasionally has a few, highly-reduced lateral branches.

DISTRIBUTION. — *Hilsenbergia apetala* occurs in western Madagascar (Fig. 2) where it grows on calcareous substrates.

VERNACULAR NAME. — Hazodomohina.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia apetala* is known from the tsingy of Namoroka and Bemaraha, both protected as Réserves Naturelles Intégrales. Populations outside of the two protected areas certainly face immediate threat. Further fieldwork will be necessary to document the size of populations within the protected areas; the reserves at Bemaraha and Namoroka are very poorly collected, so the limited number of available specimens may not prove rarity.

PARATYPES. — MADAGASCAR: *Jongkind 3280*, Prov. Mahajanga, Tsingy de Bemaraha, RHI, N of the Manambolo River, 50 m, 19°09'S, 44°49'E, fr., 29 Nov. 1996 (MO!); *Perrier de la Bâthie 17867*, Prov. Mahajanga, Réserve Naturelle de Namoroka, Ambongo, 16°26'S, 45°22'E, fl., Dec. 1926 (MO!, P!); *Réserves Naturelles: RN5617*, Prov. Mahajanga, Réserve Naturelle 8, Namoroka, dist. Soalala, Canton Andranomavo, 16°26'S, 45°22'E, fl., 31 July 1953 (P!, TEF!); *Service Forestier: SF12008 (Tata)*, Prov. Mahajanga, forêt d'Antsingy, Réserve Naturelle de Bemaraha, Antsolova, 150-750 m, 18°35'S, 44°47'E, fl., 23 Oct. 1954 (P!).

3. *Hilsenbergia bosseri* J.S. Mill., *sp. nov.*

Frutex vel arbor parva usque ad 5(-8) m alta, cortice exfoliante, ramunculis glabris. Folia decidua, alterna; lamina elliptica, interdum leviter falcata, (2.4-)3-5(-6) cm longa, 1-2 cm lata, apice obtusa usque acuta et interdum breve acuminata, basi acuta, margine integra et interdum minute revoluta, utrinque glabra; petiolo 8-

11.5(-20) mm longo. Inflorescentiae terminale, cymosae vel ex flore solitario constans. Flores bisexuales; calyx campanulato, c. 5 mm longo, 5-lobo, extus glabro, intus dense puberula; corolla alba, urceolata. Fructus drupaceus, luteus usque aurantiacus, depresso globosus, 12-16 mm longus, 13-21 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Miller & Randrianasolo 6182*, Madagascar, Prov. Toliara, 95 km W of Fort Dauphin, on Route Nationale 13, at Andalitany, 200 m, 25°08'S, 46°12'E, fr., 29 Mar. 1991 (holo-, MO!; iso-, G!, K!, MO!, P!, TAN!, WAG!).

Shrub or small tree to 5(-8) m tall, the bark smooth and exfoliating, the twigs glabrous. Leaves deciduous, alternate; blades elliptic, sometimes somewhat falcate, widest at or near the middle, (2.4-)3-5(-6) cm long, 1-2 cm wide, the apex obtuse to acute and sometimes shortly acuminate, the base acute, the margin entire and sometimes minutely revolute, glabrous on both surfaces, venation eucamptodromous, the midrib even with the adaxial surface or slightly impressed, raised on the abaxial surface, the secondary veins 4-7, faintly visible, the tertiary venation reticulate, faint; petioles 8-11.5(-20) mm long, canaliculate on the adaxial surface, glabrous.

Inflorescences terminal, small cymes of up to 12 flowers or the flowers solitary, the branches glabrous. Flowers bisexual; calyx campanulate, c. 5 mm long, 4 mm wide, 5-lobed, the lobes deltate, 1.3-1.8 mm long, glabrous on the exterior surface, densely puberulent on the interior surface and thus appearing ciliate along the margins of the lobes; corolla urceolate, with reflexed and recurved lobes, c. 5 mm long, 4 mm wide, 5-lobed, the lobes ovate, c. 2 mm long, 2 mm wide, minutely puberulent on the upper exterior surface; stamens 5, the filaments 4.5 mm long, the upper 1.8 mm free, glabrous, anthers ellipsoid, 1.3 mm long; ovary ovoid, c. 2 mm long, 2 mm wide, the style 3 mm long, the 2 stigmas capitate.

Fruits drupaceous; green to yellow or orange, then maturing blue-black or black, borne in the persistent, 6-12 mm broad calyx, globose, 12-16 mm long, 13-21 mm in diameter, the exocarp leathery, the endocarp bony, separating into 4, single-seeded pyrenes, 7-12 mm long, 5-7 mm wide, with dense parallel papery wings on the exterior surface. — Fig. 4.

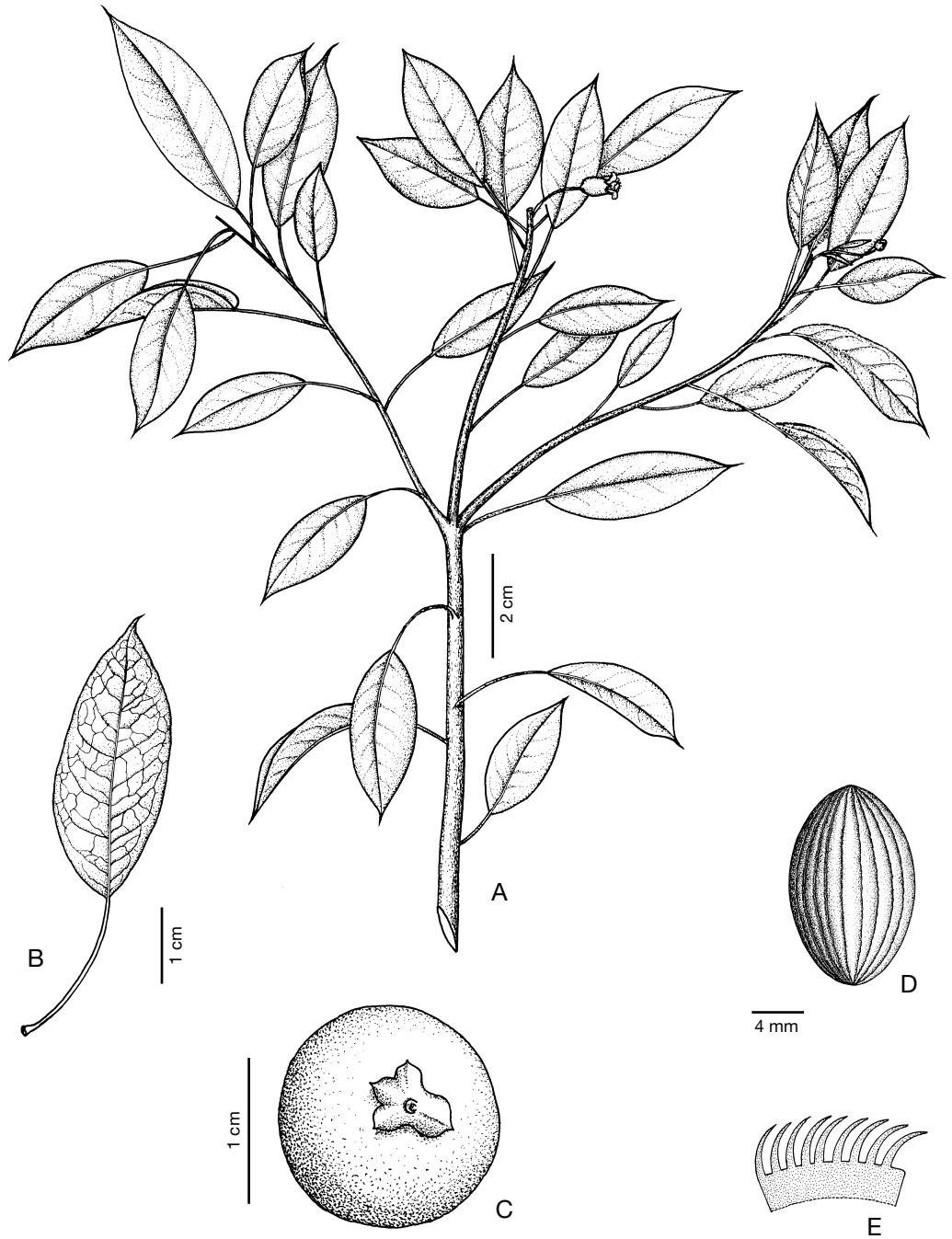


Fig. 4. — *Hilsenbergia bosseri* J.S. Mill.: **A**, flowering branch; **B**, close-up of leaf showing detailed venation; **C**, fruiting calyx showing uneven separation of the five lobes; **D**, dorsal view of pyrene; **E**, cross-section of dorsal surface of pyrene. *Service Forestier SF11717 (Capuron)*. Drawn by A. Jouy.

Hilsenbergia bosseri has the smallest leaves of any of the large-fruited members of the genus and is the only species from this group found in the dry forests between Tuléar and Ft. Dauphin. It is easily recognized by its glabrous, elliptic leaves that are 3-5 cm long. The other species with glabrous leaves are either densely branched shrubs with very small leaves (*H. croatii* and *H. leslieae*) or more northern species with leaf blades greater than 5 cm long.

This species is named in honor of Jean BOSSER who collected extensively in Madagascar, is one of the foremost authorities on its flora, and continues his prolific taxonomic contributions.

DISTRIBUTION. — *Hilsenbergia bosseri* is widespread in southern Madagascar (Fig. 2).

VERNACULAR NAMES. — Andy, Borodoka, Vatoa, Vavatoa, Voavaloa.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia bosseri* is widespread in southern Madagascar, but apparently sporadic within the region, with an Extent of Occurrence of only 220 km². Further field studies may prove this species is more common than available collections indicate.

PARATYPES. — MADAGASCAR: *Alluaud s.n.*, Prov. Toliara, Behara, 24°57'S, 46°23'E, fr., Sep. 1900 (MO!, P!); *Bosser 10480*, Prov. Toliara, environs d'Ambovombe, 25°10'S, 46°05'E, fl., Oct. 1956 (MO!, P!); *Chauvet 107*, Prov. Toliara, route d'Ifaty-Tuléar, fr., Aug. 1961 (MO!, P!, TEF!); *Cours 4632*, s.loc., fr., s.d. (MO!, P!); *Decary 8592*, Prov. Toliara, Ambovombe, 25°10'S, 46°05'E, fr., 13 Mar. 1931 (P!); *Decary 9331*, Prov. Toliara, Ambovombe, 25°10'S, 46°05'E, fr., 21 Oct. 1931 (P!); *Dumetz 1339*, Prov. Toliara, Préfecture de Fort Dauphin, Andohahela Reserve No. 11, parcelle 2, 120-1000 m, 24°53'S, 46°36'E, fr., 20 Oct. 1990 (K!, MO!, P!); *Hoffman, Ranaivojaona, Ralimanana & Randriamampionona 161*, Prov. Toliara, Parc National d'Andohahela, dirt track to Talakifeno village near Ambatohabo, 200 m, 24°52'36"S, 46°37'56"E, fr., 9 Oct. 2000 (K!); *Homolle 1711*, s.loc., fr., s.d. (MO!, P!); *Humbert 12754*, Prov. Toliara, vallée de la Manambolo, bassin du Mandrare, au NW de Maroaomby, Betsioky, forêt sèche et bush xérophile, 300-400 m, 24°30'S, 46°35'E, fr., Dec. 1933 (MO!, P!); *Humbert 20041*, Prov. Toliara, environs de Manombo, forêt d'Isonito à l'ouest d'Ankililoaka, forêt tropophile et bush xérophile sur sables roux, 80-150 m, 22°46'S, 43°36'E, fr., 28 Jan.

1947 (P!); *Humbert & Capuron 28938*, Prov. Toliara, Bevilany à l'ouest de Fort-Dauphin, bush xérophile sur terrains cristallins, 100-200 m, 25°01'S, 46°36'E, 11 Feb. 1955 (P!); *Humbert & Swingle 5499*, Prov. Toliara, bassin de la Linta, plateau calcaire à l'est du delta, 200-250 m, 24°45'S, 44°21'E, fr., 29 Aug. 1928 (MO!, P!); *Keraudren 977*, Prov. Toliara, route d'Ambovombe à Amboasary à 20 km environ d'Ambovombe, 25°05'S, 46°17'E, fr., Apr. 1960 (MO!, P!); *Miller et al. 10746*, Prov. Toliara, 50 km west of Route Nationale 10 on a dirt track north of the secondary road to Beheloka, WSW of Betsioky, 250 m, 23°44'40"S, 44°08'58"E, fr., 30 Jan. 2003 (MO, P, TAN); *Peltier 1381*, Prov. Toliara, au nord d'Ambatoveve, 23°53'S, 44°03'E, fr., 20 Nov. 1959 (P!); *Peltier 2892*, Prov. Toliara, Bevoay, près Beraketa, 24°50'S, 46°11'E, fr., 17 Jan. 1961 (P!); *Perrier de la Bathie 18652*, Prov. Toliara, entre le Mandrare et le Manambolo, 24°35'S, 46°30'E, fr., June 1932 (P!); *Phillipson & Milijaona 3578*, Prov. Toliara, 15 km NW of Ambovombe on Route Nationale 13, 150 m, 25°05'S, 45°57'E, fr., 20 Feb. 1990 (K!, MO!, P!); *Poisson 298*, Prov. Toliara, Befandry, 23°18'S, 43°42'E, fr., 2 Aug. 1911 (P!); *Réserves Naturelles: RN5046*, Prov. Toliara, Réserve Naturelle 11, Andohahela, Canton Behara, Androy, 120-1006 m, 24°57'S, 46°23'E, fr., 15 Mar. 1953 (MO!, P!); *Service Forestier: SF1523 (Begue)*, Prov. Toliara, forêt de Beara, 50 m, 24°57'S, 46°23'E, fr., 16 Sep. 1950 (P!); *Service Forestier: SF3944*, Prov. Toliara, Canton d'Amputaka, 2 km du Manombo, Beloha, 25°05'S, 44°45'E, fr., 11 Aug. 1951 (P!, TEF!); *Service Forestier: SF5301 (Ngoloka)*, Prov. Toliara, route Antanimora-Ambovombe P.K 332, 150 m, 24°14'S, 47°15'E, fr., 10 May 1952 (P!); *Service Forestier: SF11717 (Capuron)*, Prov. Toliara, sur les pentes du massif de l'Angavo, à l'est d'Antanimora, 24°51'S, 45°48'E, fl., fr., Feb. 1955 (MO!, P!); *Service Forestier: SF11740 (Capuron 11740)*, Prov. Toliara, à l'est d'Antanimora, vers la base du massif de l'Angavo, 200-530 m, 24°51'S, 45°48'E, fr., 24-25 Jan. 1955 (P!); *Service Forestier: SF12201 (Andrianaraison)*, Prov. Toliara, Androangabe, 50 m, 24°29'S, 47°03'E, fl., 6 Nov. 1954 (P!); *Service Forestier: SF12676 (Bototsalaoendry)*, Prov. Toliara, Tuléar, Ambohimahavelona, 100 m, 23°16'S, 43°54'E, fr., 27 Jan. 1955 (P!); *Service Forestier: SF15536 (Andrianaraison)*, Prov. Toliara, Amkiliroy-Ambovombe, 200 m, 25°10'S, 46°05'E, fr., 26 Jan. 1955 (P!); *Service Forestier: SF28301 (Capuron)*, Prov. Toliara, environs Est d'Antanimora, 24°14'S, 47°15'E, fr., 7 Sep. 1968 (P!, TEF!).

4. *Hilsenbergia capuronii* J.S. Mill., sp. nov.

Arbor usque ad 15 m alta, cortice laevi, ramunculis puberulis vel glabris. Folia decidua, alterna; lamina elliptica usque obovata, 3-8(-11) cm longa, 1.5-4(-5) cm lata, apice acuta vel leviter acuminata, infrequenter

obtusa, basi acuta usque obtusa, margine integra, minute revoluta, adaxialiter glabra vel sparse puberula, abaxialiter puberula vel glabra; petiolo 0.5-2(-3) mm longo. Inflorescentiae terminale, cymosae. Flores bisexuales vel fortasse unisexuales; calyce campanulato, 3.5-4 mm longo, extus dense puberulo, intus dense albo pubescente; corolla urceolata vel tubularis. Fructus drupaceus, depresso-globosus, 6-8 mm longus, 8-10 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Miller et al. 10737*, Madagascar, Prov. Toliara, Forêt d'Analava, c. 14 km N of Route Nationale 7; west of Isalo National Park; east of the Malio River, deciduous forest on sand, 670 m, 22°35'26"S, 45°08'16"E, fr., 27 Jan. 2003 (holo-, MO!; iso-, P!, TAN!).

Tree to 15 m tall, to 25 cm dbh, bark smooth, greenish, whitish in the slash, trunk channeled, the twigs puberulent to glabrous; leaves deciduous, restricted to the current season's growth, alternate; blades elliptic to obovate, the broadest point at or above the middle, 3-8(-11) cm long, 1.5-4(-5) cm wide, the apex acute or slightly acuminate, less commonly obtuse, the base acute to obtuse, the margin entire, minutely revolute, the adaxial surface glabrous or sparsely puberulent, evenly puberulent on the midrib and in a narrow band near the margin, the abaxial surface puberulent to glabrous, evenly puberulent on the midrib and secondary veins, evidently lighter in color than above, the venation brochidodromous, midrib impressed on the adaxial surface, raised on the abaxial surface, the secondary veins 5-7(-9), the tertiary veins reticulate; petioles 0.5-2(-3) cm long, evenly to sparsely puberulent, narrowly canaliculate on the adaxial surface.

Inflorescences terminal, cymose, to c. 3 cm long and up to 12-flowered, the branches puberulent. Flowers bisexual or possibly functionally unisexual, borne or pedicel-like branches 1-4 mm long; calyx campanulate, 3.5-4 mm long, 4-4.5 mm wide, 5-lobed, the lobes valvate, triangular, 1-1.5 mm long, densely puberulent on the exterior surface, densely white pubescent on the interior surface, the hairs evidently protruding from the calyx and visible with the naked eye; corolla urceolate or tubular with erect to spreading lobes, 4-5 mm long, 5-lobed, the lobes ovate, c. 1 mm long; stamens 5, the filaments 3-3.5 mm long, the upper 1.5-3 mm free, glabrous, the

anthers ellipsoid to lanceoloid, 1-1.2 mm long; ovary conical, 1-3 mm long, 1.5-2 mm wide, the style 2-3 mm long, the 2 stigmas discoid or the style lacking an apparent stigmatic surface.

Fruits drupaceous, color at maturity unknown, borne in the persistent, spreading calyx, interior pubescence of the calyx clearly visible, depressed globose, 6-8 mm long, 8-10 mm in diameter, the endocarp bony, separating into 4 single-seeded pyrenes at maturity, the dorsal surface with parallel, papery wings. — Fig. 5.

Hilsenbergia capuronii is very easily recognized by its bicolored leaves, which are relatively large among the Malagasy species, and the very distinctive pubescence on the interior surface of its calyx, easily visible in both flower and fruit. It is also unusual in having a densely puberulent midrib that is sunken into the surface of its leaves and also a thin band of pubescence along the upper leaf surface near the margin.

Hilsenbergia capuronii may be functionally dioecious. *SF15736* has stamens with full, ellipsoid anthers inserted high in the corolla tube and a style that lacks any apparent stigmatic surface, whereas *SF20594* has a gynoeceum of normal appearance, but the stamens are inserted nearly at the base of the corolla and the anthers are somewhat smaller and lanceoloid. However, as this species is known from only three flowering specimens, only two of which have dissectable flowers, additional collections or field observations will be required to confirm this possibility.

This species is named in honor of René CAPURON (1921-1971) who was one of the most prolific students of Malagasy plants. He collected extensively in Madagascar for more than 20 years and contributed to the knowledge of many plant families. At the time of his death in 1971 he had been working to complete a study of woody Boraginaceae from Madagascar. He had taken extensive notes and had tentatively assigned names to many specimens. I have largely chosen not to accept CAPURON's names here as the numerous additional collections now available indicate that many of his provisional species were not correctly delimited. Furthermore, many of the epithets that CAPURON chose were based on

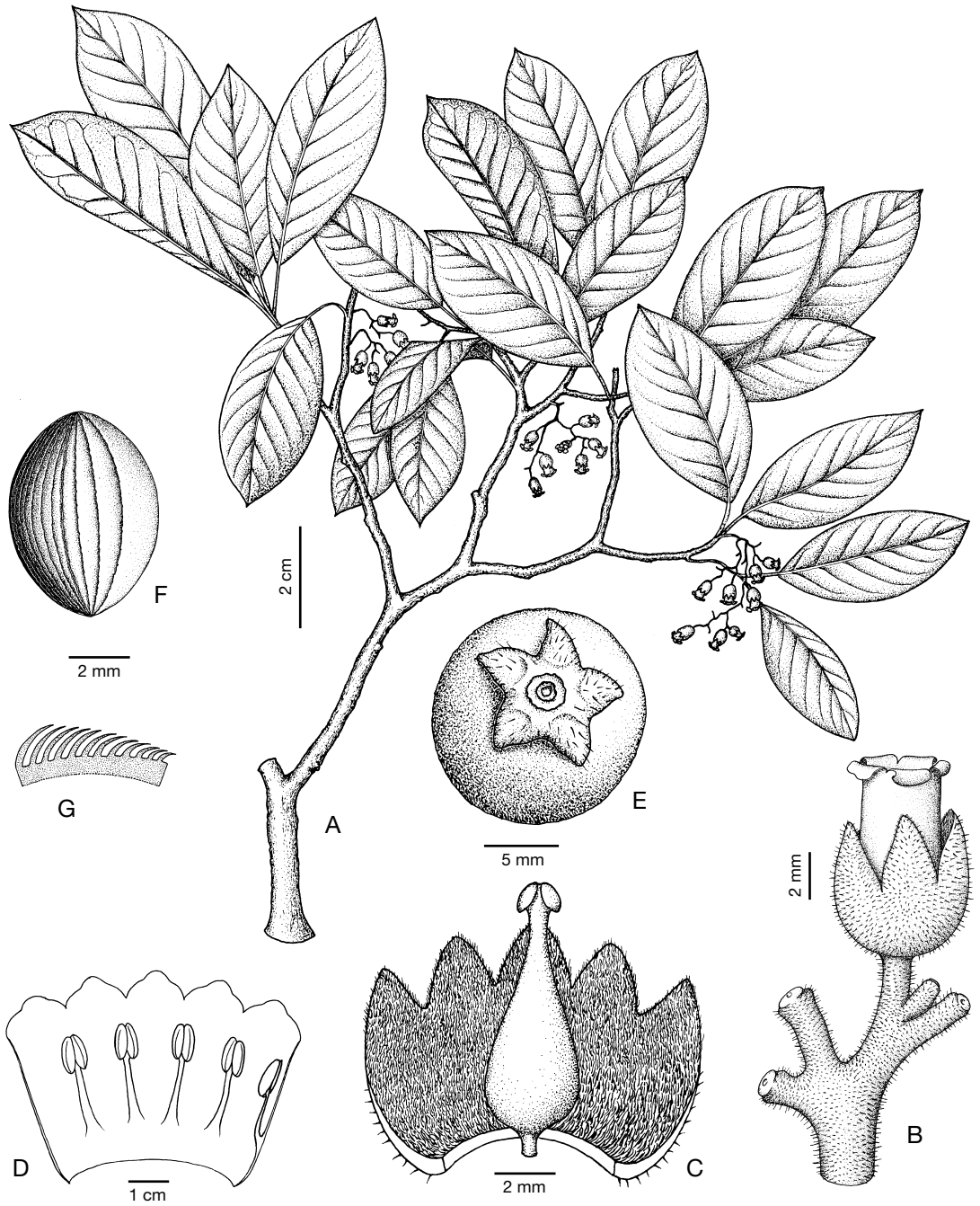


Fig. 5. — *Hilsenbergia capuronii* J.S. Mill.: **A**, flowering branch; **B**, whole flower attached to a piece of inflorescence; **C**, open calyx showing gynoecium; **D**, open corolla showing androecium; **E**, fruit, showing slightly expanded fruiting calyx; **F**, dorsal view of pyrene; **G**, cross-section of dorsal surface of pyrene. A-D, *Service Forestier SF574*; E, *Service Forestier SF4996 (Rasolofoson)*. Drawn by A. Jouy.

geographic names and recent collections demonstrate that the species are more widespread than CAPURON's names would suggest. It is, however, most appropriate to pay tribute to one of the greatest students of Malagasy trees by naming this species, which he collected numerous times during his tenure with the Service Forestier, in his honor.

DISTRIBUTION. — *Hilsenbergia capuronii* occurs on sandy soil in southern Madagascar (Fig. 6).

VERNACULAR NAMES. — Malamasafoy, Peha, Tanatananala.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia capuronii* is known from a few scattered localities in southern and western Madagascar. Although its Extent of Occurrence is rather large, its Area of Occupancy is only 70 km² and Zombitsy National Park is the only protected area where its occurrence has been recorded. In addition, other than a single individual tree that was collected in 2003, the species has not been collected for more than 30 years.

PARATYPES. — MADAGASCAR: *Humbert 29577*, Prov. Toliara, forêt de Zombitsy (Sakaraha), aux confins des bassins du Fiherenana et de l'Onilahy, forêt tropophile sur sables siliceux de l'Isalo, 600-850 m, 22°46'S, 44°42'E, ster., 26-29 Mar. 1955 (P!); *Leandri 2213*, Prov. Mahajanga, forêt de Tsiampihy et forêts côtières près de Besaraha, de Bemihia, et de Soahanina, 0-20 m, 18°35'S, 44°14'E, fr., 20 Dec. 1952 (MO!, P!); *Service Forestier: SF574 (Capuron)*, Prov. Toliara, forêt d'Analamarina (Hazoroa) au SE de Sakaraha, 500-600 m, 23°S, 44°34'E, fl., 28 Dec. 1961 (MO!, P!); *Service Forestier: SF4996 (Rasolofson)*, Prov. Toliara, Hazoroa, Sakaraha, 500 m, 23°S, 44°36'E, fr., 21 Feb. 1952 (P!); *Service Forestier: SF6851 (Capuron)*, Prov. Mahajanga, forêt de Tsienimpihy, à l'est du village de Besara, dist. Antsalova, 25 m, 18°35'S, 44°15'E, fr., 22 Dec. 1952 (P!); *Service Forestier: SF15348 (Poupon)*, Prov. Toliara, Ihera, Mahaboboka, 22°15'S, 44°16'E, fl., 2 Dec. 1955 (P!); *Service Forestier: SF15736*, Prov. Mahajanga, forêt de Ambararatakely, Mafaijijo, Maintirano, 25 m, 17°51'S, 45°21'E, fl., 21 Dec. 1955 (MO!, P!, TEF!); *Service Forestier: SF20594 (Capuron)*, Prov. Toliara, forêt d'Analamarina, Hazoroa, au SE de Sakaraha, 500-600 m, 23°S, 44°34'E, fl., 28 Dec. 1961 (MO!, P!); *Service Forestier: SF28947 (Capuron)*, Prov. Toliara, Sorita, crêtes et barres calcaires, au lieu-dit Ankiranja, à 30-35 km de Manja, sur la route de Bevoay, 198 m, 21°28'S, 44°02'E, fl., 3-4 Dec. 1969 (P!, TEF!).

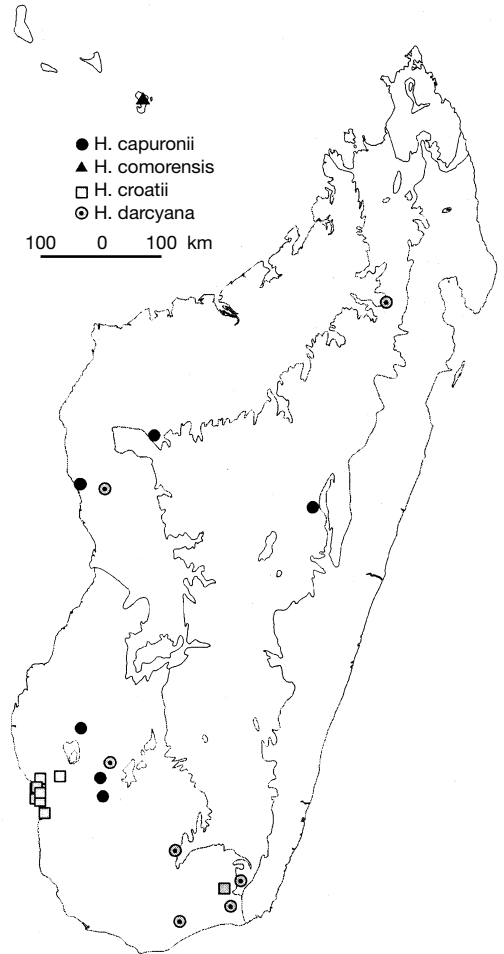


Fig. 6. — Distributions of *Hilsenbergia* species, mapped on the simplified bioclimate zones of Madagascar (after CORNET 1974; see SCHATZ 2000).

5. *Hilsenbergia comorensis* J.S. Mill., sp. nov.

Arbor usque ad 12 m alta, ramunculis glabris. Folia decidua, alterna; lamina lanceolata usque ovata, 6.5-16 cm longa, 3.3-6 cm lata, apice acuminata, basi rutundata usque obtusa, margine integra et minute revoluta, utrinque glabra vel adaxialiter puberula secus nervos principales; petiolo 15-30(-40) mm longo. Inflorescentiae cymosae, usque ad 7 cm latae. Flores non visi. Fructus drupaceus, depresso-globosus, 4-5 mm longus, 5-8 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Pascal 504*, Comores, Mayotte, Hachiroungou, 450 m, fr., 16 Apr. 1996 (holo-, P!; iso-, K!).

Tree to 12 m tall, the twigs glabrous; leaves deciduous, alternate, borne only on the current season's growth, deciduous; blades lanceolate to ovate, the widest point below the middle, 6.5-16 cm long, 3.3-6 cm wide, the apex acuminate, the base rounded to obtuse, the margin entire and minutely revolute, the adaxial surface glabrous or with short hairs along the major veins, the abaxial surface glabrous, the venation brochidodromous, the midrib impressed on the adaxial surface, raised on the abaxial surface, the secondary veins 8-12, the tertiary venation reticulate; petioles 15-30(-40) mm long, glabrous, narrowly canaliculate on the adaxial surface.

Inflorescences terminal, cymose, to 7 cm broad, the branches glabrous. Flowers unknown.

Fruits drupaceous, borne in the persistent, c. 5 mm wide calyx, orange at maturity, depressed globose, 4-5 mm long, 5-8 mm broad, the endocarp bony, separating into 4 single-seeded pyrenes at maturity, 4 mm long, 2.3 mm wide, the dorsal surface with parallel, papery wings. — Fig. 7.

Hilsenbergia comorensis is a distinctive species, perhaps most easily confused with *H. petiolaris*, from which it differs most conspicuously in having leaves that are widest below the middle, rounded to obtuse at the base, and acuminate at the apex. The leaves of *H. petiolaris*, in contrast, are to widest at the middle, acute to obtuse at the base, and obtuse to acuminate at the apex.

DISTRIBUTION. — *Hilsenbergia comorensis* is known from only two collections, both from the island of Mayotte in the Comores (Fig. 6).

VERNACULAR NAME. — Chipapou Lahi.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Critically Endangered (CR B1ab(I-iv) + 2ab(I-iv)). *Hilsenbergia comorensis* has been collected only twice on the island of Mayotte. Available habitat is both limited and threatened.

PARATYPE. — COMORES: *Pascal 890*, Mayotte, Convalescence, 400 m, fr., 19 Feb. 1997 (P!).

6. *Hilsenbergia croatii* J.S. Mill., *sp. nov.*

Frutex vel arbor parva, ramunculis glabris. Folia decidua, alterna vel dense ad apices ramunculorum

brachyblastorumve in fasciculos densos disposita; lamina late-obovata, late-elliptica, vel late-ovata usque late-depresse-ovata, 9-21 mm longa, 8-20 mm lata, apice rotundata usque emarginata, basi rotundata usque obtusa, margine integra, utrinque glabra; petiolo 4-12 (-15) mm longo. Inflorescentiae terminale, cymosae vel ex fasciculis 1- ad 3-floris constans. Flores bisexuales; calyce campanulato, 3-4 mm longo, 5 lobo, extus glabro vel margine ciliato; corolla alba, urceolata usque campanulata, 5-6 mm longa. Fructus drupaceus, aurantiacus, ovoideus usque late-ovoideus, 4-5 mm longus, 3.5-5 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Miller & Keating 4514*, Prov. Toliara, Tsivonoakely, 20-30 km N of Tuléar on the road to Morombe, 5-10 m, 23°12'S, 43°37'E, fl., 11 Nov. 1989 (holo-, MO!; iso-, P!, TAN!).

Shrub or small tree, rarely to 7 m tall, the twigs glabrous, increasingly fissured and encrusted with waxy coating with age. Leaves deciduous, alternate, but borne densely at the end of shoots or on short lateral spur shoots; blades widely obovate, widely elliptic, or widely ovate to widely depressed obovate, widely depressed elliptic, or widely depressed ovate, 9-21 mm long; 8-20 mm wide, (length:width ratio 3:2 - 2:3), the apex rounded to emarginate, the base rounded to obtuse and sometimes somewhat decurrent along the petiole, the margin entire, both surfaces glabrous, the venation brochidodromous, the midrib slightly raised or even with the leaf surface above, raised below, the secondary veins 3(-5), the tertiary venation reticulate; petioles 4-12(-15) mm long, usually nearly as long as the leaf blade, glabrous or puberulent on the adaxial surface near the base, flattened or canaliculate on the adaxial surface.

Inflorescences terminal, 1-3-flowered fascicles or up to 8-flowered cymes, the branches glabrous. Flowers bisexual, on pedicel-like inflorescence branches 1-5(-10) mm long; calyx campanulate, 3-4 mm long, 3-5 mm wide, 5-lobed, the lobes valvate, ovate to triangular, sometimes uneven, 0.7-1.5 mm long, glabrous or minutely ciliate on the margins; corolla white, urceolate to campanulate, 5-6 mm long, 4.5-5.5 mm wide, 5-lobed, the lobes ovate, erect to reflexed, 1.5-2.5 mm long; stamens 5, the filaments 2.5-3 mm long, the upper 1-2 mm free, glabrous, the anthers lanceoloid, 1-2 mm long; ovary conical, 1-

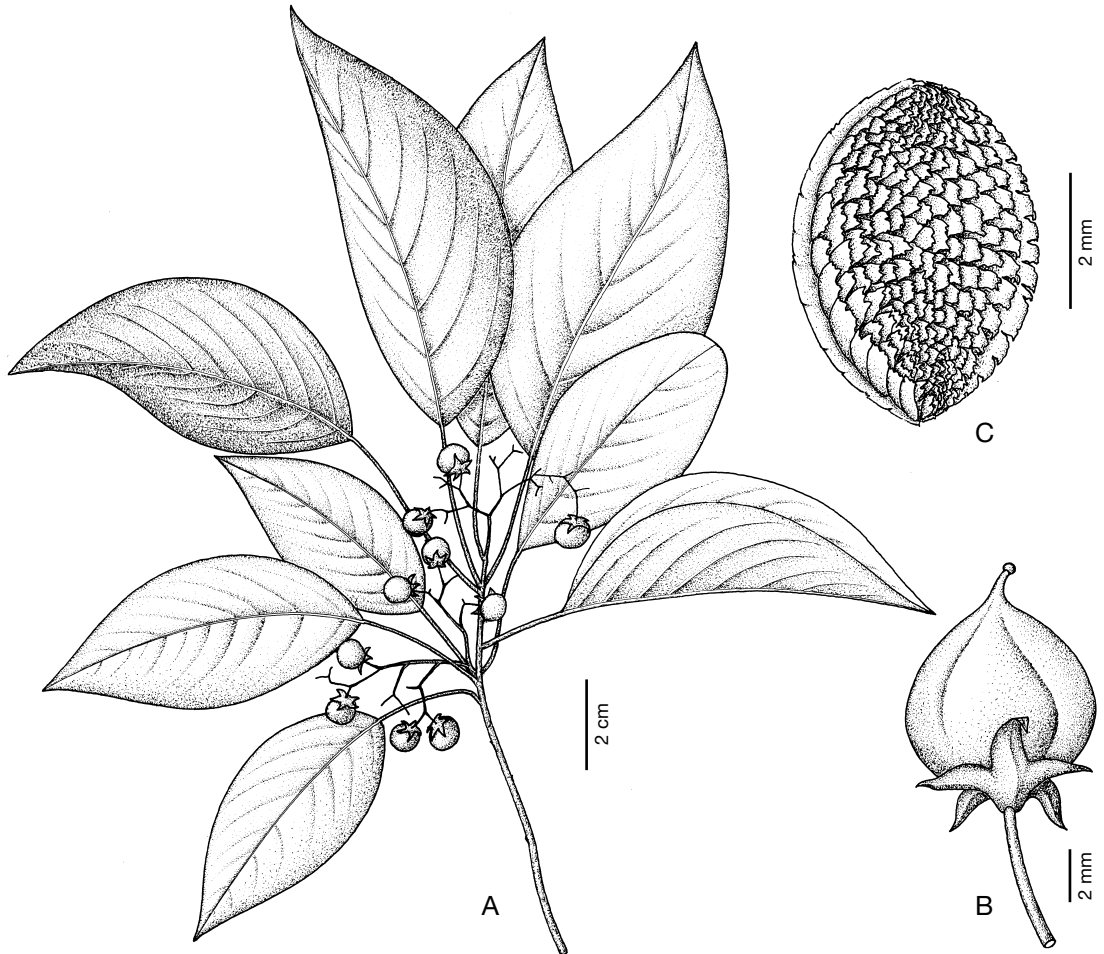


Fig. 7. — *Hilsenbergia comorensis* J.S. Mill.: **A**, fructing branch; **B**, whole fruit with persistent calyx; **C**, dorsal surface of pyrene. Pascal 504. Drawn by A. Jouy.

1.5 mm long, 0.8-1 mm wide, the style 1.5-2 mm long, the 2 stigmas capitate, angled to nearly lateral on the style apex.

Fruits drupaceous, orange at maturity, borne in the persistent, cup-shaped to spreading calyx, ovoid to broadly ovoid, 4-5 mm long, 3.5-5 mm in diameter, the endocarp bony, separating into 4 single-seeded pyrenes at maturity, 3.5 mm long, 2.5 mm wide, these ribbed on the exterior surface. — Fig. 8.

Hilsenbergia croatii is similar in appearance and probably closely related to *H. leslieae* and the two

are easily confused. The two species are quite distinct in the field, but they regularly occur sympatrically and herbarium specimens are often difficult to separate. In the field, *H. croatii*, is a more laxly branched shrub whereas *H. leslieae* is so densely three-dimensionally branched, that it is difficult to press into herbarium specimens. The two are best distinguished from herbarium material on the basis of their leaves. *H. croatii* has leaf blades that are about as long as wide, with a rounded to obtuse base, and a petiole about the same length as the blade. In contrast, *H. leslieae* has leaf blades that are distinctly longer than wide

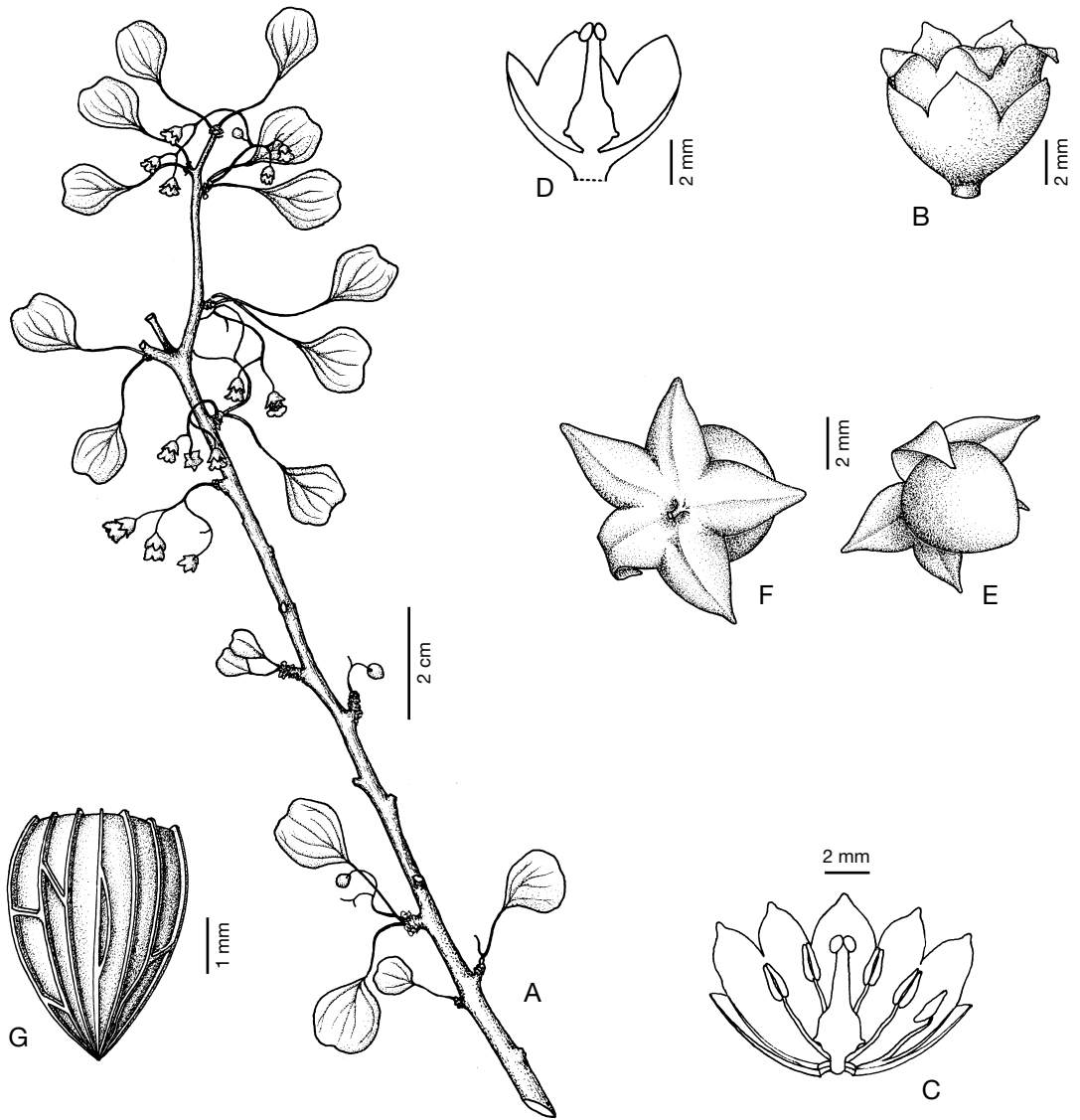


Fig. 8. — *Hilsenbergia croatii* J.S. Mill.: A, flowering branch; B, flower; C, open corolla showing androecium and gynoecium; D, open flower with corolla and androecium removed to show gynoecium; E, top view of fruit with persistent calyx; F, basal view of fruit with persistent calyx; G, dorsal view of pyrene. *Leandri 3860*. Drawn by A. Jouy.

(length:width ratio 3:1 - 3:2), with a cuneate base, and a petiole less than half of the length of the blade. Although both species produce few flowers per inflorescence, *H. croatii* occasionally produces multiply-branched cymose inflorescences with as many as 8 flowers, while inflorescences with more than 4 flowers are not known from *H. leslieae*.

Hilsenbergia croatii is named in honor of Thomas B. CROAT, one of the most prolific plant collectors in history, who made many interesting plant collections in Madagascar in 1975, including several gatherings of this species.

DISTRIBUTION. — *Hilsenbergia croatii* is known only from dry regions of southern

Madagascar (Fig. 6) on both sandy and calcareous substrates.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia croatii* is known from only two areas in southern Madagascar where its Extent of Occurrence is limited to 90 km². The forests in the vicinity of Tuléar are being both cleared and selectively logged to produce charcoal and are under great threat.

PARATYPES. — MADAGASCAR: *Bernardi* 11385, Prov. Toliara, 23-25 km N of Tuléar on the road to Manombo across the Fiherenana, 23°S, 43°40'E, fr., 11 Nov. 1967 (K!, P!); *Chauvet* 82, Prov. Toliara, environs de Tuléar, route de Sarodrano, 23°31'S, 43°44'E, 11 Mar. 1961 (P!); *Croat* 30822, Prov. Toliara, along highway near beach 12 km N of Tuléar, more than 10 m above sea level, 23°10'S, 43°40'E, fl., 5 Feb. 1975 (MO!, P!); *Croat* 30903, Prov. Toliara, along road to Morombe 16-18 km N of Tuléar, near sea level, 23°13'S, 43°40'E, fr., 6 Feb. 1975 (MO!, P!); *Decary* 18715, Prov. Toliara, Manombo, tables, 22°58'S, 43°58'E, fl., 22 Feb. 1943 (MO!, P!); *Humbert & Perrier* 2555, Prov. Toliara, environs de Tuléar, delta du Fiherenana, 2-10 m, 23°18'S, 43°36'E, fl., 14-26 Sep. 1924 (MO!, P!); *Leandri* 3860, Prov. Toliara, environs de Tuléar, route de Manombo, 0-200 m, 23°13'S, 43°40'E, 15 Nov. 1960 (P!); *Peltier* 3388, Prov. Toliara, Tsivonoa, 23°08'S, 43°37'E, fr., 11 Sep. 1961 (P!); *Perrier de la Bâthie* 19018, Prov. Toliara, dunes de Tuléar, 23°20'S, 43°40'E, fr., s.d. (P!); *Phillipson* 3450, Prov. Toliara, 38 km SW of Ampanihy, on road to Androka, 200 m, 24°50'S, 44°25'E, fr., 5 Feb. 1990 (MO!, P!); *Rabesandratana* 4036, Prov. Toliara, Ifaty, 23°09'S, 43°36'E, 13 Dec. 1993 (P!); *Service Forestier: SF9911*, Prov. Toliara, Ft. Dauphin, dunes de Mandrare, village le plus proche Tanandava, Canton Amoasary, poste Behara, 24°39'S, 46°26'E, fr., 9 May 1954 (P!, TEF!); *Service Forestier: SF27934 (Capuron)*, Prov. Toliara, sur la route de Manombo, au nord du Fiherenana, 23°13'S, 43°40'E, fr., 8-12 Nov. 1967 (P!, TEF!); *Service Forestier: SF 28970 (Capuron)*, Prov. Toliara, sables littoraux, au nord de Tuléar, sur la route de Manombo, P.K. 12-13, 23°13'S, 43°40'E, 6 Dec. 1969 (P!).

7. *Hilsenbergia darciana* J.S. Mill., sp. nov.

Arbor usque ad 6(-15) m alta, cortice exfoliante, ramunculis glabris. Folia decidua, alterna, lamina lanceolata usque anguste-elliptica vel ovata, 5-10 cm longa, 1.5-4.8 cm lata, apice acuminata, basi asymmetrica cuneata vel acuta usque obtusa, margine integra

plerumque minute revoluta, adaxialiter glabra vel raro puberula secus costam, abaxialiter glabra vel puberula; petiolo 2-28(-45) mm longo. Inflorescentiae terminale, cymosae, usque ad 3(-5) cm latae. Flores bisexuales; calyx campanulato, 4.5-5 mm longo, 5-lobo, extus glabro, intus sericeo; corolla alba, urceolata, 6-6.5 mm longa. Fructus drupaceus, luteus, globosus, 11-13(-17) mm longus, 10-15(-20) mm in diam.; pyrenis 4, alatis.

TYPUS. — *Seyrig* 5404, Madagascar, Prov. Toliara, environs d'Ampandrandava, entre Bekily et Tsivory, 1000-1100 m, 24°05'S, 45°42'E, fl., s.d. (holo-, P!).

Tree to 6(-15) m tall, to 30 cm dbh, the bark exfoliating, the twigs glabrous, waxy. Leaves deciduous, alternate; blades lanceolate to narrowly elliptic or ovate, widest near or below the middle, 5-10 cm long, 1.5-4.8 cm wide, the apex acuminate, the base asymmetrically cuneate or acute to obtuse, the margin entire and usually minutely revolute, the adaxial surface glabrous, or rarely puberulent along the midrib, the abaxial surface glabrous or rarely evenly puberulent, the venation brochidodromous, the midrib impressed or even with the adaxial surface, raised on the abaxial surface, the secondary veins 5-8, the tertiary venation reticulate; petioles 8-28(-45) mm long, glabrous or rarely sparsely puberulent, narrowly canaliculate on the abaxial surface.

Inflorescences terminal, cymose, to 3(-5) cm broad, the branches glabrous. Flowers bisexual; calyx campanulate, 4.5-5 mm long, the 5 lobes deltate, 2-2.5 mm long, acute at the apex, glabrous on the outer surface, sericeous on the inside of the lobes; corolla white, urceolate, 6-6.5 mm long, the tube 4.5-5 mm long, the 5 lobes depressed-ovate, c. 1.5 mm long, 3 mm wide; stamens 5, the filaments 4-4.5 mm long, only the upper c. 1 mm free, the anthers borne near the mouth of the corolla, obloid, c. 1 mm long; ovary ovoid, c. 2 mm long, 1.5 mm wide, the style c. 2 mm long, not divided, the 2 stigmas capitate.

Fruits drupaceous, yellow at maturity, borne in the 6-8(-10) mm broad persistent calyx, globose, 11-13(-17) mm long, 10-15(-20) mm in diameter, the endocarp bony, separating into 4 pyrenes at maturity, these 7-10(-15) mm long, 4-6(-10) mm wide, with parallel papery wings on the outer surface. — Fig. 9.

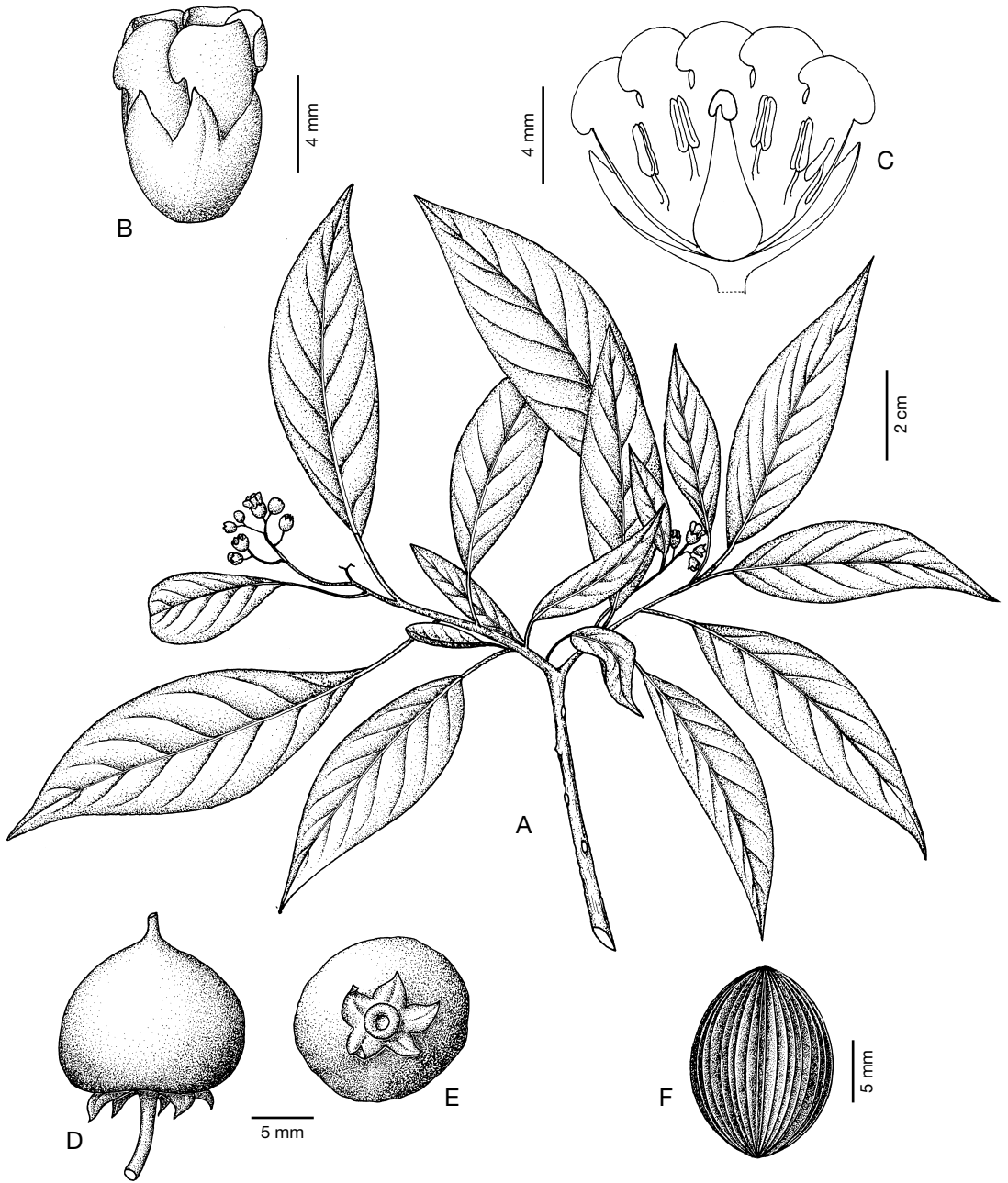


Fig. 9. — *Hilsenbergia darciana* J.S. Mill.: **A**, flowering branch; **B**, whole flower with urceolate corolla; **C**, flower with open corolla showing androecium and gynoecium; **D**, lateral view of fruit with persistent calyx; **E**, basal view of fruit with persistent calyx; **F**, dorsal view of pyrene. A-C, *Herb. Jard. Botanique 5404*; D-E, *Service Forestier: SF11930bis*. Drawn by A. Jouy.

Hilsenbergia darcyana is largely a southern species that occurs at middle elevations, from 500-1200 m. In this respect, *SF28596*, from 100-200 m near Italy in the vicinity of Ft. Dauphin is unusual in occurring at such low elevation. The two most northern collections, *Decary 14445*, from Mandritsara, and *RN7202*, from the Réserve Naturelle de Bemaraha near Soalala, are also somewhat anomalous in their distribution but are included here as they are similar in most morphological features. They do, however, differ in having larger fruits (12-17 × 15-20 mm), compared with southern populations (11-13 × 10-15 mm). The collection from Mandritsara is outstanding also in having leaves that are wider in proportion to length and a puberulent undersurface. The southern populations of this species are quite consistent morphologically and easily recognized from *H. bosseri*, the only large-fruited species in the south, by their larger, acuminate leaves.

Hilsenbergia darcyana is named in honor of William G. D'ARCY (1931-2000), who spent his botanical career at the Missouri Botanical Garden and was a leading authority on the taxonomy of Solanaceae. He collected in Madagascar in 1983 and 1987 and published the treatment of Solanaceae for the Flore de Madagascar et des Comores with Armand RAKOTOZAFY in 1994.

DISTRIBUTION. — *Hilsenbergia darcyana* is known from upland sites from southern Madagascar (Fig. 6).

VERNACULAR NAMES. — Behodiky, Lamoty Tsokaka.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia darcyana* occurs over a wide range in Madagascar, but its populations are restricted to widespread upland sites that are effectively islands, thus limiting its Extent of Occurrence to 60 km². It does occur in protected areas in the Zombitsy reserve and possibly Andohahela and Isalo National Parks but it has not been collected for 35 years.

PARATYPES. — MADAGASCAR: *Decary 14448*, Prov. Mahajanga, Mandritsara, 400-600 m, 15°50'S,

48°50'E, fr., 20 July 1939 (MO!, P!); *Humbert 13422*, Prov. Toliara, vallée de la Sakamalio, affluent de la Manambolo, bassin de Mandrare, 900-1100 m, 24°32'S, 46°41'E, fr., Dec. 1933 (P!); *Humbert 13831*, Prov. Toliara, bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, Mt. Apiky au-dessus de Mahamavo, 800-900 m, 24°55'S, 46°32'E, fr., Jan.-Feb. 1934 (P!); *Humbert, Begue & Capuron 29631*, Prov. Toliara, forêt de Zombitsy, Sakaraha, aux confins des bassins du Fiherenana et de l'Onilahy, forêt tropophile sur sables siliceux de l'Isalo, 600-850 m, 22°46'S, 44°43'E, fr., 26-29 Mar. 1955 (MO!, P!); *Réserves Naturelles: RN7202 (Ramaroson)*, Prov. Mahajanga, Antsalova, 18°39'S, 44°37'E, fr., May 1955 (P!); *Service Forestier: SF4611*, Prov. Fianarantsoa, route Ihosy-Farafangana, 22°32'S, 46°29'E, fr., 20 Mar. 1952 (P!, TEF!); *Service Forestier: SF11930bis (Capuron)*, Prov. Toliara, forêt de Zombitsy, à l'est de Sakaraha, 22°46'S, 44°43'E, fr., Mar. 1955 (MO!, P!, TEF!); *Service Forestier: SF28596 (Capuron)*, Prov. Toliara, colline gneissique au NE d'Italy, à l'ouest de Fort Dauphin, 100-200 m, 25°09'S, 45°46'E, fr., 15 Dec. 1968 (MO!, P!, TEF!); *Seyrig 295*, Prov. Toliara, environs d'Ampandrandava, entre Bekily et Tsivory, 1000-1100 m, 24°05'S, 45°42'E, fr., Nov. 1945 (P!).

8. *Hilsenbergia labatii* J.S. Mill., sp. nov.

Arbor usque ad 10(-20) m alta, cortice subtiliter fissurata, ramunculis glabris. Folia decidua, alternia; lamina late-ovata usque orbiculata, 5-10.5 cm longa, 3-7(-8) cm lata, apice obtusa usque rotundata, plumerque abrupte acuminata, basi obtusa usque acuta vel cuneata, margine integra, utrinque glabra; petiolo 1.7-4.3 cm longo. Inflorescentiae terminale, paniculata, anguste-pyramidalis, 6-10.5 cm longae. Flores bisexuales; calyce campanulato, 4-5 mm longo, 4-5-lobo, extus glabro; corolla alba vel pallide chloroleuca, tubulari, 5 lobis reflexis. Fructus drupaceus, globosus, 3-4 mm longus, 3-5 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Humbert 18924*, Madagascar, Prov. Antsiranana, collines et plateaux calcaires de l'Ankarana, 300 m, 12°54'S, 49°08'E, fl., Dec. 1937-Jan. 1938 (holo-, P!; iso-, G!, K!, MO!, P!, TEF!, WAG!).

Tree to 10(-20) m tall, to 60 cm dbh, the bark finely fissured, the stems glabrous. Leaves deciduous, borne only on the current season's growth, alternate; blades widely ovate to orbicular, 5-10.5 cm long, 3-7(-8) cm wide, the apex obtuse to

rounded and usually abruptly acuminate, the acumen usually somewhat reflexed, the margin entire, both surfaces glabrous, the venation brochidodromous, the midrib impressed near the leaf base, the secondary veins (4-)5-6(-8), the tertiary venation reticulate; petioles 1.7-4.3 cm long, narrowly canaliculate on the adaxial surface, glabrous.

Inflorescences terminal, a narrowly pyramidal panicle 6-10.5 cm long, 4-6.5 cm broad near the base, the peduncle 2.5-4 cm long, peduncle and branches glabrous. Flowers bisexual; calyx campanulate, persistent in fruit, 4-5 mm long, the lobes valvate, 4-5, sometimes tardily separating and appearing only 3 in flower, triangular to widely triangular, 1-2 mm long, 1.5-2 mm wide, glabrous; corolla white to pale greenish white, tubular with reflexed lobes, 5-lobed, the lobes widely depressed ovate, 1.5 mm long, 2 mm wide, the tube 3.5-4 mm long; stamens 5, filaments 3 mm long, the upper 1.5 mm free, glabrous, the anthers lanceoid, c. 1 mm long, the 2 sacs free and slightly divergent at the base; ovary ovoid, 1.5 mm long, 1 mm wide, the style 3 mm long, dichotomously branched at the apex, the 2 stigmas discoid.

Fruit drupaceous, color at maturity unknown, borne in the persistent, spreading calyx, globose, 3-4 mm long, 3-5 mm in diameter, 4-lobed and 4-parted at maturity, the endocarp bony, breaking into 4 single-seeded pyrenes, 3-3.5 mm long, 1.5-2 mm wide, these with thickened parallel ridges on the external surface. — Fig. 10.

Hilsenbergia labatii is the largest species of the genus, sometimes obtaining a height of 20 m. It is a very distinctive species that can be easily recognized by its paniculate inflorescence. It is named in honor of Jean-Noël LABAT who has contributed significantly to knowledge of the flora of Madagascar and the Comores through his collections and publications.

DISTRIBUTION. — *Hilsenbergia labatii* is known from only seven collections, all from calcareous substrates in extreme northern and western Madagascar (Fig. 11).

VERNACULAR NAMES. — Hazomavylahy, Talamosy, Tsarafanahy, Tsarajofy.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). The two regions where *Hilsenbergia labatii* grows are distant, thus it occurs over a wide range in Madagascar, but its distribution is restricted to calcareous substrates and its Extent of Occurrence is only 60 km². It does occur in two protected areas, the Réserve Spéciale d'Ankarana and Parc National de Bemaraha.

PARATYPES. — MADAGASCAR: *Humbert 18955*, Prov. Antsiranana, collines et plateaux calcaires de l'Ankarana, 100-350 m, 12°54'S, 49°08'E, fr., Dec. 1937-Jan. 1938 (P!); *Humbert 19156*, Prov. Antsiranana, collines et plateaux calcaires de l'Analamera, 50-400 m, 12°48'S, 49°28'E, fr., Jan. 1938 (P!); *Jongkind 3589*, Prov. Mahajanga, Tsingy de Bemaraha, RNI, N of Manambolo River, 50 m, 19°09'S, 44°49'E, fr., 18 Dec. 1996 (MO!); *Labat & Deroin 2282*, Prov. Mahajanga, près du fleuve Ambodirina, à l'est d'Ambinda, RN9, près d'Antsalova, 100-200 m, 18°38'S, 44°42'E, fr., 4 Dec. 1992 (MO!, P!); *Service Forestier: SF23146 (Capuron)*, Prov. Antsiranana, plateau de l'Ankarana, massif d'Ampatsoa, rive droite du Rodo, près de son confluent avec l'Andrafiama, 12°40'S, 49°34'E, fl., 24 Dec. 1963 (P!, TEF!); *Service Forestier: SF24456 (Capuron)*, Prov. Antsiranana, massif de l'Ambongoabo, à l'ouest de Diégo-Suarez, 12°15'S, 49°10'E, fr., 26 Jan. 1966 (P!, TEF!).

9. *Hilsenbergia leslieae* J.S. Mill., sp. nov.

Frutex vel arbor parva usque ad 5(-10) m alta, ramunculis glabris. Folia ad apice ramunculorum brachyblastorumve in fasciculos densos disposita; lamina obovata usque oblanceolata, 10-21(-30) mm longa, 6-12(-16) mm lata, apice obtusa usque rotundata vel emarginata, basi cuneata, margine integra, leviter incrassata, utrinque glabra; petiolo 2-5(-7) mm longo. Inflorescentiae terminale, cymosae. Flores bisexuales; calyce campanulato usque tubulari-campanulato, 4-4.5 mm longo, 5-lobato, extus glabro, intus apiceum versus dense pubescente; corolla alba, urceolata, 5-6 mm longa. Fructus drupaceus, ovoideus usque late-ovoideus, 4-5.5 mm longus, 3-4 mm in diam.; pyrenis 4, porcati.

TYPUS. — *Miller & Miller 3787*, Madagascar, Prov. Toliara, 14 km SE of Tuléar on the road to Sakaraha, 100 m, 23°21'S, 43°42'E, fl., 26 Dec. 1988 (holo-, MO!; iso-, K!, MO!, P!).

Shrub or small tree to 5(-10) m tall, thick-stemmed, densely branched, the twigs glabrous, often glaucous and densely waxy with age. Leaves

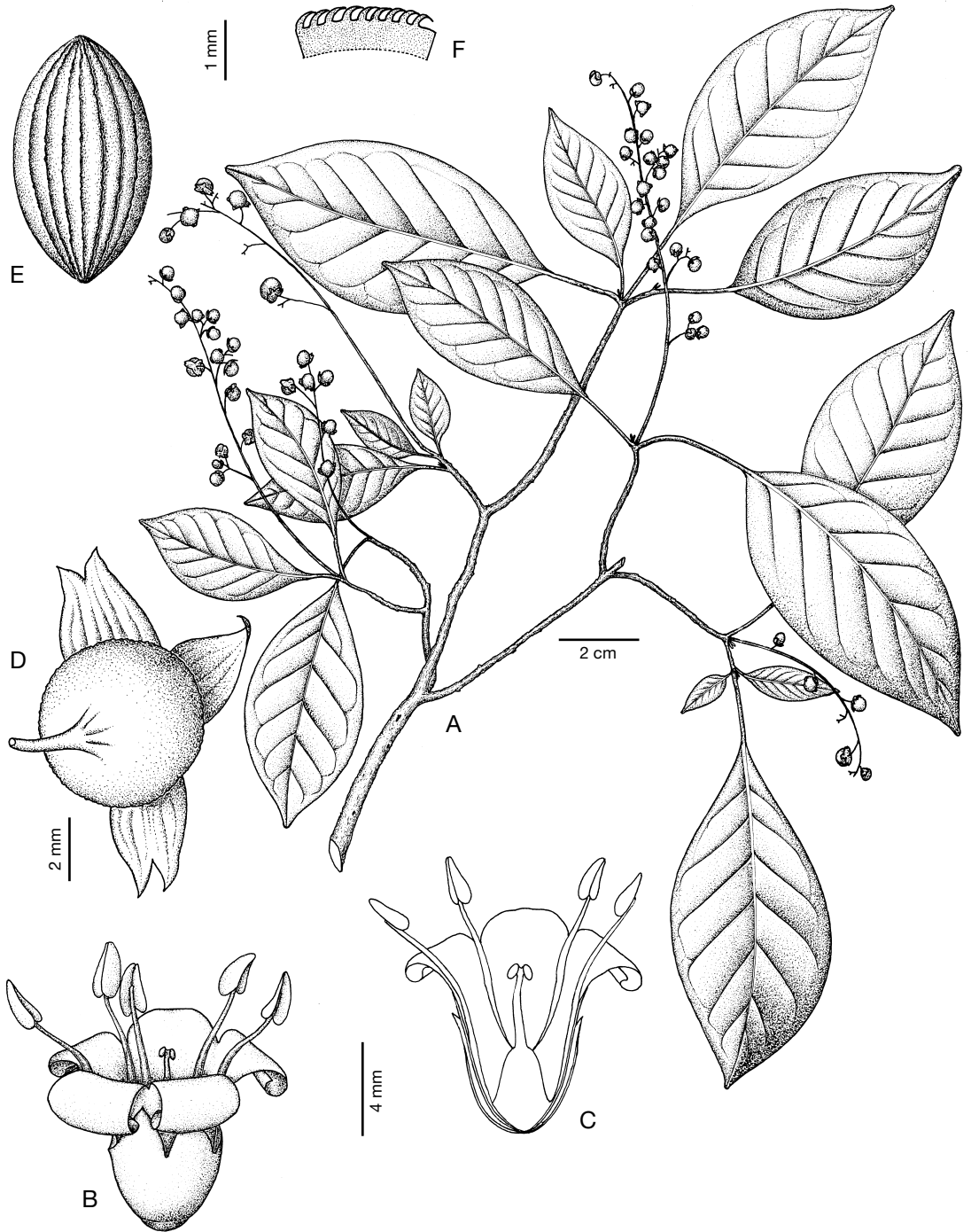


Fig. 10. — *Hilsenbergia labatii* J.S. Mill.: **A**, fruiting branch; **B**, whole flower; **C**, open flower showing androecium and gynoecium; **D**, young fruit with persistent calyx; **E**, dorsal view of pyrene; **F**, cross-section of dorsal surface of pyrene. A, D, E, F, *Labat 2282*; B, C, *Humbert 18924*. Drawn by A. Jouy.

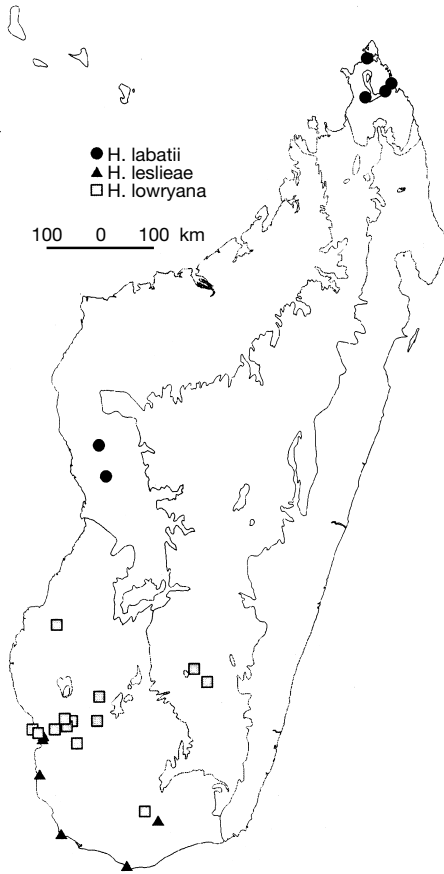


Fig. 11. — Distributions of *Hilsenbergia* species, mapped on the simplified bioclimate zones of Madagascar (after CORNET 1974; see SCHATZ 2000).

fasciculate at branch tips or on short lateral spur shoots, deciduous; blades obovate to oblanceolate, 10-21(-30) mm long, 6-12(-16) mm wide, (length:width ratio 3:1-3:2), the apex obtuse to rounded or emarginate, the base cuneate, the margin entire, slightly thickened, both surfaces glabrous, rarely minutely ciliate along the margin near the leaf base, the venation obscurely brochidodromous, the midrib even with the leaf surface, raised slightly below, the secondary veins 3-4, often indistinct, the tertiary venation reticulate; petioles 2-5(-7) mm long, less than half the length of the blade, or nearly sessile on young leaves, glabrous or rarely minutely puberulent, prominently canaliculate on the adaxial surface.

Inflorescences terminal, reduced cymes of 1-3(-4) flowers, the branches glabrous. Flowers bisexual, on pedicel-like inflorescence branches 2-6 mm long; calyx campanulate to tubular-campanulate, 4-4.5 mm long, 3-4 mm wide, 5-lobed, the lobes valvate, triangular, 1-1.5 mm long, densely pubescent on the apical part of the interior surface, the outer surface glabrous; corolla white, urceolate, 5-6 mm long, 3-4 mm wide, 5-lobed, the lobes erect to spreading, ovate, 1-2 mm long; stamens 5, the filaments 3-4 mm long, the upper 1-2 mm free, glabrous, the anthers ellipsoid, 1-1.5 mm long; ovary conical, 1.2-1.5 mm long, 0.8-1 mm wide, the style 1.5-2 mm long, the 2 stigmas capitate and terminal.

Fruits drupaceous, color at maturity unknown, borne in the persistent cup-shaped to spreading calyx, ovoid to broadly ovoid, 4-5.5 mm long, 3-4 mm in diameter, the endocarp bony, separating into 4 pyrenes at maturity, c. 4 mm long, c. 2.5 mm wide, ridged on the exterior surface. — Fig 12.

Hilsenbergia leslieae is variable in habit, usually being an erect shrub or small tree, sometimes reaching 10 m in height (e.g. *Humbert 28919*), but occasionally is low and prostrate (e.g. *SF28553*, from wind-swept areas near Cap Sainte-Marie). This species appears to be closely related to, and is easily confused with, *H. croatii* and the differences between them are discussed under that species.

Hilsenbergia leslieae is named in honor of my wife, Leslie MILLER, who accompanied me during field studies for this project, including the collection of the type specimen.

DISTRIBUTION. — *Hilsenbergia leslieae* occurs in southern Madagascar (Fig. 11) on calcareous substrates.

VERNACULAR NAMES. — Taikoaky, Tsingena.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia leslieae* occurs at scattered localities in southern Madagascar, but it is infrequently collected and its Extent of Occurrence is only 60 km². It is known to occur in the Réserve Naturelle Intégrale de Tsimanampetsotsa.

PARATYPES. — MADAGASCAR: *Chauvet 190*, Prov. Toliara, route Sarodrano, Tuléar, fl., fr., 23°28'S, 43°46'E, 13 Nov. 1961 (P!, TEF!); *Humbert 5403*, Prov. Toliara, du lac Tsimanampetsotsa, au delta de la Linta, près d'Itampolo, 1-10 m, 25°02'S, 44°04'E, fl., 17-24 Aug. 1928 (P!); *Humbert 28919*, Prov. Toliara, environs d'Antanimora, 20-25 km au SSE, bush xérophile sur terrains cristallins, 200-500 m, 24°49'S, 45°40'E, fl., 6-9 Feb. 1955 (P!); *Perrier de la Bathie 4434*, Prov. Toliara, dunes au nord de Tsimanampetsotsa, 24°03'S, 43°43'E, fl., fr., June 1910 (P!); *Phillipson 3042*, Prov. Toliara, SE of Tuléar on Route Nationale 7, 15 km from town, near La Table, 75 m, 23°25'S, 43°47'E, fl., 28 Dec. 1988 (P!); *Phillipson, Labat & Du Puy 3450*, Prov. Toliara, 38 km SW of Ampanihy, on road to Androka, calcareous plateau, 200 m, 24°50'S, 44°25'E, fr., 5 Feb. 1990 (P!); *Service Forestier: SF11723 (Capuron)*, Prov. Toliara, sur les pentes du massif de l'Angavo, à l'est d'Antanimora, 200-530 m, 24°49'S, 45°40'E, fl., 24-25 Jan. 1955 (P!); *Service Forestier: SF25252*, Prov. Toliara, Tsimandaha, Antanimora, Dist. Ambovombe, 330 m, 24°49'S, 45°40'E, ster., 28 Oct. 1964 (P!); *Service Forestier: SF 25255*, Prov. Toliara, Tsimandaha, Antanimora, Dist. Ambovombe, 330 m, 24°49'S, 45°40'E, ster., 28 Oct. 1964 (MO!, P!); *Service Forestier: SF28553 (Capuron)*, Prov. Toliara, Cap Sainte-Marie et environs Nord du Cap, 25°34'S, 45°09'E, fl., 17 Dec. 1968 (P!).

10. *Hilsenbergia lowryana* J.S. Mill., sp. nov.

Frutex vel arbor usque ad 10 m alta, cortice exfoliante, ramunculis glabris. Folia decidua, alterna; lamina elliptica, 1.5-5.5 cm longa, 0.8-3 cm lata, apice acuminata, basi cuneata usque decurrente, margine integra, basim versus involuta, adaxialiter glabra vel sparsim puberula secus costam, abaxialiter puberulenta vel fere glabra; petiolo 1-2.5(-3) cm longo. Inflorescentiae terminale, cymosae. Flores bisexuales; calyce campanulato, 3.5-4 mm longo, 5-lobo, extra glabro; corolla alba, campanulata, 4.5-5.5 mm longa. Fructus drupaceus, depresso-globosus, 3.5-4.5 mm longus, 4-5 mm in diam.; pyrenis 4, porcati.

TYPUS. — *Service Forestier: SF28492 (Capuron)*, Madagascar, Prov. Fianarantsoa, vestiges de forêt tropophile, dans la vallée de la Menarahaka, à l'est d'Ihoso, 22°19'S, 46°16'E, fl., 19 Dec. 1968 (holo-, P!; iso-, MO!, P!, TEF!).

Shrub or tree to 10 m tall, the bark exfoliating, the twigs glabrous. Leaves deciduous, alternate, borne only on the current season's growth; blades

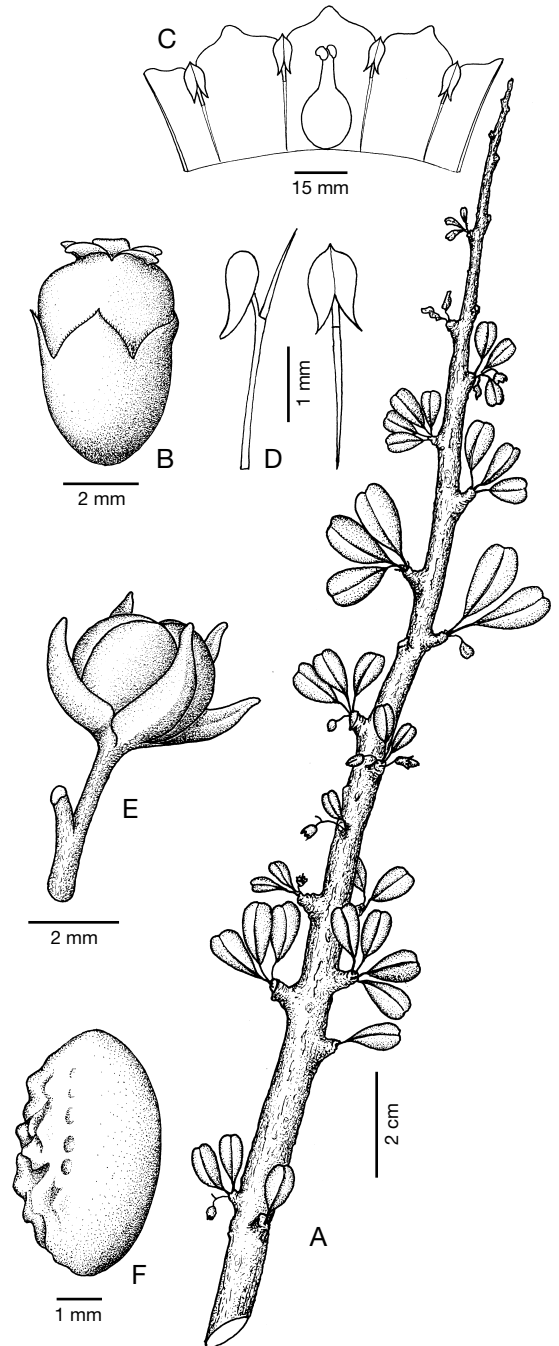


Fig. 12. — *Hilsenbergia leslieae* J.S. Mill.: **A**, flowering branch; **B**, whole flower; **C**, open corolla with androecium and gynoecium; **D**, lateral and frontal view of anther; **E**, whole fruit with persistent calyx; **F**, lateral view of pyrene. A-D, *Miller & Miller 3787*; E, F, *Phillipson et al. 3450*. Drawn by A. Jouy.

elliptic, 1.5-5.5 cm long, 0.8-3 cm wide, the apex acuminate, the base cuneate to decurrent, the margin entire, slightly thickened and distinctly involute near the base, the adaxial surface glabrous or with a few scattered hairs along the midrib, the abaxial surface evenly to sparsely puberulent or nearly glabrous, the venation brochidodromous, the midrib even with the adaxial surface or slightly impressed near the base, raised on the abaxial surface, the secondary veins 4-6, noticeably parallel, the tertiary venation reticulate; petioles 1-2.5(-3) cm long, glabrous, tightly canaliculate on the adaxial surface.

Inflorescences terminal, cymose, the branches glabrous. Flowers bisexual; calyx campanulate, 3.5-4 mm long, 3-4 mm wide, 5-lobed, the lobes valvate, triangular, 2-2.5 mm long, glabrous on both surfaces but sometimes minutely puberulent on the margins of the lobes; corolla campanulate, 4.5-5.5 mm long, 4.5-5 mm wide, 5-lobed, the lobes ovate, 1.3-1.7 mm long; stamens 5, the filaments 3-3.5 mm long, the upper 2-2.7 mm free, glabrous, the anthers ellipsoid c. 1 mm long; ovary conical, 1.5-2 mm long, 1-1.5 mm wide, the style 2-2.2 mm long, dichotomously branched at the apex or not, the 2 stigmas capitate.

Fruits drupaceous, color at maturity unknown, borne in the persistent, cup-shaped to spreading calyx, depressed globose, 3.5-4.5 mm long, 4-5 mm in diameter, the endocarp bony, separating into 4, single-seeded pyrenes at maturity, 3-4 mm long, 2-2.5 mm wide, ridged. — Fig. 13.

Hilsenbergia lowryana can be recognized by long-petiolate leaves with blades that are elliptic and nearly glabrous. HUMBERT's collections note that the fruits of this species are edible and that the wood is used for heating. With the exception of a single sterile specimen I was able to make in 2003, this species has not been collected since 1969. It occurs to the east of Tuléar, in the region that supplies most of the charcoal to the city. There is evidence that this species is being selectively gathered, as it is valued as a fuelwood, and its exploitation has significantly reduced its abundance and narrowed its distribution.

It is named in honor of Porter P. LOWRY II, a close friend and professional colleague, who has

done so much to promote the study of the Malagasy flora, who has contributed through his own collections and publications, and who accompanied me on several field trips in Madagascar.

DISTRIBUTION. — *Hilsenbergia lowryana* is known only from southwestern Madagascar (Fig. 11).

VERNACULAR NAMES. — Lambora, Lamboro, Lambotaha, Malamasafoy.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia lowryana* occurs at scattered localities in southern Madagascar. However, with the exception of a single collection in 2003, it has not been collected for more than 30 years and it has not been recorded from any protected areas, although it is known from near the Parc National de Zombitsy.

PARATYPES. — MADAGASCAR: *Humbert 11556*, Prov. Toliara, basse vallée du Fiherenana, forêt et bush sur calcaire, 50-200 m, 23°18'S, 43°36'E, fr., Nov. 1933 (P!); *Humbert 20200bis*, Prov. Toliara, vallée de l'Onilahy près de Tongobory, à Ranomay, forêt xérophile des coteaux et plateaux calcaires rocaillieux, 80-200 m, 23°34'S, 44°20'E, stér., 6-8 Feb. 1947 (P!); *Miller et al. 10742*, Prov. Toliara, Km 64 on Route Nationale 7, W of Toliara, deciduous forest; highly disturbed with trees cut, on calcareous rock, 360 m, 23°10'22"S, 44°03'45"E, ster., 29 Jan. 2003 (MO!, P!, TAN!); *Service Forestier: SF5914 (Bototsalaendry)*, Prov. Toliara, Andamasiny-Vineta, Km 90, route Tuléar - Tananarive, 23°01'S, 44°15'E, fl., 8 Nov. 1952 (MO!, P!); *Service Forestier: SF12599 (Dinard)*, Prov. Toliara, Tuléar, 23°21'S, 43°40'E, fr., 20 Oct. 1954 (P!); *Service Forestier: SF15597*, Prov. Toliara, Vineta, Behena, Majaboboka, Tuléar, 480 m, 23°01'S, 44°15'E, fl., 20 dec. 1955 (P!, TEF!); *Service Forestier: SF20753 (Capuron & Chauvet)*, Prov. Toliara, Andranovory, route de Tuléar - Sakaraha, au PK 47, à 2 km à l'est d'Andronahimaly, 400 m, 23°15'S, 44°01'E, fl., 8 Jan. 1962 (P!); *Service Forestier: SF27853bis (Capuron)*, Prov. Fianarantsoa, vestiges de forêt dans le haut bassin de la Menarahara, à l'est d'Ihosa, 22°19'S, 46°16'E, fl., 5 Nov. 1967 (P!, TEF!); *Service Forestier: SF27944 (Capuron)*, Prov. Toliara, Andranovory, formations de transitions entre le bush et la forêt trophophile, vers le PK 48 de la route Tuléar - Sakaraha, 23°16'S, 44°E, fl., 8-12 Nov. 1967 (P!, TEF!); *Service Forestier: SF28937 (Capuron)*, Prov. Toliara, Sorita, crêtes et barres calcaires, au lieu-dit Ankiranja, à 30-35 km de Manja, sur la route de Bevoay, 198 m, 21°32'S, 44°E, fl., 3-4 Dec. 1969 (P!,

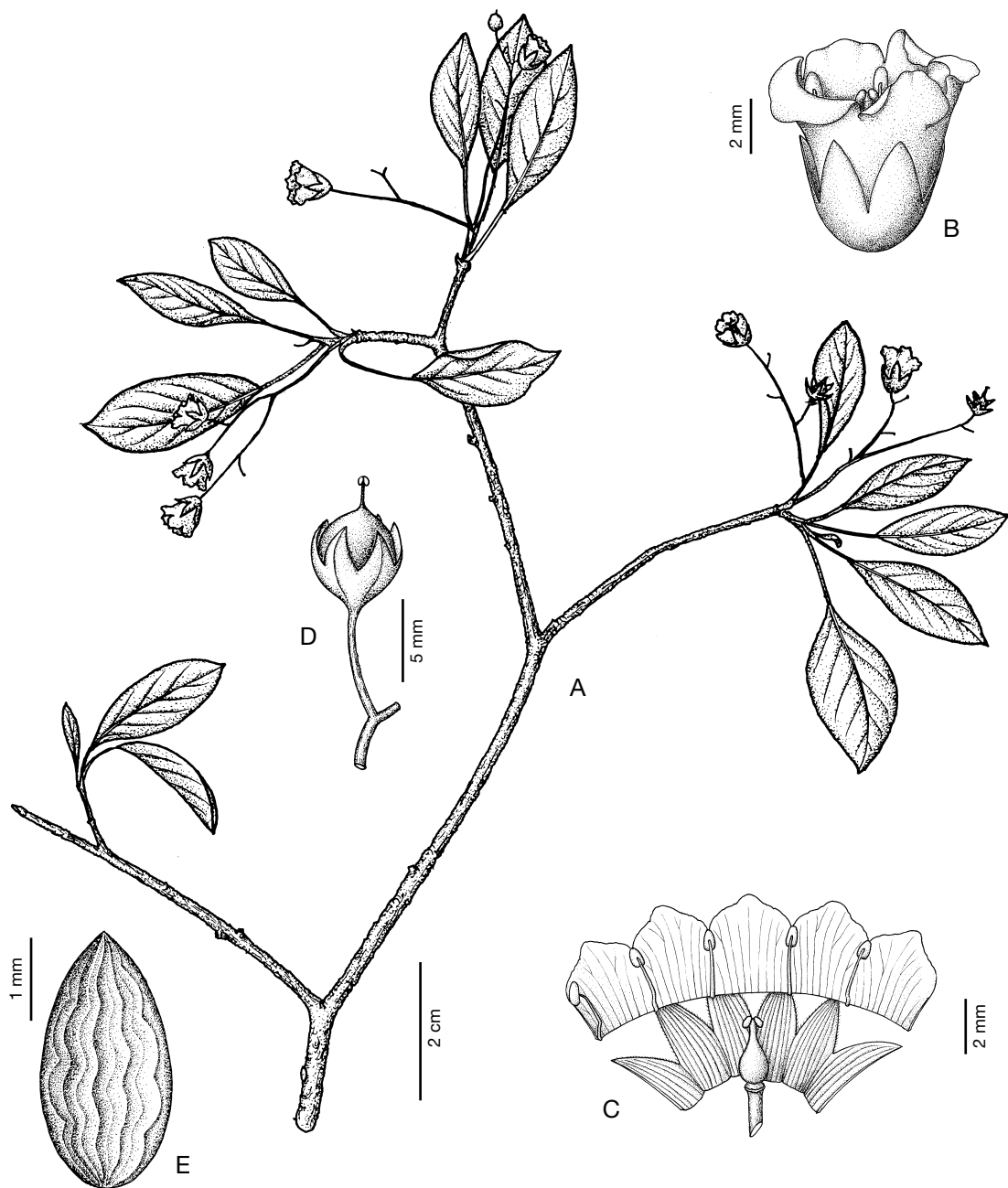


Fig. 13. — *Hilsenbergia lowryana* J.S. Mill.: **A**, flowering branch; **B**, whole flower; **C**, flower with opened calyx showing gynoecium and opened corolla showing androecium; **D**, whole fruit with persistent calyx; **E**, dorsal surface of pyrene. A-C, *Service Forestier*: SF28492 (Capuron); D, E, *Humbert 11556*. Drawn by A. Jouy.

TEF!); *Service Forestier: SF4-R-82*, Prov. Toliara, forêt d'Ankazomalanga, près d'Andranovory, canton Maromiandra, 700 m, 22°46'S, 44°42'E, ster., 30 Nov. 1953 (MO!, P!); *Service Forestier: SF112-R-226*, Prov. Toliara, au nord du village d'Ankilimilopaka dans la savane arborée, canton Bekitro, 24°40'S, 45°27'E, ster., 18 May 1954 (P!); *Service Forestier: SF921-R-1*, Prov. Toliara, J.B. 10, Beando, 400 m, 23°10'S, 44°04'E, ster., 14 Feb. 1955 (P!).

11. *Hilsenbergia lyciacea* (Thulin) J.S. Mill., comb. nov.

Bourreria lyciacea Thulin, Nord. J. Bot. 7: 415 (1987).
— Type: *Thulin & Warfa 4506*, Somolia, Middle Juba Region, 14 km on the Jelib-Camsuma road, near Shek Ahmed Yare, 6 May 1983 (holo-, UPS; iso-, K!, MOG).

Shrub or small tree to 6 m tall, densely branched, the newly emerging twigs puberulent, later glabrous and often with a thin waxy surface layer. Leaves alternate, but mostly in fascicles at the tips of branches and on short lateral spur shoots, deciduous; blades elliptic to obovate, the broadest point at or above the middle, 8-22 (-25) mm long, 3-10(-14) mm wide, the apex obtuse to rounded or emarginate, the base acute to cuneate, the margin entire and tightly revolute, the adaxial surface scabrous, evidently rough to the touch, the hairs from a basal, multi-cellular cystolith, the abaxial surface densely tomentose to scabrid or completely glabrous; petioles 1-4 (-6) mm long, scabrous to stiffly pubescent or tomentose, strongly canaliculate on the adaxial surface.

Inflorescences terminal, small cymes with up to 5(-10) flowers, the peduncles 5-10 mm long, the branches stiffly pubescent to nearly glabrous. Flowers bisexual or apparently female, on pedicel-like branches 1-5 mm long; calyx campanulate, 3-4 mm long, 3.5-5 mm wide, 5-lobed, the lobes valvate, triangular, 1.5-2 mm long, densely pubescent to glabrous on the exterior surface, glabrous to sparsely pubescent on the inside of the lobes; corolla white to pale yellow-green, campanulate, 4-6 mm long, 4-6 mm wide, 5-lobed, the lobes erect to spreading, broadly ovate and crisped along the margin, 1-1.5 mm long; stamens 5, the filaments 1-3 mm long, the upper

0.8-2.2 mm free, glabrous, the anthers ellipsoid to lanceoloid 0.6-1 mm long; ovary conical, 1-2 long, 1-1.5 mm wide, the style 1-2.5 mm long, the 2 stigmas capitate.

Fruits drupaceous, color at maturity unknown, borne nearly enclosed in the persistent, cup-shaped calyx, globose, 4-5 mm long, 4-5 mm in diameter, the endocarp bony, separating into 4 single-seeded pyrenes, 2.5-3 mm long, 1.5-1.7 mm wide, ridged on the exterior surface.

Hilsenbergia lyciacea has previously been reported only from Kenya, Somalia, and Ethiopia. The Malagasy populations are quite similar in appearance to those from continental Africa, differing only in sometimes having a greater number of flowers per inflorescence. In addition, the calyx in the Malagasy populations ranges from completely glabrous to densely pubescent while the African populations have calyces that are consistently glabrous. Because of these differences, the full description provided above is based only on the Malagasy populations to demonstrate both similarities and differences from the original description by THULIN (1987), which was based solely on East African plants. This species is somewhat similar to *Bourreria teitensis* (Gurke) Thulin, which occurs in Kenya, Tanzania, and Somalia, but that species differs in having larger leaves and glandular pubescence on the inflorescence branches.

CAPURON described *H. lyciacea* as dioecious and collected two individuals from the same population (*SF28987*, male; *SF28988*, female) in excellent flowering condition. The plant that CAPURON labeled male, looks very much like those found in normal bisexual *Hilsenbergia* flowers, with stigmas and stamens borne at nearly the same height; no fruit are evident setting on the specimen. The plant that CAPURON labeled female has a gynoeceum very similar to that from other plant, but has stamens that are noticeably smaller, with the filaments only 1 mm long and attached only at the very base, and anthers that are reduced in size and have not dehisced; this specimen has fruits of several developmental stages present in addition to the flowers. Lacking paired collections, the interpretation of breeding

systems from other populations is not so straight forward. Some specimens appear to have bisexual flowers, some exhibit flowers with very reduced stamens, and some collections having flowers with full size stamens (morphologically similar to CAPURON's male plant) have developing fruits evident on the herbarium specimens. While it is thus apparent that variability exists in the sexual system of this species, additional field studies will be necessary in order to fully understand the variation present.

This species is reported to be used as an indigenous medicine in Madagascar to treat diarrhea and hemoraging (Humbert 20240).

DISTRIBUTION. — *Hilsenbergia lyciacea* is known from southern Somalia, Ethiopia, and eastern Kenya and also occurs in southwestern Madagascar (Fig. 14).

VERNACULAR NAMES. — Adriamanindry, Hazomara, Nato.

CONSERVATION STATUS. — Provisional IUCN Red List Category (Malagasy populations): Endangered (EN B2ab(i-iv)). *Hilsenbergia lyciacea* is known from scattered localities in southern Madagascar, where it is provisionally endangered, but it also occurs in east Africa (THULIN 1987). It is known to occur in the Réserve Naturelle Intégrale de Tsimanampetsotsa and the dry parcel of the Parc National d'Andohahela.

MATERIAL EXAMINED. — MADAGASCAR: *Decary 3059*, Prov. Toliara, Behara, terrain cristallin, 24°57'S, 46°23'E, fl., 1 Sep. 1924 (P!); *Decary 3076*, Prov. Toliara, Behara, terrain cristallin, 24°57'S, 46°23'E, fl., 1 Sep. 1924 (P!); *Decary 9354*, Prov. Toliara, Beteny, 24°27'S, 46°26'E, fl., 22 Nov. 1931 (P!); *Humbert 2943bis*, Prov. Toliara, de la vallée de la Sakamena à la vallée de La Sakoa, bassin de l'Onilagy, à l'est de Betioky, vers 300 m, 23°45'S, 44°33'E, fr., 16 Mar. 1955 (P!); *Humbert 20240*, Prov. Toliara, environs du lac Tsimanampetsotsa, 2-200 m, 24°08'S, 43°47'E, fl., 14 Feb. 1947 (P!); *Methuen s.n.*, Prov. Toliara, Ampanihy, 24°42'S, 44°45'E, fl., 29 Oct. 1911 (K!); *Miller et al. 10743*, Prov. Toliara, 20 km NE of Tuléar on Route Nationale 7, La Table, deciduous forest on limestone, 130 m, 23°24'33"S, 43°47'02"E, ster., 29 Jan. 2003 (MO!, P!, TAN!); *Miller & Miller 3782*, Prov. Toliara, 14 km SE of Tuléar on the road to Sakaraha, 100 m, 23°21'S, 43°42'E, ster., 26 Dec. 1988 (P!); *Miller & Schatz*

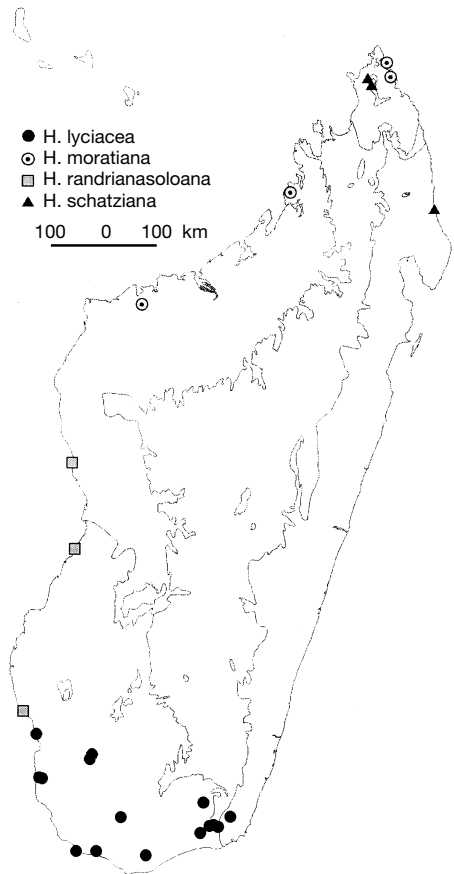


Fig. 14. — Distributions of *Hilsenbergia* species, mapped on the simplified bioclimate zones of Madagascar (after CORNET 1974; see SCHATZ 2000).

3744, Prov. Toliara, 12 km W of Tuléar on the road to Sakaraha, low deciduous forest on the plateau above Tuléar, 150 m, 23°21'S, 43°42'E, fl., 12 Dec. 1988 (MO!); *O'Connor 42*, Prov. Toliara, Berenty, 25°01'S, 46°17'E, fl., Dec. 1984 (K!); *O'Conner 68*, Prov. Toliara, Berenty, 25°01'S, 46°17'E, fl., 4 Nov. 1984 (K!); *Phillipson 2441*, Prov. Toliara, Beza Mahafaly Reserve, near Betioky, Parcelle 2, 180 m, 23°40'S, 44°35'E, fl., 23 Oct. 1987 (K!, MO!, P!); *Phillipson 2835*, Prov. Toliara, Réserve d'Andohahela, Parcelle 2, NE of Amboasary near Hazofotsy, 100 m, 24°50'S, 46°32'E, fl., 7 Dec. 1988 (K!, MO!, P!); *Phillipson 2961*, Prov. Toliara, Réserve d'Andohahela, Parcelle 2, near Hazofotsy, 75 m, 24°50'S, 46°32'E, fr., 22 Dec. 1988 (K!, MO!, P!); *Phillipson & Rabesihanaka 3145*, Prov. Toliara, Réserve de Tsimanampetsotsa, NW corner of Reserve, 50 m, 24°04'S, 43°46'E, fl., fr., 11 Jan. 1989 (K!, MO!, P!); *Raveohitra 2400*, Prov. Toliara,

préfecture de Fort-Dauphin, sur la route Ambovombe-Toliara, à 10-20 km de Tsihombe, 25°19'S, 45°29'E, fr., 19 Oct. 1990 (MO!); *Rakotomalaza 586*, Prov. Toliara, Andohahela, RNI, parcelle 2, ENE Ihazofotsy, bord de la route, près du campement 6, 120 m, 24°49'S, 46°37'E, fl., 12 Dec. 1995 (MO!); *Réserves Naturelles: RN9428 (Rakotoson)*, Prov. Toliara, Andohahela, RNI, Marotoka, Behara, dist. Amboasary, 24°57'S, 46°23'E, fl., 22 June 1957 (P!, TEF!); *Service Forestier: SF34-R-18*, Prov. Toliara, 20 km sur la route Ampanihy - Tranoroa, 24°42'S, 45°04'E, ster., 11 Dec. 1953 (P!); *Service Forestier: SF8536 (Capuron)*, Prov. Toliara, aux environs d'Ambatoabo, dist. de Fort Dauphin, 24°51'S, 46°41'E, fl., s.d. (P!); *Service Forestier: SF22263 (Capuron)*, Prov. Toliara, plateau calcaire aux environs de la Table, Tuléar, 23°20'S, 43°40'E, fr., 12 Dec. 1962 (MO!, P!, TEF!); *Service Forestier: SF27999 (Capuron)*, Prov. Toliara, entre Amboasary et Ranomainty, 24°41'S, 46°53'E, fr., 17 Nov. 1967 (MO!, P!, TEF!); *Service Forestier: SF28987 (Capuron)*, Prov. Toliara, calcaires et argiles sur la route d'Ampanihy à Bevoalavo, au sud de l'embranchement de Befotaka, 25°15'S, 44°20'E, fl., 10 Dec. 1969 (MO!, P!); *Service Forestier: SF28988 (Capuron)*, Prov. Toliara, calcaires et argiles sur la route d'Ampanihy à Bevoalavo, au sud de l'embranchement de Befotaka, 25°15'S, 44°20'E, fl., 10 Dec. 1969 (MO!, P!, TEF!).

12. *Hilsenbergia moratiana* J.S. Mill., sp. nov.

Arbor usque ad 8 m alta, cortice in laminas exfoliante, ramunculis glabris. Folia decidua, alterna; lamina lanceolata usque lanceolata-ovata, interdum leviter falcata, 6-14.5 cm longa, 2-5.5 cm lata, apice acuminata usque attenuata vel acuta, basi acuta usque obtusa, margine integra, utrinque glabra; petiolo 1.5-5 cm longo. Inflorescentia terminale interdum ut videtur subterminalis, cymosa, 3-13 cm latae. Flores bisexuales; calyce campanulato, 3.5-5 mm longo, 5-lobo, extus glabro vel granulati usque minute puberulo, intus dense puberulo usque tomentosus; corolla alba, urceolata, 4-6 mm longa. Fructus drupaceus, aurantiacus, globosus, 6-8 mm longus, 6-7 mm in diam.; pyrenis 4, matures non visis.

TYPUS. — *Service Forestier: SF24435 (Capuron)*, Madagascar, Prov. Antsiranana, forêt d'Orangéa, à l'est de Diégo-Suarez, 12°15'S, 49°24'E, fl., fr., 25 Jan. 1966 (holo-, P!; iso-, MO!, P!).

Tree to 8 m tall, 30 cm dbh, the bark exfoliating in plates, the twigs glabrous. Leaves deciduous, alternate; blades lanceolate to lance-ovate, the widest point below the middle, sometimes somewhat falcate, 6-14.5 cm long, 2-5.5 cm

wide, the apex acuminate to attenuate or acute, the base acute to obtuse, the margin entire, glabrous on both surfaces, the venation brochidodromous, the midrib even with or slightly impressed on the adaxial surface, raised on the abaxial surface, the secondary veins 8-13, the tertiary venation reticulate; petioles 1.5-5 cm long, glabrous, canaliculate on the adaxial surface.

Inflorescences terminal or appearing subterminal and lateral as shoot elongation continues, cymose, 3-13 cm broad, the peduncle 1.5-3 cm long, the branches glabrous, with small leaf-like bracts subtending the flowers, these 2.5-3 mm long, pubescent on the adaxial surface. Flowers bisexual; calyx campanulate, 3.5-5 mm long, 4-5 mm wide, 5-lobed, the lobes deltate, 1.5-2 mm long, glabrous or granular to minutely puberulent on the exterior surface, densely puberulent to tomentose on the interior surface and appearing ciliate on the margin of the lobes; corolla white, urceolate, the tube 4-6 mm long, 5-lobed, the lobes widely to depressed-ovate, 1-1.5 mm long, 1.5 mm wide; stamens 5, the filaments 4-5 mm long, the upper 1-1.5 mm free, glabrous, the anthers ellipsoid, 1.5-2 mm long; ovary ovoid, 1.5-2 mm long, 1.5-2 mm wide, the style 3-4 mm long, the 2 stigmas capitate.

Fruits drupaceous, orange at maturity, borne in the 8-12 mm broad persistent calyx, globose 6-8 mm long, 6-7 mm in diameter, the endocarp bony, separating into 4 pyrenes at maturity, mature pyrenes not seen. — Fig. 15.

Hilsenbergia moratiana is similar in appearance to *H. schatziana*, and the two are probably closely related, but it is easily distinguished from that species by the small, leafy bracts that it has in its inflorescence. It is named in honor of Prof. Philippe MORAT who has collected extensively in Madagascar, published prolifically on the taxonomy of the Malagasy flora, and has provided much encouragement and support for this study.

DISTRIBUTION. — *Hilsenbergia moratiana* occurs on sandy substrates in northern Madagascar (Fig. 14).

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(I-iv)). *Hilsenbergia moratiana* is known only from three

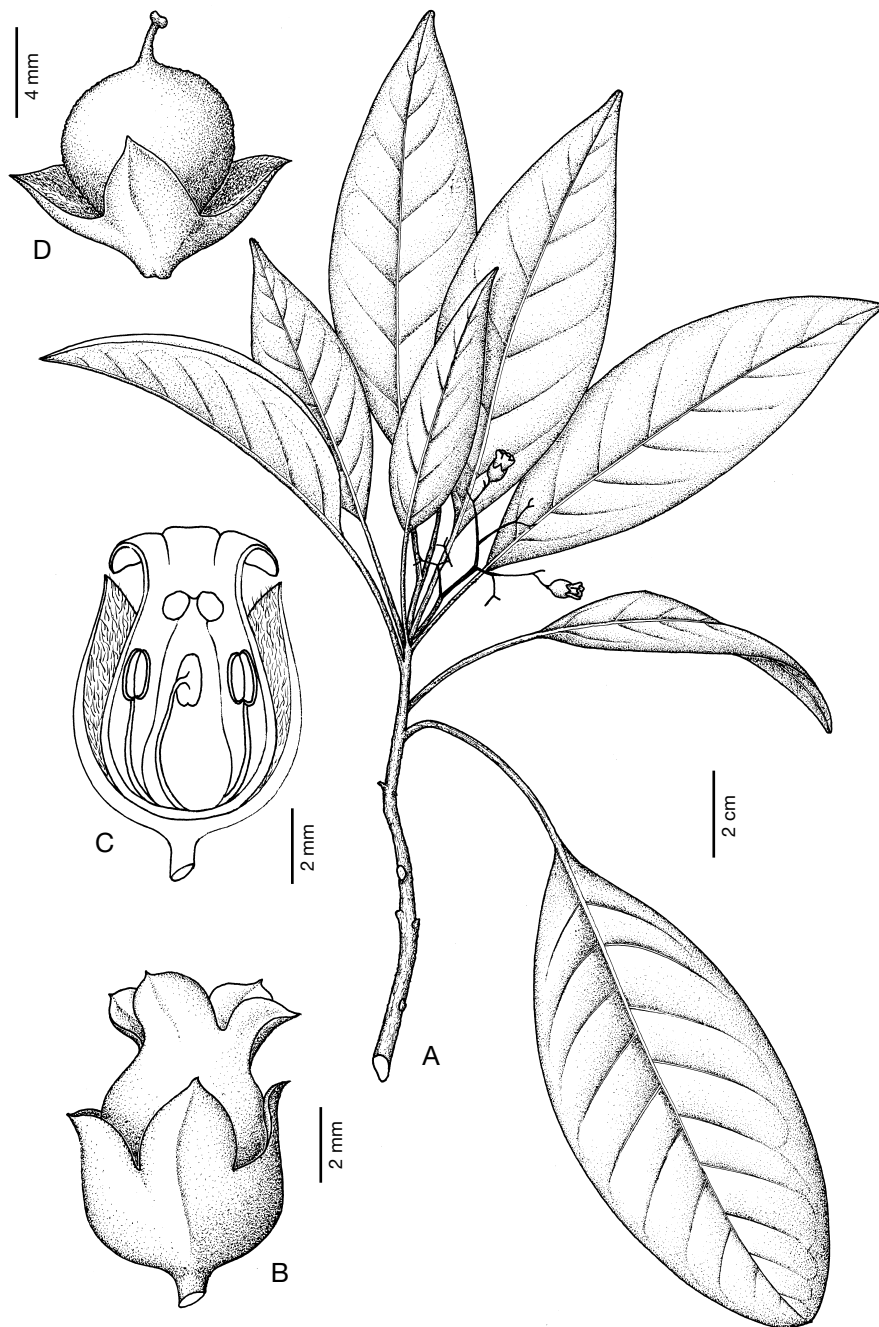


Fig. 15. — *Hilsenbergia moratiana* J.S. Mill.: **A**, flowering branch; **B**, whole flower; **C**, open flower showing androecium and gynoecium; **D**, whole fruit with persistent calyx. *Service Forestier*: SF24435 (Capuron). Drawn by A. Jouy.

scattered localities in northern Madagascar, none of which are currently protected. Its Extent of Occurrence is limited to 40 km².

PARATYPES. — MADAGASCAR: *Perrier de la Bâthie* 1793, Prov. Mahajanga, bois sablonneux, Manongarivo, Ambongo, 16°16'S, 45°22'E, fl., Oct. 1904 (MO!, P!); *Service Forestier: SF26-R301*, Prov. Mahajanaga, Analanitsiny, Amboloboza, 14°25'S, 47°49'E, ster., 25 Jan. 1955 (P!); *Service Forestier: SF24485 (Capuron)*, Prov. Antsiranana, sables, près d'Antsoha, à l'ouest de la baie de Rigny, 12°29'S, 49°28'E, fl., 27 Jan. 1966 (P!, TEF!); *Service Forestier: SF24689 (Capuron)*, Prov. Antsiranana, partie sud de la forêt d'Orangea, à l'est de Diégo-Suarez, 12°15'S, 49°24'E, fr., 24 June 1966 (P!, TEF!); *Service Forestier: SF28750 (Capuron)*, Prov. Antsiranana, forêt d'Orangea, sur sables, à l'est de Diégo-Suarez, 12°15'S, 49°24'E, fl., fr., 1 Feb. 1969 (P!, TEF!).

**13. *Hilsenbergia nemoralis* (Gürke) J.S. Mill.,
comb. nov.**

Ehretia nemoralis Gürke, in Engler A. & Prantl K., Die Natürlichen Pflanzenfamilien IV. 3a: 336 (1893). — *Bourreria nemoralis* (Gürke) Thulin, Nord. J. Bot. 7: 415 (1987). — Lectotype (here designated): *Holst 2814*, Tanzania, Tanga District, Amboni, (B; iso-, K!).

Ehretia litoralis Gürke, in Engler, Pflanzenw. Ost-Afr. C: 335 (1895). — Lectotype (here designated): *Holst 2115*, Tanzania, Tanga (B; iso-, K!).

While VERDCOURT (1991) indicated that this species might be only varietally distinct from *H. petiolaris*, the two appear easily distinguished and I have maintained it as separate.

DISTRIBUTION. — *Hilsenbergia nemoralis* occurs in coastal areas of eastern Africa from Kenya to Mozambique (THULIN 1987; MARTINS 1990; VERDCOURT 1991).

**14. *Hilsenbergia orbicularis* (Hutch. & E.A. Bruce) J.S. Mill.,
comb. nov.**

Ehretia orbicularis Hutch. & E.A. Bruce, Kew Bull. 1941: 159 (1941). — *Bourreria orbicularis* (Hutch. & E.A. Bruce) Thulin, Nord. J. Bot. 7: 415 (1987). — Type: *J.B. Gillett 4472*, Somalia, Afard, 690 m, 48°08'E, 10°10'N, fl., 26 Oct. 1932 (holo-, K!).

Hilsenbergia orbicularis is a poorly known species from Ethiopia and Kenya and additional collections will be required to clarify its relationship with *H. teitensis*. The two are similar in appearance, are the only two species of the genus with glandular hairs, and appear closely related.

DISTRIBUTION. — *Hilsenbergia orbicularis* occurs in Somalia and eastern Ethiopia (THULIN 1987; VERDCOURT 1991).

**15. *Hilsenbergia petiolaris* (Lam.) J.S. Mill.,
comb. nov.**

Ehretia petiolaris Lam., Encycl. Méth. Bot. A: 527 (1785). — *Bourreria petiolaris* (Lam.) Thulin, Nord. J. Bot. 7: 414 (1987). — Type: *Cultivé au jardin du Roi*, Mauritius (holo-, P-LAM!). *Hilsenbergia ehretia* Meisn., Pl. Vasc. Gen. Comment.: 198 (1840). — Lectotype (here designated): *Sieber Fl. Maurit. II: 160*, Mauritius (P!; iso-, K!, PR!, PRC!).

Hilsenbergia petiolaris is one of only two species that occur in both eastern Africa and the Indian Ocean. It is similar in appearance to *H. nemoralis* from east Africa, from which it differs in being consistently glabrous on the lower surface of its leaves, and *H. comorensis* from the Comores, from which it differs in having elliptic leaf blades that are widest at the middle and obtuse to acute at the base; *Hilsenbergia comorensis* has leaf blades that are ovate to lanceolate, widest below the middle, and rounded at the base.

DISTRIBUTION. — *Hilsenbergia petiolaris* occurs in coastal areas of eastern Africa from Kenya to Mozambique and also in the Mascarenes (THULIN 1987; MARTINS 1990; VERDCOURT 1991).

**16. *Hilsenbergia randrianasoloana* J.S. Mill.,
sp. nov.**

Arbor parva, cortice fissurato, ramunculis puberulis. Folia decidua, alterna; lamina elliptica usque obovata, 2.5-5.5 cm longa, 1-3.5 cm lata, apice acuta usque obtusa vel leviter acuminata, basi acuta usque obtusa, margine integra, revoluta, utrinque sparsim strigillosa;

petiolo 0.5-3.5 cm longo. Inflorescentia floresque non visi. Fructus drupaceus, depresso-globosus, 3-4 mm longus, 4-5 mm in diam.; pyrenis 4, porcati.

TYPUS. — *Service Forestier*: SF15554, Madagascar, Prov. Toliara, Morondava, forêt d'Antanambao, 20°17'S, 44°17'E, fr., 8 Feb. 1956 (holo-, P!; iso-, K!, MO!, P!, TEF!).

Small tree, the bark fissured, the twigs puberulent. Leaves deciduous, borne on the current season's growth, alternate; blade elliptic to obovate, the broadest point at or above the middle, 2.5-5.5 cm long, 1-3.5 cm wide, the apex acute to obtuse or slightly acuminate, the base acute to obtuse, the margin entire, tightly revolute, the adaxial surface sparsely, but evenly, strigillose, the hairs appressed and parallel, the abaxial surface sparsely, but evenly, strigillose, the hairs not all parallel, the venation brochidodromous, the midrib slightly impressed on the adaxial surface, raised on the abaxial surface, the secondary veins 3-5, the tertiary venation reticulate; petioles 0.5-3.5 cm, narrowly canalicate on the adaxial surface, strigillose. Flowers unknown.

Fruits drupaceous, color at maturity unknown, borne in the persistent spreading calyx, the calyx lobes not fully separating so the fruiting calyx 3-5-lobed, globose, 3-4 mm long, 4-5 mm in diameter, the endocarp bony, separating into 4, single-seeded pyrenes at maturity, c. 3 mm long, 2 mm wide, prominently ridged on the exterior surface. — Fig. 16.

Hilsenbergia randrianasoloana is an apparently rare tree of southwestern Madagascar that differs from other members of the genus in having leaves that are strigillose on the lower surface and inflorescences that are reduced to only a single branch, thus appearing racemose or nearly so. *Hilsenbergia randrianasoloana* is named in honor of my friend and fellow researcher Armand RANDRIANASOLO, a specialist who has contributed significantly to our understanding of the taxonomy of Malagasy Anacardiaceae and who has often traveled with me and helped support my interest in the flora of Madagascar in numerous ways.

DISTRIBUTION. — *Hilsenbergia randrianasoloana* is known from only three collections from

southwest Madagascar (Fig. 14) where it occurs on basalt.

VERNACULAR NAMES. — Korindy, Vatoa.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia randrianasoloana* is known from only three scattered localities along the west coast of Madagascar, none of which are protected, and it has not been collected for nearly 50 years.

PARATYPES. — *Humbert 20059*, Prov. Toliara, Manambo Atsimo, environs de Manombo, colline basaltique d'Ambatomainty, 150 m, 22°57'S, 43°27'E, ster., 29-30 Jan. 1947 (P!); *Service Forestier*: SF24617 (*Capuron*), Prov. Mahajanga (Menabe), tables basaltiques au SW du Cap Kimby, Antsalova, 18°52'S, 44°14'E, fr., 1 Apr. 1966 (P!, TEF!).

17. *Hilsenbergia schatziana* J.S. Mill., *sp. nov.*

Arbor 10-15 m alta, ramunculis glabris. Folia decidua, alterna; lamina elliptica, (3.5-)5-9(-16) cm longa, 2.4-5.5(-7.5) cm lata, apice acuta usque acuminata, basi cuneata vel acuta usque obtusa, margine integra, utrinque glabra. Inflorescentiae terminalis vel subterminalis, cymosae, 3-7 cm latae. Flores bisexuales; calyce campanulato, 5-6 mm longo, 5-lobo, extus glabro, intus tomentosus; corolla alba, campanulata, c. 7 mm longa. Fructus drupaceus, depresso-ovoideus, 9-12 mm longus, 9-12 mm in diam.; pyrenis 4, alatis.

TYPUS. — *Service Forestier*: SF11302 (*Capuron*), Madagascar, Prov. Antsiranana, massif de la Montagne d'Ambre, bassin de la rivière des Makis, 600 m, 12°37'S, 49°09'E, fl., 13 Oct. 1954 (holo-, P!; iso-, MO!, P!, TEF!).

Tree 10-15 m tall, the twigs glabrous. Leaves deciduous, alternate; blades elliptic, the widest point near or just below the middle, (3.5)5-9(-16) cm long, 2.4-5.5(-7.5) cm wide, the apex acute to acuminate, the base cuneate or acute to obtuse, the margin entire, both surfaces glabrous, the venation brochidodromous, the midrib even with or slightly impressed in the adaxial surface, raised on the abaxial surface, the secondary veins 4-6, the tertiary venation reticulate; petioles (1-)2-4(-6) cm long, glabrous, canalicate on the adaxial surface.

Inflorescences terminal or subterminal, cymose, 3-7 cm broad, the peduncles 1-2.5 cm long, glabrous, bracts lacking. Flowers bisexual;

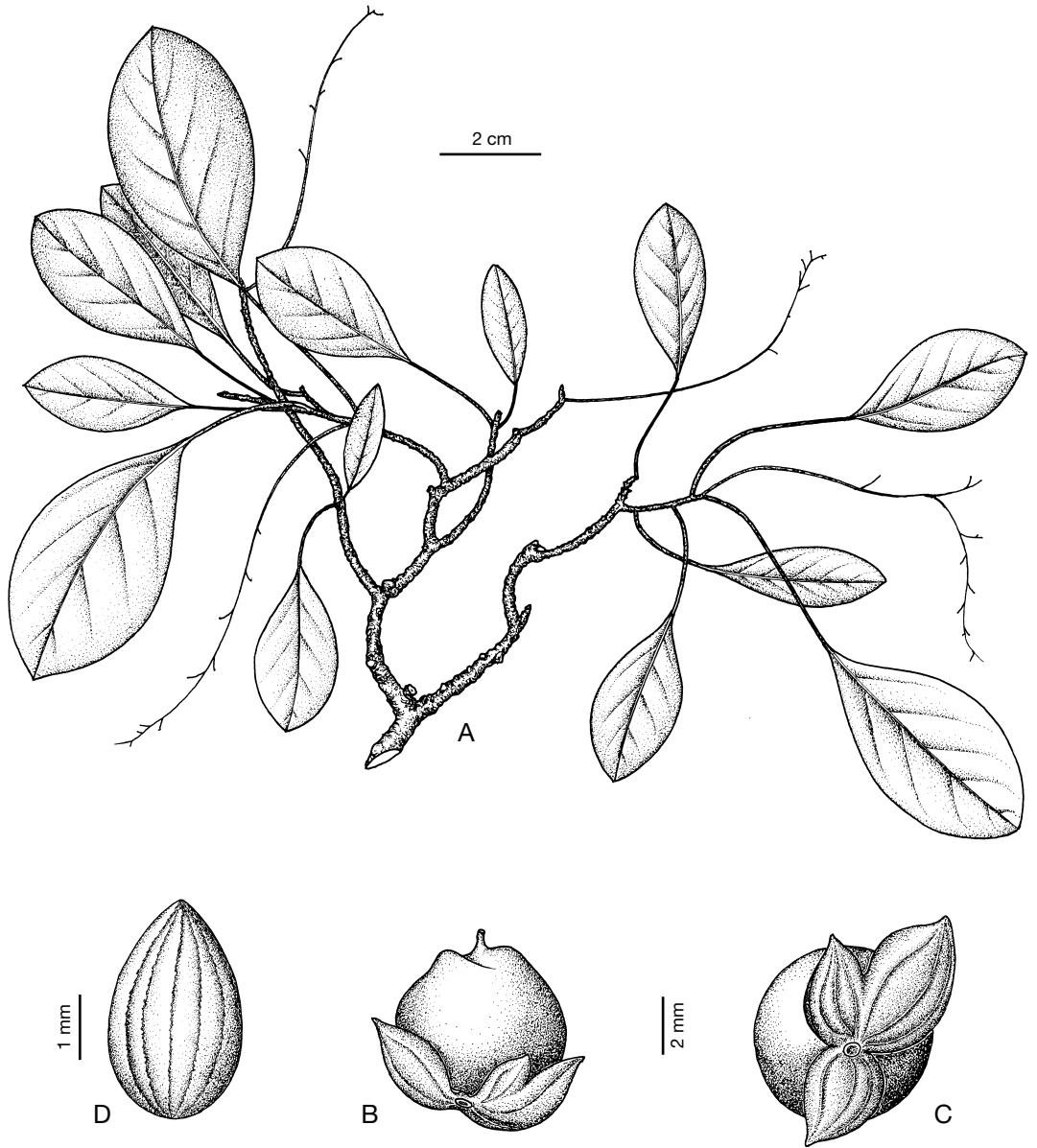


Fig. 16. — *Hilsenbergia randrianasoloana* J.S. Mill.: **A**, fruiting branch; **B**, lateral view of whole fruit with persistent calyx; **C**, basal view of whole fruit with persistent calyx; **D**, dorsal view of pyrene. *Service Forestier: SF15554*. Drawn by A. Jouy.

calyx campanulate, 5-6 mm long, 6 mm wide, 5-lobed, the lobes deltate to triangular, 2.3-3 mm long, glabrous on the outer surface, tomentose on the inner surface; corolla white, campanulate, c. 7 mm long, c. 7 mm wide, 5-lobed, the lobes

widely ovate, c. 2 mm long, c. 2 mm wide; stamens 5, the filaments 5 mm long, the upper 2-2.5 mm free, glabrous, the anthers ellipsoid, 2 mm long; ovary ovoid, c. 2 mm long, c. 2 mm wide, the style 3 mm long the 2 stigmas capitate.

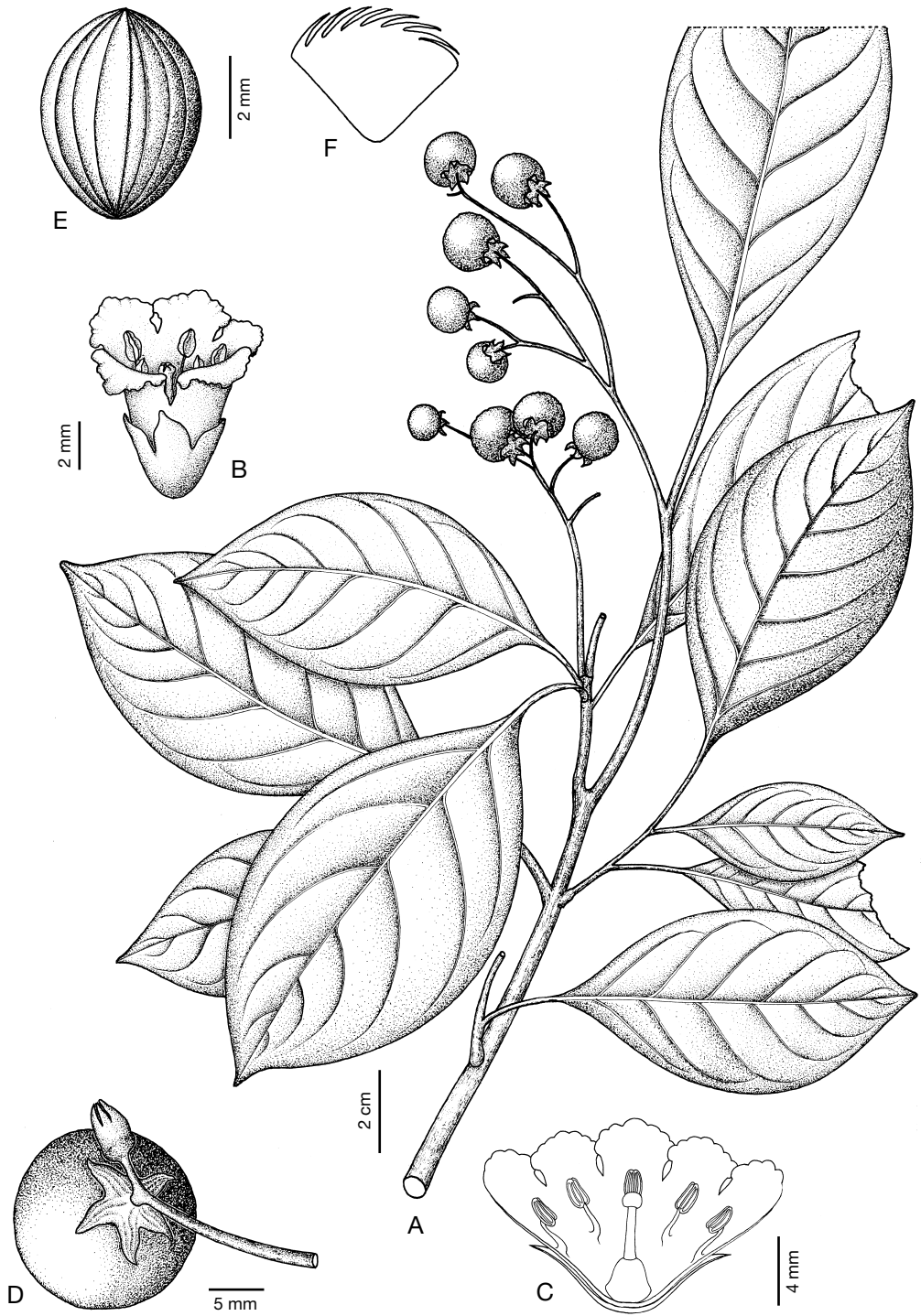


Fig. 17. — *Hilsenbergia schatziana* J.S. Mill.: **A**, fruiting branch; **B**, whole flower; **C**, flower with opened corolla showing androecium and gynoecium; **D**, whole fruit with persistent calyx; **E**, dorsal surface of pyrene; **F**, cross-section of dorsal surface of pyrene. *Service Forestier: SF27741 (Capuron)*. Drawn by A. Jouy.

Fruits drupaceous, borne in the 6-9 mm broad persistent calyx, depressed ovoid, 9-12 mm long, 9-12 mm in diameter, the endocarp bony, separating into 4 pyrenes at maturity, these 8-9 mm long, c. 4 mm wide, with papery wings on the exterior face. — Fig. 17.

Hilsenbergia schatziana is apparently a substrate specialist restricted to northern Madagascar and is distinct from other members of the genus in its large fruits, glabrous leaves, c. 7 × 7 mm corolla, and in lacking bracts in its inflorescence. It is named in honor of my colleague George SCHATZ, a leading authority on the flora of Madagascar, who's guide to the woody plant genera, and numerous other publications, have contributed so much to our understanding of the systematics and evolution of Malagasy plants.

DISTRIBUTION. — *Hilsenbergia schatziana* is known from only four collections, all from northern Madagascar (Fig. 14). It may be restricted to basalt.

CONSERVATION STATUS. — Provisional IUCN Red List Category: Endangered (EN B2ab(i-iv)). *Hilsenbergia schatziana* is known from only two populations in northern Madagascar, one of which occurs within Montagne d'Ambre National Park, and it has not been collected for nearly 50 years.

PARATYPES. — MADAGASCAR: *Service Forestier*: SF7210, Prov. Antsiranana, forêt d'Ambre, 12°37'S, 49°09'E, fr., 26 Mar. 1953 (K!, MO!, P!, TEF!); *Service Forestier*: SF11276 (*Capuron*), Prov. Antsiranana, massif de la Montagne d'Ambre, 1000 m, 12°37'S, 49°09'E, fl., 8-14 Oct. 1954 (K!, MO!, P!); *Service Forestier*: SF27741 (*Capuron*), Prov. Antsiranana, table basaltique d'Ambanitazana, près d'Andrapengy, au nord d'Antalaha, 14°40'S, 50°12'E, fr., 11 Apr. 1967 (G!, GH!, K!, MO!, P!, TEF!, WAG!).

18. *Hilsenbergia teitensis* Gurke

Boraginaceae, in Engler A., Die Pflanzenwelt Ost-Africas und der Nachbargebiete C: 336, Berlin. — Lectotype (here designated): *Holst 2409*, Tanzania, Nyika (B; iso-, K!).

Hilsenbergia teitensis is morphologically similar to both *H. lyciacea* and *H. orbicularis* and it dif-

fers from both in having a completely undivided style with two stigmas opposite one another on the apex. It differs further from *H. lyciacea* in having glandular hairs on the leaves and generally more flowers in its inflorescence.

DISTRIBUTION. — *Hilsenbergia teitensis* occurs in northeastern Tanzania, eastern Kenya, and southern Somalia (THULIN 1987; VERDCOURT 1991).

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REFERENCES

- BROWNE P. 1756. — *The Civil and Natural History of Jamaica in Three Parts*. London.
 CANDOLLE A.P. de 1845. — *Ehretia*. In *Prodromus Systematis Naturalis Regni Vegetabilis*, Paris. 9: 502-512.
 CAVANILLES A.J. 1799. — *Icones et Descriptiones Plantarum*. Madrid.
 DUCKE A. 1925. — Plantes nouvelles ou peu connues de la région amazonienne (III^e partie). *Archiv. Jard. Bot. Rio de Janeiro* 4: 1-210.

- DU PUY D.J. & MOAT J. 1996. — A refined classification of the vegetation types of Madagascar, and their current distribution: 205-218, in LOURENÇO W.R. (ed.), *Biogéographie de Madagascar*. Éditions de l'ORSTOM, Paris.
- GOTTSCHLING M. & HILGER H. 2001. — Phylogenetic analysis and character evolution of *Ehretia* and *Bourreria* (Ehretiaceae, Boraginales) and their allies based on ITS1 sequences. *Bot. Jahrb. Syst.* 123: 249-268.
- GOTTSCHLING M., HILGER H., WOLF M. & DIANE N. 2001. — Secondary structure of the ITS1 transcript and its application in a reconstruction of the phylogeny of Boraginales. *Plant Biol.* 3: 629-636.
- IUCN 2001. — *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.
- JOHNSTON I.M. 1949. — Studies in the Boraginaceae XVIII. Boraginaceae of the southern West Indies. *J. Arnold Arbor.* 30: 111-138.
- JOHNSTON I.M. 1950. — Studies in the Boraginaceae XIX. A noteworthy species from tropical America. *J. Arnold Arbor.* 31: 172-179.
- JOHNSTON I.M. 1951. — Studies in the Boraginaceae XX. Representatives of three subfamilies in eastern Asia. *J. Arnold Arbor.* 32: 1-26, 99-122.
- LOTT E.J. & MILLER J.S. 1986. — *Bourreria rubra* (Boraginaceae), a new species from coastal Jalisco, Mexico. *Ann. Missouri Bot. Gard.* 73: 216-218.
- LOUREIRO J. 1790. — *Flora Cochinchinensis*. Lisbon.
- MARTINS E.S. 1990. — Boraginaceae: 59-110, in LAUNERT E. & POPE G.B. (eds.), *Flora Zambeziaca* 7(4): London.
- MIERS J. 1869. — On the Ehretiaceae. *Contr. Bot.*: 224-256.
- MILLER J.S. 1989. — A revision of the new world species of *Ehretia* (Boraginaceae). *Ann. Missouri Bot. Gard.* 76: 1050-1076.
- MILLER J.S. 1999. — New Boraginaceae from tropical America 1: new species of *Bourreria* and *Tournefortia* from Costa Rica and a note on the publication of *Cordia collococca*. *Novon* 9: 230-235.
- MILLER J.S. 2002. — A revision of *Ehretia* (Boraginaceae) for Madagascar and the Comoro Islands. *Adansonia*, sér. 3, 24: 137-157.
- MILLER J.S. & NOWICKE J.W. 1990. — Dioecy and a reevaluation of *Lepidocordia* and *Antrophora* (Boraginaceae: Ehretioideae).
- MILLER J.S. & SIROT B. 1997. — A new species of *Bourreria* (Boraginaceae) from Costa Rica. *Novon* 7: 395-397.
- NOWICKE J.W. & MILLER J.S. 1991. — Boraginaceae, in DASSANAYAKE M.D. (ed.), *A revised handbook to the flora of Ceylon*. American Publishing Co., New Delhi.
- RETIEF E. & VAN WYK A.E. 2001. — The genus *Ehretia* (Boraginaceae: Ehretioideae) in southern Africa. *Bothalia* 31: 9-23.
- RICHARDSON A.T. 1977. — Monograph of the genus *Tiquilia* (*Coldenia*, sensu lato), Boraginaceae: Ehretioideae. *Rhodora* 79: 467-572.
- SCHULZ O.E. 1911. — *Beurreria*, in URBAN, *Symb. Antill.* 7: 45-71.
- STRUWE L., ALBERT V.A. & BREMER B. 1994. — Cladistics and family level classification of the Gentianales. *Cladistics* 10: 175-206.
- SWARTZ O. 1788. — *Nova Genera & Species Plantarum*. Stockholm.
- THULIN M. 1987. — *Bourreria* (Boraginaceae) in Tropical Africa. *Nord. J. Bot.* 7: 413-417.
- VERDCOURT B. 1991. — Boraginaceae, in POLHILL R.M. (ed.), *Flora of tropical East Africa*, London.

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