

Revision of the Malagasy species of the genus *Tricalysia* (Rubiaceae)

TIANJANAHARY RANARIVELO-RANDRIAMBOAVONJY¹, ELMAR ROBBRECHT²,
ELISABETH RABAKONANDRIANINA³ and PETRA DE BLOCK^{2*}

¹Royal Botanic Gardens, Kew Lot II J 131 B, Ambodivoanjo, Ivandry, 101 Antananarivo, Madagascar

²National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium

³Université d'Antananarivo, Faculté des Sciences, Département de Biologie et Ecologie Végétales, BP 906, 101 Antananarivo, Madagascar

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The Malagasy representatives of the large African genus *Tricalysia* (tribe Coffeeae *s.l.*) are revised. Three Malagasy species were hitherto recognized in the genus, namely *T. cryptocalyx*, *T. madagascariensis*, and *T. ovalifolia*. In this study, two species, *T. boiviniana* and *T. leucocarpa*, are transferred from the genus *Hypobathrum* and seven new species and two new subspecies are described, raising the species number for *Tricalysia* to a total of 12. This marked increase in species number is a recurring pattern for many Malagasy genera in systematically poorly known families such as Rubiaceae. All the species are described in detail and illustrated, and a list of exsiccatae and a distribution map are provided. Furthermore, the characters of the Malagasy taxa are compared with those of the continental African species, and their infrageneric status is discussed. With the exception of *T. ovalifolia*, a member of subgenus *Empogona*, all Malagasy species belong to subgenus *Tricalysia*. Because of their unisexual flowers, these species cannot be accommodated within one of the four existing sections in subgenus *Tricalysia*. A new section, *Androgyne*, is therefore recognized. © 2007 National Botanic Garden of Belgium. Journal compilation © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 155, 83–126.

ADDITIONAL KEYWORDS: *Androgyne* – Coffeeae *s.l.* – dioecy – *Hypobathrum* – intra-ovarian trichomes – Madagascar.

INTRODUCTION

With more than 100 species, *Tricalysia* is one of the larger genera of the African Rubiaceae. The coffee-like habit – the genus is the largest of Chevalier's (1947) 'faux-caféiers' – makes the genus easily recognizable, but the recognition of species is notoriously difficult. A taxonomic revision was therefore started at the herbarium of the National Botanic Garden of Belgium (BR) in 1978, and resulted in a series of papers surveying all continental African groups and investigating the tropical Asian relatives, in the past also frequently considered to belong to *Tricalysia* (Robbrecht, 1978, 1979a, 1980, 1982, 1983, 1987; Ali

& Robbrecht, 1991). Our studies segregated the genus *Sericanthe* (17 continental African species, most formerly in *Tricalysia*) and recognized and revised two subgenera: subgenus *Tricalysia*, with five sections (*Probletostemon*, *Tricalysia*, *Rosea*, *Ephedranthera*, and an unnamed Madagascan section characterized by unisexual flowers), and subgenus *Empogona*, with two sections (*Empogona* and *Kraussiopsis*). The tropical Asian representatives were believed to belong to two genera, *Diplospora* and *Discospermum*, closely and more distantly related to *Tricalysia*, respectively. A single species was found to be common to the African continent and Madagascar and other Indian Ocean Islands: *Tricalysia ovalifolia* Hiern (belonging to section *Empogona*). Our revision proved (Robbrecht, 1979a: 279) that its later redescriptions from

*Corresponding author. E-mail: deblock@br.fgov.be

Madagascar (as *Hypobathrum albicaule*), Aldabra (as *Tricalysia cuneifolia*), and the Comoro Islands (as *Hypobathrum comorense*) are synonymous.

The present paper aims to finish our work on *Tricalysia* by dealing with the Malagasy representatives, the only group for which the species have not yet been revised. It attempts to delimit and document the species, to establish and discuss their chorology, and to test the initial hypothesis (Robbrecht, 1987) that the Malagasy species (except *T. ovalifolia*) represent a fifth section in subgenus *Tricalysia*.

With the present paper, our long-term investigation of the genus enters its fourth decade. It is consequently not astonishing that the tribal position of *Tricalysia*, quite problematic when we started working on it, has changed several times over this period. *Tricalysia* was described by Richard (1830, 1834) in the tribe Cordiereae, a totally artificial assemblage for only three genera: *Cordia* (= *Alibertia*, now Gardenieae), *Tricalysia*, and *Myrmecodia* (now Psychotrieae). Classical systems (for example, Schumann, 1891) placed the genus in the Gardenieae, a then much wider concept of this tribe. Details of the subsequent taxonomic positions (Ixoreae *s.l.* = Coffeae *sensu latissimo*/Gardenieae subtribe Diplosporinae) until the publication of Robbrecht's (1988) survey of the family are given by Robbrecht (1987: 40). Recent phylogenetic analysis based on morphological and genomic data (Andreasen & Bremer, 2000), sampling six of the 13 genera concerned, proposed the merging of the Coffeae (*s.s.*, *Coffea*, and *Psilanthus* only) with the Diplosporinae. The tribal name Coffeae must be used for this widened concept. It should be borne in mind that this Coffeae *s.l.* of the 2000s seriously differs from the Coffeae *sensu latissimo* of the 1970s.

MATERIAL AND METHODS

The present revision was undertaken on preserved samples and herbarium material from the following institutions: BR, K, P, TAN, and TEF. Measurements, colours, and other details given in the descriptions are based on herbarium specimens, data derived from field notes (herbarium labels), and observations during fieldwork by two of the four authors. Vernacular names and uses are given as listed by the collectors. The plant material studied is listed by province and alphabetically by collector.

Material collected by personnel of the Malagasy 'Service des Eaux et Forêts' and the 'Conservation des Réserves Naturelles et Parcs Nationaux de Madagascar' was given consecutive numbers in the series SEFM (suffix -SF) and CRNPNM (suffix -RN) (Dorr, 1997). As it is often impossible to retrieve names and collecting numbers of individual collectors within

these series, the specimens are listed here under their series number. The following abbreviations are used in the lists of material studied: fir., fraisana (commune); fiv., fivondronana (district); fl, flowering; fok., fokotany (canton); fr, fruiting; PK, point kilométrique; RN, Route Nationale; RNI, Réserve Naturelle Intégrale; st, sterile.

MORPHOLOGY

This section discusses the features of the endemic Malagasy species, all belonging to subgenus *Tricalysia*. *T. ovalifolia*, present in Madagascar but a recent colonist from the African continent, belongs to subgenus *Empogona* and has the following features characteristic for this subgenus: long pedicels (up to 1.6 cm long) with free and alternate or subopposite bracteoles; a short calyx tube (0.5–0.7 mm long) and rounded calyx lobes of roughly the same length (0.3–0.6 mm long); anthers with relatively long sterile apical appendages (1–2 mm long); fruits first white, turning black at complete maturity. Moreover, *T. ovalifolia* has hermaphroditic flowers, as is the case in all other continental African species of the genus. This species is not discussed further in this morphological overview (see Robbrecht, 1979a for a detailed discussion of this subgenus).

VEGETATIVE FEATURES

The Malagasy species of *Tricalysia* are mostly shrubs or, less often, small trees and do not exceed 10 m in height. Rhizomatous undershrubs, a habit typical for certain continental African species from dry vegetation types (such as *T. cacondensis* Hiern; Bridson, 2003), are absent in Madagascar. The leaves are opposite, the leaf base cuneate to acute or attenuate, the tip acuminate, more rarely acute to obtuse. Heterophylly, occurring in a few continental African taxa (D. M. Bridson, Royal Botanic Gardens, Kew, pers. comm.), is absent in the Malagasy representatives. Domatia are generally present and belong to most common types found in the Rubiaceae. The presence/absence of domatia and domatia type are often variable at the species level and have limited taxonomic importance. Other characters, such as tertiary venation, do not show much variation. Leaf texture, size, and shape, pubescence, and colour (in the dried state), by contrast, are useful characters for distinguishing species.

The stipules consist of a truncate or triangular sheath and a narrow awn. The length of the stipular awn, although somewhat variable within species, provides a good distinguishing character for several species.

Collecters are present inside the stipules, the bracts and bracteoles, the calyculi (see below) and the

calyces. Robbrecht (1979a, 1980, 1982, 1983, 1987) already noted the high variation in colleter morphology within the continental African representatives of *Tricalysia*. The Malagasy species show the same high diversity in colleter morphology (Randriamboavonjy, 2000: fig. 10).

INFLORESCENCES AND FLOWERS

The inflorescences are axillary, opposite, and sessile to shortly pedunculate. Co-axillary inflorescences (serial buds resulting in two or even three superposed inflorescences in each axil; see Robbrecht, 1979a: 250 and Robbrecht, 1987: 48, fig. 4) were observed in most species, but are rare. The number of flowers per inflorescence is low, varying from one to nine. Reduction of floral primordia is common, resulting, for example, in impoverished five-flowered thyrses (i.e. two lateral flowers and a central triad), three-flowered inflorescences (consisting only of a central triad), or even a solitary flower. The reduction also results in flowers subtended by not one but two (or even three) calyculi, a situation alluded to by the name *Tricalysia*. Many genera of the Rubiaceae with unisexual flowers (for example, in the tribe Vanguerieae) have considerably fewer flowers on female than on male inflorescences. This was not observed for the Malagasy *Tricalysia*.

Paired bracts and bracteoles are fused to form calyculi. These are cup-shaped and morphologically very similar to the calyx. They are mostly provided with two shorter and two longer awns, of stipular and foliar origin. Often the stipular awns are inconspicuous or completely absent, but, in some species, the foliar appendages are subfoliaceous (for example, up to 25 mm long in *T. ambrensis* ssp. *ambrensis* and *T. analamazaotrensis*). In certain species, for example *T. ambrensis*, the calyculi are sometimes split longitudinally as a result of the development of the calyx. All inflorescence parts (peduncle, inflorescence axes, calyculi, calyces) are green. They are glabrous to densely pubescent with whitish hairs.

Flowers are white (corolla, style and stigma, filaments) and four- to seven-merous, with five- to six-merous flowers most common. Flower merosity is somewhat variable at the species level, but can be a good distinguishing character for certain species. *T. humbertii*, *T. orientalis*, and *T. perrieri* are the only species characterized by four-merous flowers. This feature was once thought to be useful to distinguish the Asian *Diplospora* (four-merous) from the African *Tricalysia* (five-merous to pleiomerous) (Schumann, 1891). Although the Asian taxa are consistently tetramerous (only a single flower on an individual shrub being occasionally pentamerous; Ali & Robbrecht, 1991), the continental African *Tricalysia* are variable,

notably four- to pleiomerous (Robbrecht, 1985: 334). We found here that the same holds for the Malagasy taxa (excluding the three above-mentioned species).

The calyx consists of a tubular part (0.75–2.5 mm long) which is truncate or provided with minute or somewhat more developed teeth or subulate lobes (0.1–0.8 mm long). In species with long calyx tubes, such as *T. analamazaotrensis*, the calyx occasionally shows a longitudinal split, resulting from the development of the corolla.

The corolla is hypocrateriform and rather small, the tube varying in length between 2 and 7.5 mm; the lobes are 2.5–7 mm long. The longest corolla tubes occur in *T. madagascariensis* (5–7.5 mm) and *T. ambrensis* ssp. *coriacea* (3–7 mm). In most taxa, the corolla tube is shorter than or subequal to the corolla lobes. This is especially obvious in functionally female flowers, which have shorter corolla tubes than hermaphroditic or functionally male flowers (see 'Floral biology' section). In a few taxa, *T. ambrensis* var. *coriacea* and *T. madagascariensis*, the corolla tube is shorter or longer than the corolla lobes. Only *T. orientalis* possesses corolla tubes that are consistently longer than the corolla lobes. The corolla is glabrous outside, except in *T. madagascariensis* and *T. perrieri* ssp. *perrieri*, and glabrous inside, except for a densely pubescent zone in the region of the throat.

The stamens are sessile or borne on short filaments, attached in the throat, and exerted completely or for most of their length. A minute sterile apical appendix occurs. Filaments and anthers are glabrous, except in *T. perrieri* ssp. *perrieri*, which has sparsely pubescent thecae.

The style is exerted and, at anthesis, the stigma is situated between or above the anthers. The length of style and stigma is 4–8 mm in most taxa, but 6–9.5 mm in *T. ambrensis* var. *coriacea* and 8.5–11.5 mm in *T. madagascariensis*. The stigma is bilobed and 0.5–2.5(–3.5) mm long. The style is completely glabrous, except in *T. madagascariensis* and *T. perrieri* ssp. *perrieri*.

The ovary is bilocular (but see discussion on functionally male flowers below). Fleshy placentas are attached to the upper half of the septum and have two to eight loosely impressed ovules. In one species, *T. analamazaotrensis*, intra-ovarian trichomes were consistently present. The trichomes are few and situated on the septum in the region of the placenta. They are not visible in the fruiting stage. Intra-ovarian trichomes are rare within the Rubiaceae [only described for the Malagasy genus *Lemyrea* (A.Chev.) A.Chev. & Beille (Beille, 1939) and the tropical Asian *Jackiopsis* Ridsdale (Puff & Igersheim, 1994)], and were hitherto not known to occur in *Tricalysia*.

The Malagasy representatives differ from all continental members of subgenus *Tricalysia* in being dioecious or gynodioecious. The presence of unisexual flowers in Malagasy *Tricalysia* has been discussed previously by Capuron (1973: 144–146) and Robbrecht (1980: 92–94; 1987: 64–66). Earlier on, Hooker (1873: 96) was the first to remark on the dioecious nature of the Malagasy *Tricalysia* species, which he included in the genus *Diplocrater*, now a synonym of *Tricalysia*.

FRUITS AND SEEDS

The fruits of the Malagasy *Tricalysia* species are berry-like drupes. They are relatively small (4–16 × 4–11 mm), bilocular, with a fleshy mesocarp and a thin endocarp. The exocarp is glabrous, except in *T. perrieri* ssp. *perrieri*. Most species have spherical or subspherical fruits, except for *T. ambrensis* and *T. analamazaotrensis*, which have distinctly ellipsoid fruits. Young fruits are green, turning whitish, and then yellow–orange, and mature fruits are red. The fruits dry blackish brown to orange–brown, a character which seems to have some taxonomic value at the species level.

The seeds are dark brown, smooth, and small (3–11 × 2–7 mm). The largest seeds are found in *T. ambrensis* ssp. *ambrensis* (9–11 × 4.5–7 mm), the smallest in *T. boiviniana* (3.5–5 × 2–2.75 mm). The seed number varies between two and 16 per fruit: two to four seeds per fruit in *T. ambrensis* ssp. *ambrensis* and *T. madagascariensis*, six to ten in *T. majungensis*, 6–16 in *T. boiviniana*, and three to nine in all other species. Seed shape is dependent on the number of seeds per fruit. In fruits with few seeds, they are hemispherical (two seeds per fruit) or, in the case of two seeds per locule, tetartospherical (i.e. in the shape of a quadrant of a sphere; Robbrecht, 1978: 6). A higher number results in seeds shaped like a segment of an orange, laterally flattened ellipsoid seeds with one convex and one somewhat concave side, or angular seeds.

The hilum is narrow, linear, and shallow. In some species, it may be somewhat curved.

The seed coat consists of several layers of crushed endotestal cells and a single layer of large, parenchymatic, tannin-filled exotesta cells, covered by a thin cuticle. The exotesta cells are polygonal in surface view (Randriamboavonjy, 2000: photographs 7–8).

FLORAL BIOLOGY

Seven Malagasy species (*T. analamazaotrensis*, *T. boiviniana*, *T. cryptocalyx*, *T. leucocarpa*, *T. majungensis*, *T. orientalis*, and *T. perrieri*) were found to be dioecious. Superficially, the flowers look perfect, but

they are either functionally male or functionally female. In functionally male flowers, the gynoecium is not developed, that is, the locules in the ovary are empty (no placentas or ovules present) or not formed at all. In functionally female flowers, the anthers are not functional, neither opening nor producing viable pollen grains. No differences were observed in the number of flowers in male and female inflorescences. For most species, too few flowering specimens were available to show differences between functionally male and female flowers with regard to the length of the corolla tube, corolla lobes, style, stigmata, anthers, and filaments. This was not the case, however, for *T. cryptocalyx*. Functionally female flowers were observed to have larger ovaries, shorter corolla tubes and lobes, a shorter style, and smaller anthers borne on shorter filaments. *T. ambrensis*, *T. dauphinensis*, and *T. madagascariensis* are probably gynodioecious, possessing both perfect and functionally female flowers (no male flowers were found except in *T. ambrensis* ssp. *coriacea*). All flowers therefore have well-developed gynoecia with placentas and ovules. Again, functionally female flowers were observed to have shorter corolla tubes and lobes, a shorter style, and smaller anthers than perfect flowers (*T. ambrensis*).

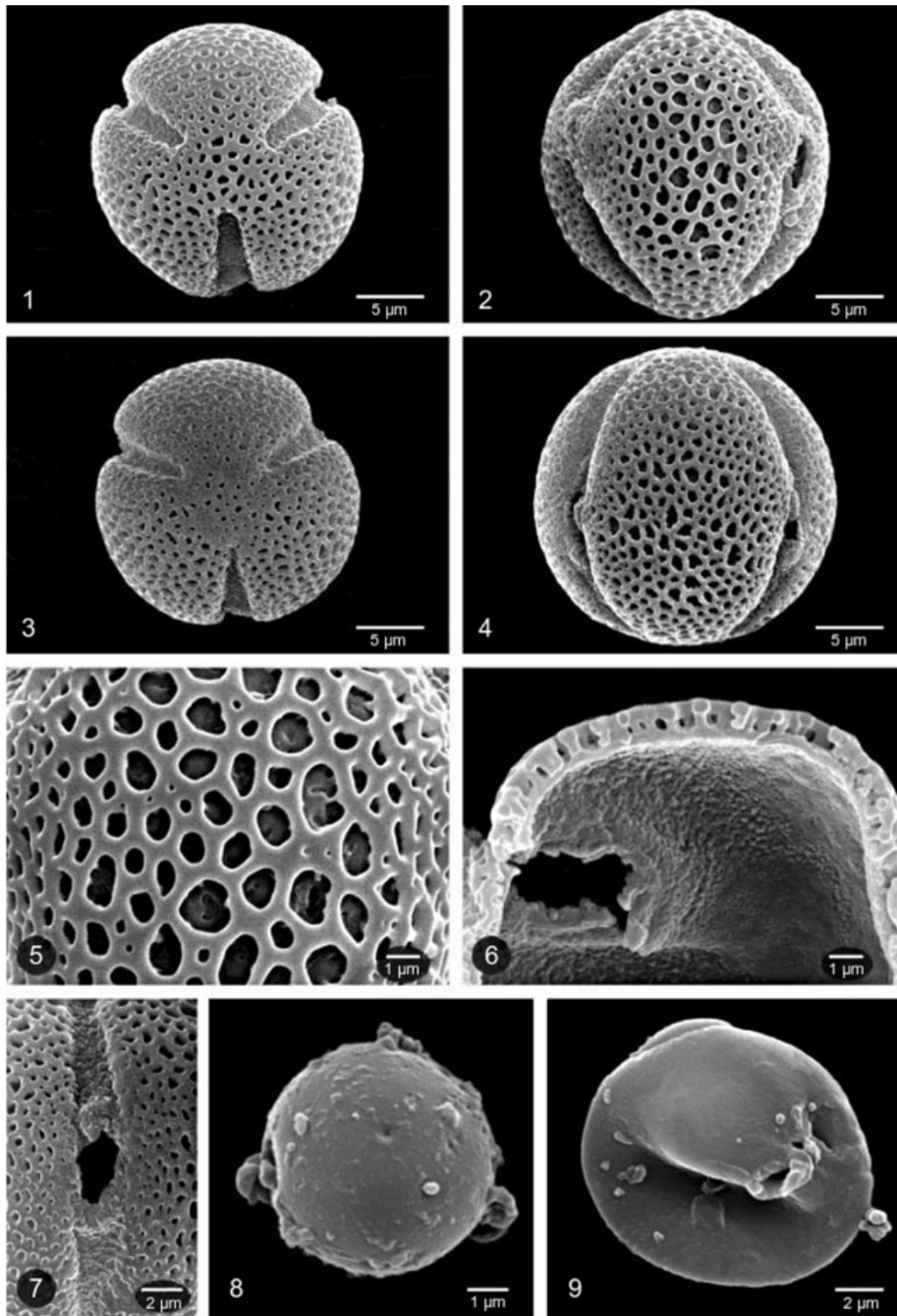
For *T. humbertii*, only perfect flowers were seen. The study of more flowering material, however, might well reveal this species to show some degree of dioecy.

POLLEN MORPHOLOGY

The genus *Tricalysia* is stenopalynous. The pollen grains of the Malagasy species are similar to those of the continental African representatives: small-sized, three-zonocolporate, circular with somewhat sunken colpi in polar view, subspheroidal in equatorial view, with reticulate sexine (Figs 1–7; see also Randriamboavonjy, 2000: pls 1A–D, 2). Polar and equatorial axes vary in length between 15 and 25 µm in pollen from functionally male or hermaphroditic flowers. Pollen grains in functionally female flowers are 6–8 µm in diameter and not ornamented (Figs 8, 9; see also Randriamboavonjy, 2000: pl. 1E, F); these are uncharacteristically small and clearly nonviable. In functionally female flowers, anthers are either not opened at all, or, if they are, the pollen is not disseminated but remains in the thecae as an undifferentiated mass.

ECOLOGY AND CHOROLOGY

Tricalysia ovalifolia is a recent colonist from continental Africa. The species is widespread in the eastern and northern coastal regions and occurs in all



Figures 1–9. Pollen of Malagasy *Tricalysia*. Figs 1–7. Pollen from functionally male flowers. Figs 8, 9. Pollen from functionally female flowers. Fig. 1. Polar view, *T. majungensis* (coll. ignot. 6372 -RN). Fig. 2. Equatorial view, *T. majungensis* (coll. ignot. 6372 -RN). Fig. 3. Polar view, *T. cryptocalyx* (Descoings 3242). Fig. 4. Equatorial view, *T. cryptocalyx* (Descoings 3242). Fig. 5. Mesocolpium, *T. majungensis* (coll. ignot. 6372 -RN). Fig. 6. Pollen grain wall, *T. cryptocalyx* (Descoings 3242). Fig. 7. Ecto-aperture, *T. majungensis* (coll. ignot. 6372 -RN). Figs 8, 9. Nonviable pollen from functionally female flowers, *T. cryptocalyx* (De Block et al. 762). Scale bars: 5 µm (Figs 1–4), 2 µm (Figs 7, 9), 1 µm (Figs 5, 6, 8).

woody littoral formations, such as scrub, thicket, and semi-deciduous or deciduous dry forests.

The 11 endemic Malagasy species have colonized both humid and dry woody vegetation. Six species occur in humid rain forest from low altitude to submontane regions. This is the case for *T. ambrensis*, *T. analamazaotrensis*, *T. leucocarpa*, and *T. orientalis*. Two species are more coastal in distribution, notably *T. dauphinensis* in the south-east and *T. boiviniana* in the north-west. Four other species grow in deciduous or semi-deciduous dry forests at low altitudes. *T. madagascariensis*, *T. majungensis*, and *T. perrieri* ssp. *perrieri* occur mainly on sandy soil, *T. humbertii* and *T. perrieri* ssp. *antsalovensensis* on calcareous soil. *T. cryptocalyx* is the most widespread species. It occurs throughout the Central Plateau in high plateau and gallery forest, but is nowadays mostly found in remnant forest patches and in degraded vegetation.

Except for the widespread *T. cryptocalyx* and *T. ovalifolia*, the Malagasy *Tricalysia* have relatively narrow distributions. The genus is distributed in the two major vegetation domains recognized in Madagascar: the Western and Eastern Malagasy regional centres of endemism (White, 1983). *T. madagascariensis*, *T. majungensis*, *T. perrieri*, *T. humbertii*, and *T. ovalifolia* occur in the western domain (Région de l'Ouest, Domain de l'Ouest; Humbert, 1955), whereas the other species of the genus occur in the Eastern Malagasy regional centre of endemism (Région de l'Est; Humbert, 1955), notably in the Domaine du Centre, Domaine de l'Est, and the Domaine du Sambirano (Humbert, 1955).

ANDROGYNE, A NEW SECTION TO ACCOMMODATE THE MALAGASY SPECIES

The generic delimitation of the genus *Tricalysia* and its infrageneric classification were treated exhaustively by Robbrecht (1978, 1979a, 1980, 1982, 1983, 1987). He segregated the African genus *Sericanthe* and recognized two subgenera within *Tricalysia*: subgenus *Tricalysia*, with five sections (*Probletostemon*, *Tricalysia*, *Rosea*, *Ephedranthera*, and an unnamed Madagascan section characterized by unisexual flowers), and subgenus *Empogona*, with two sections (*Empogona* and *Kraussiopsis*).

In Madagascar, the two subgenera are represented: subgenus *Empogona* with a single species and subgenus *Tricalysia* with 11 endemic species. *T. ovalifolia* Hiern is the only species common to the African continent, Madagascar, and other Indian Ocean Islands. It clearly belongs to subgenus *Empogona* section *Empogona* (see 'Morphology' above).

The other Malagasy species belong to subgenus *Tricalysia*, but do not fit easily into the existing sec-

tions. Certain characters typical for one section or another are present in some species. For example, *T. perrieri* ssp. *perrieri* possesses a pubescent style and pubescent anthers, typical for section *Probletostemon*, but the other characters of that section do not match (large pleiomerous flowers, free bracteoles, large fruits with thick sclerotic wall). Sessile anthers, partly included in the corolla tube at anthesis, occur in several Malagasy species. This is typical for section *Ephedranthera*. However, in that section, two floral morphs occur, with the stigma either exerted or deeply included in the corolla tube. This was certainly never observed in Malagasy *Tricalysia*.

The Malagasy species would fit within section *Tricalysia* (bracts and bracteoles fused into calyculi, fruits drupaceous, endocarp thin) were it not that the flowers in this section are hermaphroditic (Robbrecht, 1987: 71). It seems, therefore, opportune to place the Malagasy representatives of the genus in a section of their own. This was suggested by Robbrecht (1987: 65–66), who gave a provisional (Robbrecht, 1980: 92) name, but left the formal description of the section until after a revision had been carried out. The idea of a Malagasy section, characterized solely by floral biological adaptations, was followed by other authors, such as Bridson (2003: 465).

TAXONOMIC TREATMENT

TRICALYSIA A.RICH.

Tricalysia A.Rich. in DC., *Prodr.* 4: 445 (Sept. 1830); Richard, *Mém. Fam. Rubiac.* 144 (Dec. 1830) & *Mém. Soc. Hist. Nat. Paris* 5: 224 (1834).

Generic description (restricted to the Malagasy species; features relating uniquely to *T. ovalifolia* are given in square brackets): Gynodioecious, dioecious [or hermaphroditic] shrubs or small trees. Leaves opposite, petiolate, often with domatia. Stipules interpetiolar, consisting of a sheath and a needle-like awn. Inflorescences axillary and opposite, sessile or shortly pedunculate, one- to several-flowered, usually relatively compact; bracts and bracteoles fused into calyculi [or bracteoles free]; calyculi cup-shaped, with foliar appendages awn-like or subfoliaceous and stipular appendages awn-like but often inconspicuous. Flowers four- to seven-merous, sessile to shortly [to long] pedicellate. Calyx usually with well-developed tube and minute triangular or subulate teeth. Corolla white, hypocrateriform; corolla lobes spreading or reflexed, contorted to the left; throat or upper half of corolla tube pubescent inside. Stamens attached in the throat, sessile or with short filaments; anthers medifixed, partly or completely exerted at anthesis, with sagittate base and sterile apical

appendage. Disc annular. Ovary two-locular; placenta attached to the upper half of the septum; two to eight ovules loosely impressed in placental tissue. Style exerted, often overtopping the anthers; stigma bilobed. Functionally female flowers with anthers not opening and/or not containing well-developed pollen; functionally male flowers with locular cavities not developed or, if they are present, then reduced and empty or with rudimentary placentas. Fruits drupaceous, subspherical or ellipsoid, red [or black] at maturity; calyx persistent. Seeds 2–16/fruit, dark brown; hilum shallow, narrow, linear, often somewhat curved; endosperm horny; embryo with inferior radicle; seed coat with exotestal cells parenchymatic, filled with tannins.

Subgenus Empogona (Hook.f) Robbrecht, *Bull. Jard. Bot. Nat. Belg.* **49**: 259 (1979)

Empogona Hook.f., *Hook. Ic. Pl.* **11**: 72, t. 1091 (1871); Bentham & Hooker f., *Gen. Pl.* **2**: 94 (1873); Hiern in Oliv., *Fl. Trop. Afr.* **3**: 114 (1877); Schumann in Engler & Prantl, *Nat. Pflanzenfam.* **4(4)**: 80 (1891).

Tricalysia sect. *Empogona* (Hook.f) Brenan, *Kew Bull.* **1947**: 55 (1947) & **1953**: 111 (1953).

Hypobathrum sect. *Empogona* (Hook.f) Baillon, *Adansonia* **12**: 204 & 212 (1878).

Tricalysia sect. *Kraussia* auct. non (Harv.) Hiern: Hiern in Oliv., *Fl. Trop. Afr.* **3**: 118 (without indication of rank) (1877) & Schumann in Engler & Prantl, *Nat. Pflanzenfam.* **4(4)**: 81 (1891).

Hypobathrum sect. *Kraussia* auct. non (Harv.) Baillon: Baillon, *Adansonia* **12**: 208 & 212 (1878).

Malagasy representative: only *T. ovalifolia* Hiern.

Subgenus Tricalysia

Section *Androgyne* Robbrecht, sect. nov.

Diagnosis: Propter bracteas bracteolasque ad calyculos connatas et fructus rubros manifeste ad subgenus *Tricalysiam* pertinet, ubi ab aliis sectionibus removendum est ob statum dioecium gynodioeciumve.

Type species: Madagascar, *Tricalysia cryptocalyx* Baker.

Endemic to Madagascar with the following representatives: *T. ambrensis* Randriamb. & De Block; *T. analamazaotrensis* Homolle ex Randriamb. & De Block; *T. boiviniana* (Baill.) Randriamb. & De Block; *T. cryptocalyx* Baker; *T. dauphinensis* Randriamb. & De Block; *T. humbertii* Randriamb. & De Block; *T. leucocarpa* (Baill.) Randriamb. & De Block; *T. madagascariensis* (Drake ex Dubard.) A.Chev.; *T. majungensis* Homolle ex Randriamb. & De Block;

T. orientalis Homolle ex Randriamb. & De Block;
T. perrieri Homolle ex Randriamb. & De Block.

TRICALYSIA AMBRENSIS RANDRIAMB. & DE BLOCK, SP. NOV. (FIG. 10)

Type: MADAGASCAR. Antsiranana Province, Montagne d'Ambre NP, près du Cascade Antakarana, *De Block, Rakotonasolo & Randriamboavonjy 1313* (holo-: BR; iso-: BR, G, K, MO, P, TAN, WAG).

Diagnosis: Ab omnibus aliis sectionis *Androgyne* speciebus Madagascaris incolis differt inflorescentiis laxis atque fructibus ellipsoideis usque ad 16 mm longis.

Description: Gynodioecious shrubs or small trees, 2.5–10 m high; flowering branches moderately stout, flattened, and bisulcate, glabrous; youngest internodes brownish, smooth; older internodes greyish or fawnish. Leaves with petioles 4–10 mm long, canalliculate adaxially, glabrous. Blades elliptic or somewhat ovate or obovate, 7.5–14 × (2.7–)3.2–5.5 cm, papyraceous to subcoriaceous, drying green or brown above and paler below, glabrous on both surfaces; tip acuminate, acumen 7–18 mm long; base cuneate or rarely somewhat attenuate; 6–11 pairs of secondary nerves; tuft domatia conspicuous. Stipules with sheath 1.5–3 mm high, glabrous outside; awn (1–)1.5–4 mm long. Inflorescences (1–)3–(5)-flowered, pedunculate [peduncle 1.5–4(–6) mm long], lax; axes 1–4(–8) mm long, glabrous; pedicels 0(–1) mm long, glabrous; bracts and bracteoles fused into calyculi, usually one per flower; calyculi cupular, glabrous or rarely sparsely ciliate or with sparse hairs on the foliar awns, foliar appendages awn-like (1–4 mm long) or subfoliaceous (up to 20 × 8 mm), stipular awns up to 1 mm long but often inconspicuous or absent. Flowers 5–(6)-merous; bud rounded; calyx glabrous outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1.2–2.3 mm long; calyx lobes triangular to narrowly triangular, ≤ 0.5 mm long; corolla tube 2–4.5 mm long, 1.2–1.5 mm wide at the base and 2–2.8 mm wide at the throat, glabrous outside, glabrous inside except for a dense ring of hairs at the throat; corolla lobes 3–4.5 mm long, glabrous; anthers sessile, 1.5–3.5 mm long, glabrous, apical sterile appendix minute; ovary 1–2 mm high, glabrous, two ovules loosely immersed in each placenta; style and stigma 4–8 mm long, glabrous, stigmatic lobes 1–2.5 mm long; hermaphroditic flowers: corolla tube 3–4.5 mm long, corolla lobes 3–4.5 mm long, anthers 2–3.5 mm long, style and stigma 6–8 mm long; functionally female flowers: corolla tube 2–2.5 mm long, corolla lobes 3–3.5 mm long, anthers not opening and/or not containing well-

KEY TO THE MALAGASY TAXA OF *TRICALYSIA*

- 1a. Inflorescences very lax, glabrous; pedicels (1.5–)3–16 mm long; bracteoles not fused into calyculi, positioned *c.* halfway up on the pedicel, subopposite or alternate, broadly triangular, 1–1.5 mm long. Fruits first white, turning black when mature.....2 (subgenus *Empogona*)
- 1b. Inflorescences compact or lax, glabrous or pubescent; pedicels 0–3 mm long; bracteoles fused into calyculi. Fruits first white, then yellow–orange, turning red when mature.....3 (subgenus *Tricalysia* section *Androgyne*)
- 2a. Stems glabrous, except for the youngest internodes and the adaxial side of the petioles which may be puberulous; leaves entirely glabrous; pedicels, bracteoles, and ovary glabrous.....*T. ovalifolia* var. *ovalifolia*
- 2b. Stems more densely and persistently pubescent; petioles pubescent all around; leaves with midrib puberulous on both surfaces, especially near the leaf base; pedicels, bracteoles, and sometimes also ovary pubescent.....*T. ovalifolia* var. *glabrata*
- 3a. Youngest internodes, petioles, and stipules densely pubescent with very fine, short, appressed hairs; leaves coriaceous, lanceolate (narrowly elliptic) or rarely elliptic or somewhat obovate or ovate, (2.0–)2.5–8.5(–10) × (0.5–)0.8–3 cm; tip obtuse, acute or rarely very weakly acuminate; domatia conspicuous.....*T. cryptocalyx*
- 3b. Youngest internodes, petioles, and stipules glabrous or pubescent; leaves coriaceous or papyraceous, of different shape and size or, if like *T. cryptocalyx*, then papyraceous; tip acuminate, rarely weakly acuminate, acute or obtuse; domatia conspicuous or not.....4
- 4a. Corolla moderately to densely pubescent outside (at least from the middle of the corolla tube upwards); style at least partly pubescent; anther thecae sparsely pubescent; fruits moderately to densely pubescent; leaves often moderately or densely pubescent on both surfaces; young internodes densely pubescent with erect hairs; inflorescences compact, all parts densely pubescent; flowers 4(–5)-merous; calyx densely covered with appressed hairs outside, lobes triangular to subulate, 0.4–0.75 mm long.....*T. perrieri* ssp. *perrieri*
- 4b. Corolla (outside) and style glabrous or, if pubescent then flowers not four-merous; thecae glabrous; fruits glabrous; leaves glabrous on both surfaces or pubescence restricted to midrib and/or secondary nerves or leaf base; young internodes glabrous or sparsely pubescent, rarely densely pubescent but, if so, then not with erect hairs; inflorescences lax or compact, all parts glabrous or pubescent; flowers four- to seven-merous; calyx glabrous or sparsely to densely pubescent outside, lobes only rarely > 0.5 mm long.....5
- 5a. Corolla moderately to densely pubescent outside (at least from the middle of the corolla tube upwards); corolla tube 5–7.5 mm long; style at least partly pubescent; flowers five- to seven-merous; calyx tube 1.5–2.5 mm long, densely pubescent with short appressed hairs outside, faintly ridged longitudinally; fruits spherical, with two to four seeds; inflorescences compact; youngest internodes glabrous; older internodes fawnish, often flaking.....*T. madagascariensis*
- 5b. Corolla glabrous outside; corolla tube usually < 5 mm long; style glabrous; flowers 4- to 6(–7)-merous; calyx tube ≤ 1.5 mm long, or, if longer, then either not densely pubescent over its whole area or flowers four-merous; fruits spherical or ellipsoid, usually with more seeds; inflorescences compact or lax; youngest internodes glabrous or pubescent; older internodes usually not fawnish but, if fawnish, then inflorescences lax, calyx glabrous or sparsely pubescent outside and fruits ellipsoid.....6
- 6a. Leaves narrowly elliptic, papyraceous to subcoriaceous.....7
- 6b. Leaves usually not narrowly elliptic, or, if so, then coriaceous.....9
- 7a. Fruits ellipsoid, 7–13 × 6.5–11 mm; calyx tube 1.5–2.3 mm long, lobes 0.4–0.8 mm long; stipular awns (0.5–)1.5–5.5 mm long; inflorescences usually one-flowered; calyculi with foliar appendages awn-like (1.5–5 mm long) or subfoliaceous.....*T. analamazaotrensis*
- 7b. Fruits spherical, 6–9.5 × 5–8 mm; calyx tube 1–1.5 mm long, lobes < 0.5 mm long; stipular awns 0.5–2(–3) mm long; inflorescences one- to nine-flowered; calyculi with foliar appendages awn-like (< 1.5 mm long) or rarely subfoliaceous.....8
- 8a. Leaves with five to seven pairs of secondary nerves; inflorescences one- to nine-flowered, subsessile, compact, all parts densely pubescent; at least upper half of calyx moderately to densely pubescent outside; filaments 1–1.5 mm long; flowers (5)–6-merous; dioecious.....*T. majungensis*
- 8b. Leaves with six to ten pairs of secondary nerves; inflorescences (1)–3(–5)-flowered, shortly pedunculate (peduncle 0.5–4 mm long), lax, all parts glabrous or moderately to densely pubescent; calyx glabrous or sparsely to moderately pubescent; filaments 0.5–1 mm long; flowers (4)–5(–7)-merous; gynodioecious.....*T. dauphinensis*
- 9a. Inflorescences (1)–3–9-flowered, compact, all parts including calyces moderately or densely pubescent; calyculi with foliar awns ≤ 1 mm long or absent; flowering branches stout, youngest internodes deep red or rarely reddish brown (in dry condition), not rapidly becoming fawnish; stipules with sheath at least partly sparsely to moderately puberulous outside, awn relatively short (0.5–2 mm long); ovary dark brown to blackish when dry and strongly contrasting with the paler calyx and the other inflorescence parts; filaments 1(–1.5) mm long; six to eight ovules/locule; (6)–8–16 seeds/fruit.....*T. boiviniana*

9b. Not the above character combination.....	10
10a. Flowers 4(–5)-merous; calyx with 4(–5) lobes.....	11
10b. Flowers 4(–)5–6(–7)-merous; calyx with 4(–)5–6(–7) lobes.....	13
11a. Leaves glabrous, coriaceous, or subcoriaceous; youngest internodes glabrous, older internodes fawnish; petioles and stipules glabrous; stipular awn (1–)2–5 mm long; inflorescences usually three-flowered, coaxillary inflorescences not common; corolla tube 4–5.5 mm long; corolla lobes 2.5–3.5 mm long, glabrous.....	<i>T. orientalis</i>
11b. Leaves glabrous but commonly midrib pubescent, papyraceous, or subcoriaceous; youngest internodes sparsely to densely pubescent; older internodes never becoming fawnish; petioles and stipules glabrous or sparsely to densely pubescent; stipular awn 0.75–2 mm long; inflorescences one- to five-flowered, coaxillary inflorescences common in some specimens; corolla tube (2–)3–4.25 mm long; corolla lobes (2.5–)3–4 mm long, glabrous but often ciliate ..	12
12a. Calyx densely pubescent outside, with subulate lobes; flowering branches, petioles, and stipules densely pubescent; stipular awn 0.75–2 mm long; inflorescences compact, all parts densely pubescent, pedicels 0(–1) mm long; calyculi with foliar awns up to 1.5 mm long or rarely subfoliaceous (up to 5 mm long).....	<i>T. perrieri</i> ssp. <i>antsalovensis</i>
12b. Calyx glabrous or sparsely to moderately pubescent outside, truncate or nearly so; flowering branches, petioles, and stipules glabrous to densely pubescent; stipular awn 0.1–1(–1.5) mm long; inflorescences compact in flowering stage, lax in fruiting stage, all parts glabrous or pubescent, pedicels 0.5–3 mm long; calyculi with foliar awns up to 1 mm long or inconspicuous.....	<i>T. humbertii</i>
13a. Leaves coriaceous, 9.5–20 × 3.5–7.5 cm.....	14
13b. Leaves papyraceous or subcoriaceous, 2–14 × 1–5.5 cm.....	15
14a. Flowering branches glabrous, older internodes greyish or fawnish; leaves with conspicuous tuft domatia; inflorescences (1–)3–(5)-flowered, pedunculate [peduncle 1.5–4(–6) mm long], lax (especially in fruiting stage); floral bud rounded at the tip; calyx glabrous or rarely sparsely pubescent outside; fruits ellipsoid, drying brown.....	<i>T. ambrensis</i> ssp. <i>coriacea</i>
14b. Flowering branches sparsely to moderately pubescent or glabrous, older internodes brown or reddish brown, not fawnish; leaves with inconspicuous ciliate pit or tuft domatia; inflorescences three- to nine-flowered, subsessile (sometimes shortly pedunculate in fruiting stage, peduncle ≤ 2 mm long), compact; floral bud acuminate at the tip; calyx moderately to densely pubescent outside; fruits subspherical, drying orange–brown.....	<i>T. leucocarpa</i>
15a. Inflorescences one- or, rarely, three-flowered; calyx lobes 0.4–0.8 mm long; dioecious.....	<i>T. analamazaotrensis</i>
15b. Inflorescences only rarely one-flowered; calyx lobes < 0.5 mm long; gynodioecious.....	16
16a. Flowering branches, petioles, stipules glabrous; calyx glabrous outside, 1.2–2.3 mm long; inflorescences very lax, almost completely glabrous; calyculi with foliar appendages awn-like (1–4 mm long) or subfoliaceous (up to 20 × 8 mm); floral bud rounded at tip; two ovules per locule; fruits ellipsoid, 11–16 × 7–11 mm; two to four seeds per fruit, 9–11 × 4.5–7 mm.....	<i>T. ambrensis</i> ssp. <i>ambrensis</i>
16b. Flowering branches, petioles, stipules glabrous or pubescent; calyx glabrous or pubescent outside, 1–1.5 mm long; inflorescences lax, glabrous, or pubescent; calyculi with foliar appendages awn-like (< 1 mm long) or rarely subfoliaceous (up to 5 mm long); floral bud shortly acuminate at tip; (2–)3–(4) ovules per locule; fruits spherical or only slightly longer than wide, 6.5–9 × 5–8 mm; four to eight seeds per fruit, 3.5–6.5 × 2–4.5 mm.....	<i>T. dauphinensis</i>

developed pollen, c. 1.5 mm long, style and stigma 4–5 mm long. Fruits ellipsoid, 11–16 × 7–11 mm, red when mature, drying brown, glabrous. Seeds 2–4 per fruit, 9–11 × 4.5–7 mm.

Distribution: Only known from Montagne and Forêt d'Ambre (Antsiranana Province) (Fig. 11A).

Ecology: In humid evergreen forest; altitude: 700–1475 m.

Phenology: Flowering: December–January(–March); fruiting: May–August.

Vernacular names: kafeala.

Material studied: MADAGASCAR. Antsiranana Province: Parc National de Montagne d'Ambre, v.1993 (fr), *Andrianantoanina, Solotiana & Bezara 102* (BR, K, MO, P); Parc National de Montagne d'Ambre, Campement de Chris, viii.1993 (fr), *Andrianantoanina & Rocseohelher 304* (BR, K, MO); Forêt d'Ambre, iii.1953 (fl, fr), *coll. ignot. 7195-SF* (P); Montagne d'Ambre, v.1954 (fr), *coll. ignot. 9957-SF* (BR, P, TEF); Montagne d'Ambre, i.1960 (fl), *Cours & Humbert 5373* (BR, P); Montagne d'Ambre, i.1960 (fl), *Cours & Humbert 5374* (P); Montagne d'Ambre, i.1960 (fl), *Cours & Humbert 5375* (BR, P); Montagne d'Ambre,

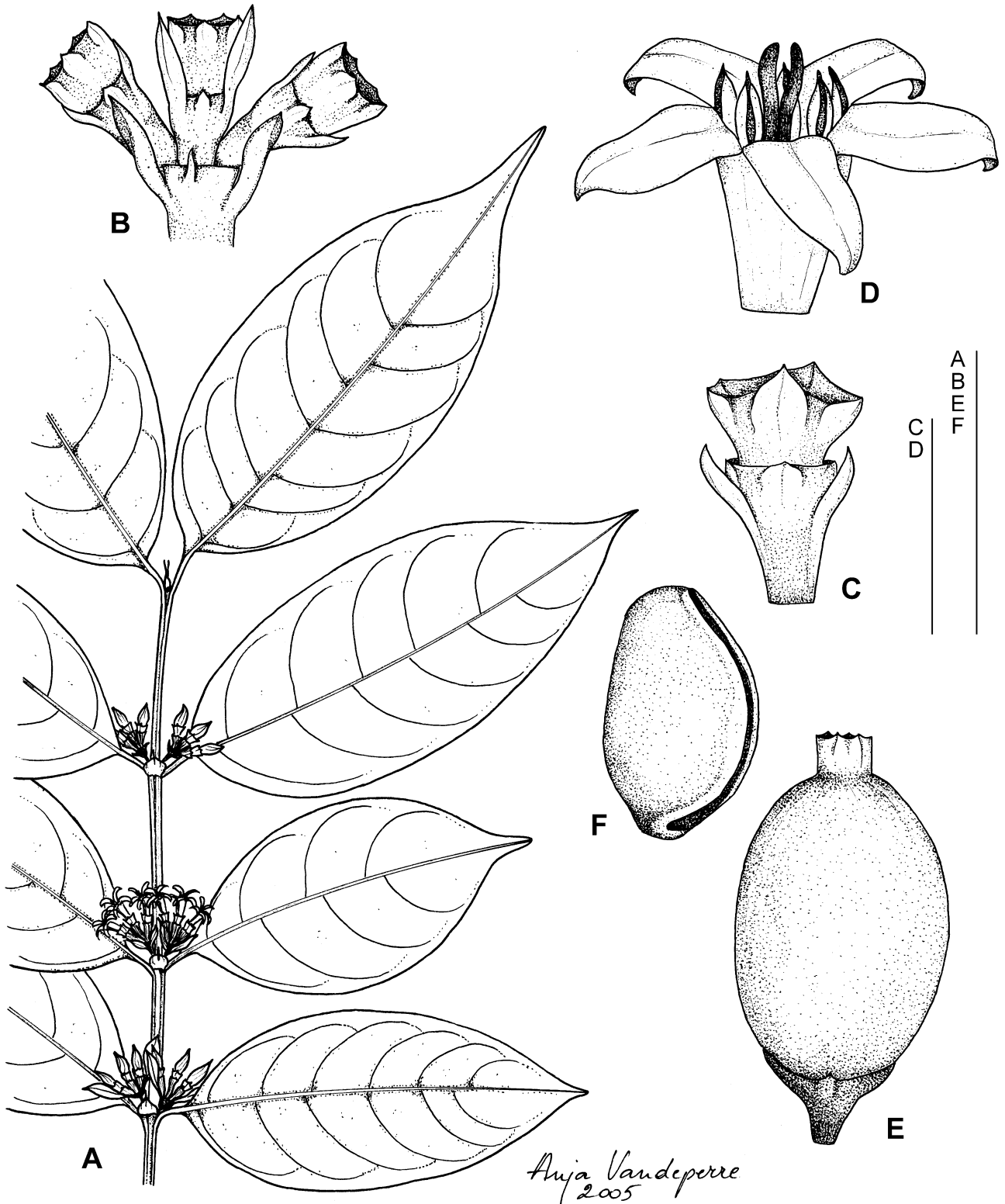


Figure 10. *Tricalysia ambrensis* Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, inflorescence $\times 4$; C, calyx and calyculus $\times 6$; D, corolla $\times 6$; E, fruit $\times 2$; F, seed $\times 4$. A, B, *De Block et al.* 1313; C, D, *Cours & Humbert* 5373; E, F, *Andrianantoanina & Rocseohclher* 304.

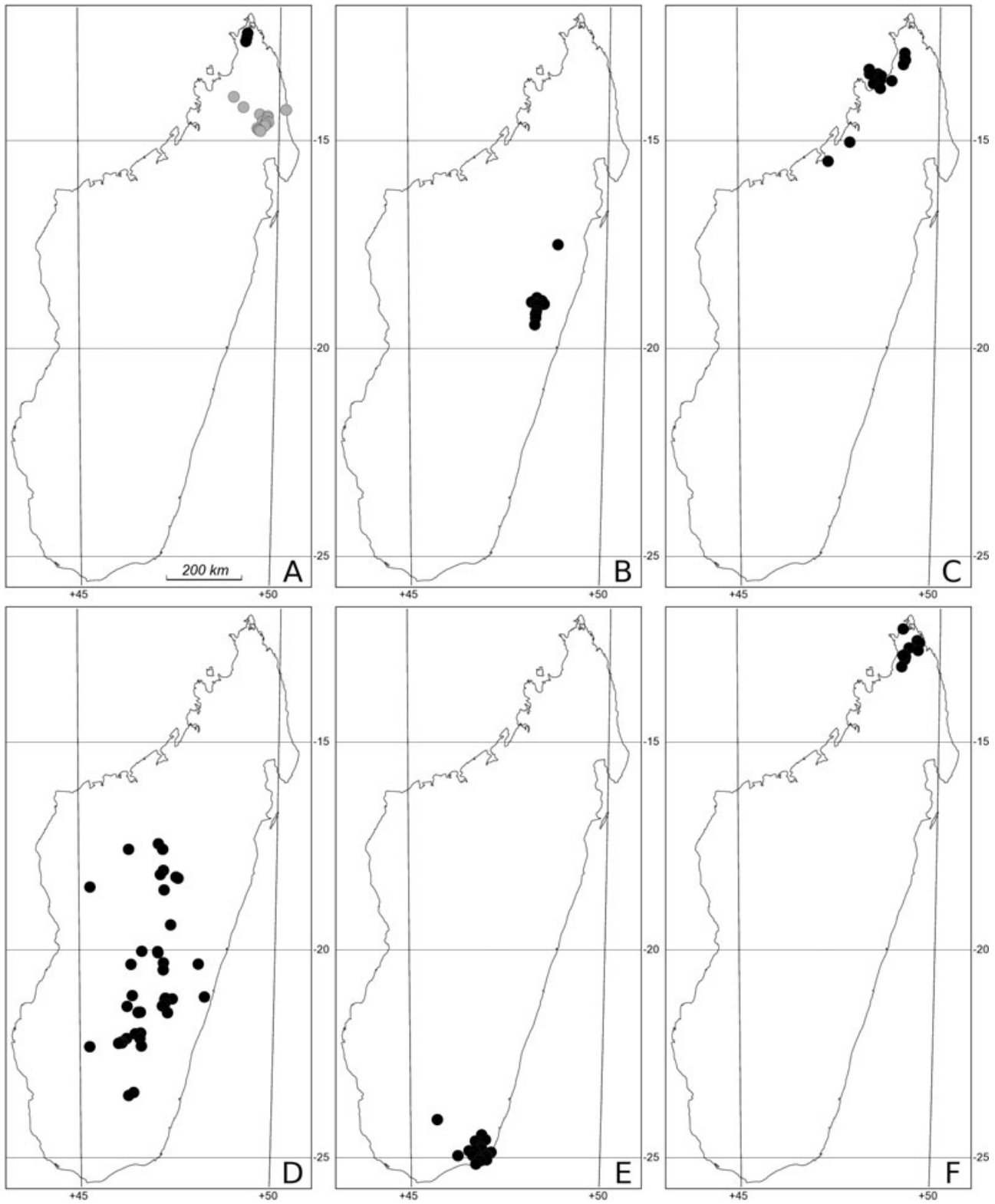


Figure 11. Distribution maps of *Tricalysia*. A, *T. ambrensis* ssp. *ambrensis* (black circles) and ssp. *coriacea* (grey circles); B, *T. analamazaotrensis*; C, *T. boiviniana*; D, *T. cryptocalyx*; E, *T. dauphinensis*; F, *T. humbertii*.

forêt de Roussettes, i.1960 (fl), *Cours & Humbert 5376* (P); Montagne d'Ambre National Park, piste vers Bemanevika, v.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 978* (BR, K, MO, P, TAN, WAG); Montagne d'Ambre National Park, piste vers Bemanevika, v.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 979* (BR, K, MO, P, TAN); Montagne d'Ambre NP, près du Cascade Antakarana, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1313* (BR, G, K, MO, P, TAN, WAG); Forêt d'Ambre, xii.1959–i.1960 (fl), *Humbert 32088* (BR, P); Forêt d'Ambre, xii.1959–i.1960 (fl), *Humbert 32102* (BR, K, P); Forêt d'Ambre, xii.1959–i.1960 (fl), *Humbert 32119* (BR, P); Forêt d'Ambre, xii.1959–i.1960 (fl), *Humbert 32132* (BR, P); Forêt d'Ambre, xii.1959–i.1960 (fl), *Humbert 32135* (BR, P); Montagne d'Ambre, vers la Grande Cascade, xii.1959–i.1960 (fl), *Humbert 32133* (P); Forêt d'Ambre, vers le sommet, xii.1959–i.1960 (fl), *Humbert 32137* (BR, P); Parc National de Montagne d'Ambre, vi.1995 (fr), *Razafimandimbison 118* (BR, K, MO). Without locality or date: *Homolle 50* (P) (fr); *Homolle 51* (P) (fr); *Homolle 52* (P) (fr); *Homolle 120* (P) (fr).

TRICALYSIA AMBRENSIS RANDRIAMB. & DE BLOCK
SSP. CORIACEA RANDRIAMB. & DE BLOCK, **SSP.**
NOV.

Type: MADAGASCAR. Antsiranana Province, montagnes entre la Haute Andramonta (bassin de la Lokoho) et Mafaika (bassin de l'Antainambalana), *Humbert & Capuron 24845* (holo-: P; iso-: BR).

Diagnosis: Foliorum laminis coriaceis majoribusque et etiam inflorescentiarum partibus pubescentibus a ssp. *ambrensi* differt.

Description: Differs from ssp. *ambrensis* as follows. Leaves with petioles 3–5 mm long. Blades 12–20 × 4–6 cm, acumen 10–30 mm long, coriaceous. Stipules with sheath 1.5–2 mm high; awn 0.5–2 mm long. Inflorescences lax, but less so than in ssp. *ambrensis*, all parts sparsely to moderately pubescent with appressed hairs; calyculi with foliar awns up to 2.5 mm long or inconspicuous, never subfoliaceous. Flowers with calyx 1–1.75 mm long, truncate or with minute teeth, glabrous or rarely sparsely pubescent; functionally male flowers: corolla tube 3–7 mm long, corolla lobes 4–4.5 mm long, anthers subsessile, 2–2.5 mm long, style and stigma 6–9.5 mm long; functionally female flowers not seen, placentation unknown. Fruits 8.5–13 × 7–9.5 mm. Seeds 3–4(–6) per fruit, 5.5–9 × 3–5.5 mm.

Distribution: Northern Madagascar: occurring in Antsiranana Province, in the region of Marojejy and Anjanaharibe-Sud (Fig. 11A).

Ecology: In humid evergreen forest on lateritic soil; altitude: 0–1400 m.

Phenology: Flowering: December–January; fruiting: April–September.

Vernacular names: kafeala.

Notes: (1) The specimens belonging to this taxon were tentatively grouped with *T. ambrensis*, mainly because of their lax inflorescence structure and ellipsoid fruits, although these characters are less pronounced than in that taxon. There are many quantitative differences, such as the larger leaves with a longer acumen, the shorter stipules and petioles, the less developed calyculi and calyces, and the smaller seeds and fruits. Qualitative differences are the coriaceous leaves and the pubescence of the inflorescence parts. There is no information about placentation type, but the seed number is sometimes higher than in *T. ambrensis*. Also puzzling is the flower size, with corolla tubes 3–7 mm long and shorter than, equal to, or longer than the lobes (corolla tubes only up to 4.5 mm long in ssp. *ambrensis*, shorter than or equal to the lobes). A possible explanation is the fact that, although, for *T. ambrensis*, perfect and functionally female flowers were seen, only functionally male flowers were observed in this taxon. In other Malagasy *Tricalysia* species, it was noted that the latter possess longer corolla tubes than the former (see 'Floral biology' section). In any case, very few specimens with mature flowers were seen for both subspecies [two for ssp. *ambrensis*, three for ssp. *coriacea* (in one specimen, the corolla tubes were 3 mm long; in the other, they were 6–7 mm long)]; therefore, flower descriptions may need to be amended when more flowering material becomes available. The relationship between *T. ambrensis* ssp. *ambrensis* and this taxon remains unclear until further material can be studied. It may well be that new collections will lead to the recognition of two species instead of two subspecies. (2) The large coriaceous leaves of ssp. *coriacea* are reminiscent of *T. leucocarpa*. However, the latter possesses more compact inflorescences, spherical fruits, and the calyx is always pubescent.

Material studied: MADAGASCAR. Antsiranana Province: S d'Analamanara (près de Tsaratanana), entre Sambava et Antsirabe-Nord, xii.1966 (fl), *Capuron 27176-SF* (P, TEF); au cours de la descente du Marojejy, iv.1949 (fr), *Cours 3596* (BR, P, TAN); Andapa, vii.1956 (fr), *coll. ignot. 7989-RN* (BR, P, TAN); Sambava, iv.1956 (fr), *coll. ignot. 8220-RN* (BR, P, TAN, TEF); Sambava, iv.1956 (fr), *coll. ignot. 8250-RN* (BR, P, TAN); canton Maroambihy, district Sambava, vi.1957 (fr), *coll. ignot. 9011-RN* (BR, P);

vallée de la Lokoho, près d'Ambalavoniho, i.1949 (fl), *Humbert & Cours 22802* (BR, P); montagnes entre la Haute Andramonta (bassin de la Lokoho) et Mafaika (bassin de l'Antainambalana), i.1951 (fl), *Humbert & Capuron 24845* (BR, P); montagnes N de Mangindrano (Haute Maevarano), jusqu'aux sommets d'Ambohimirahavavy (partage des eaux Mahavavy-Androranga), xii.1950–ii.1951 (fl), *Humbert & Capuron 25006* (P); RN de Marojejy, N slopes of Ambatosoratra, ii.1989 (fr), *Miller 4213* (K, MO, P); Marojejy RN, 3.5 km à vol d'oiseau de Marovato et 2 km à vol d'oiseau de Sarahandrano, v.1995 (fr), *Rasoavimbahoaka 635* (MO, P, TAN); Andapa, Doany, Betsomanga, environs à 11.2 km SE de Doany, v.1995 (fr), *Rasoavimbahoaka 701* (K, MO, P); SW d'Andapa, Réserve Spécial d'Anjanaharibe-Sud, aux environs des sommets, v–vi.1994 (fr), *Ravelonarivo, Raymond & Bekamisy 180* (BR, K, MO, P); Préf. d'Antalaha, sous-préf. d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, commune Bealampona, quartier Befingotra, village Andranotsarabe, suivant RN d'Andapa vers Bealalana, piste est 1 km à côté droite du ruisseau Andranotsarabe, ix.1994 (fr), *Ravelonarivo, Rabesonina & Ramainty 368* (K, MO, P); Fiv. Andapa, fir. Bealampona, fok. Befingotra, Réserve Spéciale Intégrale d'Anjanaribe-Sud, environs 37 km SW d'Andapa par la RN d'Andapa-Bealalana, 3 km SE de l'ancien village de Mandritsarahely, piste vers Ranomafana, iv.1995 (fr), *Ravelonarivo & Rabesonina 738* (MO, P); Sous-préf. d'Andapa, commune rurale d'Ambodimanga I, quartier d'Andilandrano, environs de Hiakan'ny Zamandrabosy, 6 km W d'Andilandrano, dans la réserve d'Anjanaharibe-Sud, v.1995 (fr), *Ravelonarivo & Rabesonina 770* (K, MO, P, TAN).

TRICALYSIA ANALAMAZAOTRENSIS HOMOLLE EX
RANDRIAMB. & DE BLOCK, **SP. NOV.** (FIG. 12)

Type: MADAGASCAR. Toamasina Province, forêt d'Analamaoatra, *Perrier de la Bâthie 6904* (holo-: & iso-: P).

Diagnosis: Ab omnibus aliis sectionis *Androgynis* speciebus Madagascaris incolis differt foliorum laminis parvis papyraceis-subcoriaceis apice saepium acuminatis, inflorescentiis 1(–3)floris breviter pedunculatis, floribusque breviter pedicellatis etiamque fructibus ellipsoideis.

Description: Dioecious shrubs, 1.5–4 m high; flowering branches slender, glabrous, or sparsely to densely pubescent with short appressed or spreading hairs; youngest internodes reddish brown or brown; older internodes somewhat rough and flaking, greyish to greyish brown. Leaves with petioles

1–5 mm long, canaliculate adaxially, glabrous or sparsely to densely pubescent with short appressed or spreading hairs. Blades elliptic to ovate or rarely narrowly so, 2–10.5 × 1–3 cm, papyraceous to subcoriaceous, drying brown to dark brown or rarely greenish above and paler below, glabrous on both surfaces but midrib sometimes sparsely to densely pubescent on one or both leaf surfaces; tip short to long acuminate or rarely weakly acuminate or acute, acumen 0.3–2.5 cm long; base cuneate to attenuate; 7–12 pairs of secondary nerves; domatia conspicuous, varying from ciliate pit to tuft. Stipules rapidly becoming corky, sheath 1–2 mm high, glabrous or sparsely to densely pubescent with short appressed or spreading hairs outside; awn (0.5–)1.5–5.5 mm long. Inflorescences one- or rarely three-flowered, shortly pedunculate (peduncle 0.5–3 mm long), lax, all parts glabrous or sparsely to densely covered with short appressed hairs; axes 0–1 mm long; pedicels 0–1 mm long; bracts and bracteoles fused into calyculi, usually two per flower; calyculi cupular, foliar appendages awn-like, 1.5–5 mm long, or subfoliaceous and up to 7 mm long, stipular awns inconspicuous or absent. Flowers (4–)5–6-merous; bud acuminate; calyx glabrous or sparsely to densely covered with short appressed hairs outside, densely covered with long, appressed hairs and with scattered colleters inside; calyx tube 1.5–2.3 mm long; calyx lobes triangular or subulate, 0.4–0.8 mm long; corolla tube (3–)4–5 mm long, 1.25–1.75 mm wide at the base and c. 2 mm wide at the throat, glabrous outside, glabrous but with a dense ring of long white hairs in the upper half inside; corolla lobes 4–5 mm long, glabrous but ciliate or sparsely ciliate near the tip; anthers sessile, their bases included in corolla tube, erect at anthesis, 1.5–3 mm long, glabrous, apical sterile appendix minute; ovary 1–1.5 mm high, glabrous; style and stigma 5.5–8 mm long, glabrous, stigmatic lobes 1.5–2.5 mm long; functionally female flowers: anthers not opening and/or not containing well-developed pollen, two to three ovules loosely impressed in a large placenta; functionally male flowers: ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas. Fruits ellipsoid, 7–13 × 6.5–11 mm, red when mature, drying brown, glabrous. Seeds 3–5 per fruit, 5–9.5 × 3.5–6 mm.

Distribution: Restricted to the Moramanga region; abundantly collected from Perinet-Analamazaotra and along the road from Moramanga to Anosibe An'ala (Toamasina Province) (Fig. 11B).

Ecology: In mid-altitudinal, humid evergreen forest; altitude: 750–1100 m.

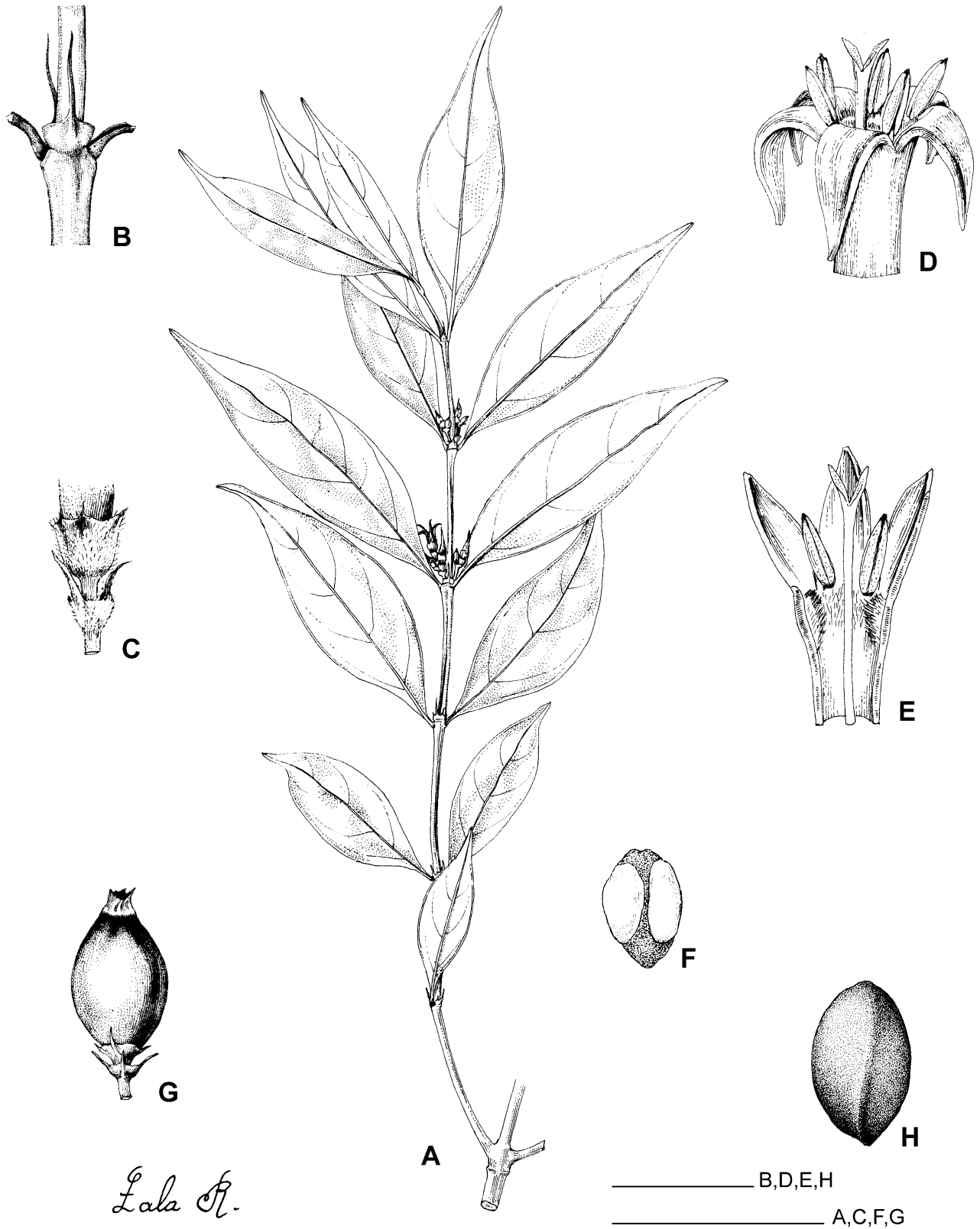


Figure 12. *Tricalysia analamazaotrensis* Homolle ex Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, stipule $\times 3$; C, calyx and calyculus $\times 4$; D, corolla $\times 6$; E, corolla longitudinally cut $\times 6$; F, frontal view of placenta $\times 4$; G, fruit $\times 2$; H, seed $\times 3$. A–C, *Bosser 7709*; D–F, *De Block et al. 861*; G, H, *De Block et al. 915*.

Phenology: Flowering: October–April, with peak in January–February; fruiting: March–November.

Vernacular names: kafeala.

Notes: (1) A few specimens (e.g. *Baron 2314, 3069 & 3070*) differ from the other material by larger leaves, shorter awns, and by the fact that the bark rapidly turns buff. Otherwise, they fit well within *T. analamazaotrensis*. (2) The pubescent specimens of this species sometimes resemble *T. cryptocalyx*. *T. analamazaotrensis* can be recognized by its less coriaceous leaves with acuminate tips, its inflorescences with one or few (up to three) flowers, and the rougher pubescence on the shoots.

Material studied: MADAGASCAR. Toamasina Province: Périnet, ix.1951 (fr), *Benoist 1210* (P); Périnet, ii.1955 (fl, fr), *Bosser 7709* (P, TAN); Périnet, vii.1944 (fr), *coll. ignot. (Ecole forestière) s.n.* (BR, P); Antaniditra, Périnet, vi.1950 (fr), *coll. ignot. 1408-SF* (P, TAN, TEF); Befoza, Périnet, iii.1950 (fr), *coll. ignot. 1815-SF* (P, TAN, TEF); Analamazaotra, x.1936 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 2155* (P); Anosibe, Moramanga, i.1951 (fl), *coll. ignot. 2179-SF* (P, TAN, TEF); Antsahatsaka, Périnet, i.1950 (fl), *coll. ignot. 3519-SF* (P, TAN, TEF); Analamazaotra, vi.1938 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 3732* (P); forêt d'Ambodivato, district Moramanga, v.1952 (fr), *coll. ignot. 5076-SF* (BR, P, TEF); Ampasanampano, village Ambohibolakely, canton Marovoay, district Moramanga, vi.1963 (fr), *coll. ignot. 21230-SF* (P, TEF); Sandrangato, canton et district Moramanga, x.1964 (fr), *coll. ignot. 21873-SF* (P, TEF); Andrianariana, village Ambodiakatra, canton et district Moramanga, ix.1964 (fr), *coll. ignot. 21941-SF* (P, TEF); RN 2, PK 99 from Antananarivo, 12 km before Moramanga, ii.1999 (fl), *De Block & Rakotonasolo 836* (BR, MO, TAN); PK 32 on road from Moramanga to Anosibe An'ala, ii.1999 (fl), *De Block & Rakotonasolo 844* (BR, K, MO, TAN); Parc d'Analamazaotra, ii.1999 (fl), *De Block & Rakotonasolo 861* (BR, K, MO, TAN); PK 33 on road from Moramanga to Anosibe An'ala, v.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 915* (BR, G, K, MO, P, TAN, WAG); S de Moramanga, ii.1930 (fl), *Decary 7030* (BR, P); S de Moramanga, ii.1930 (fl), *Decary 7034* (BR, P); Moramanga, vii.1942 (fr), *Decary 17914* (P); station forestière d'Andasibe, Périnet, xii.1989 (fl), *Evrard 11223* (BR, P); entre Sandrangato et Anosibe, S de Moramanga, xi.1952 (fr), *Leandri & Capuron 1518* (P); Analamazaotra, iv.1912 (fl), *Perrier de la Bâthie 4002* (P); forêt d'Analamazaotra, without date (fl), *Perrier de la Bâthie 6904* (P); Analampanga, rive droit du Mangoro, x.1927 (fl), *Perrier de la Bâthie 18271* (P); NW de la RNI de Zahamena, 1 km SE du village

d'Antenina, commune d'Imerimandroso, Ambaton-drazaka, viii.1994 (fr), *Randrianjanaka & Zafy 204* (BR, K, MO, P); forêt d'Analamazaotra, Périnet, xii.1934 (fl), *Ursch 38* (P). Not located: forêt d'Analamihilana, xii.1944 (fr), *Cours 2016* (BR, P); Ahondrona, canton Périnet, village Manarintsoa, à proximité d'une ancienne voie decauville, iv.1965 (fr), *coll. ignot. 25156-SF* (P, TEF). Without locality or date: *Baron 1623* (K, P) (fr); *Baron 2314* (K, P) (fr); *Baron 3069* (K, P) (fr); *Baron 3070* (K) (fr); *Homolle E5* (BR, P) (st); *Homolle 2015* (P) (fl).

TRICALYSIA BOIVINIANA (BAILL.) RANDRIAMB. & DE BLOCK, COMB. NOV. (FIG. 13)

Hypobathrum boivinianum Baill., *Adansonia* **12**: 208 (1878). *Types*: MADAGASCAR. Antsiranana Province, Nossi-Be, *Boivin 2069* (lecto-: P; isolecto-: P; designated here), *Richard 360* (syn-: P; isosyn-: P) & *647* (syn-: P; isosyn-: P).

Pentasporea madagascariensis Boivin, nomen in herb. (Boivin 2069).

Tricalysia acuminata Vatke, nomen nudum, cited in Palacky, *Cat. Pl. Madag.* **4**: 55 (1906) (see note).

Description: Dioecious large shrubs or, rarely, small trees, up to 6 m high; flowering branches stout, flattened, and often bisulcate, glabrous or rarely sparsely to moderately pubescent with short appressed hairs; young internodes smooth, deep red or rarely reddish brown, not rapidly becoming fawnish. Leaves with petioles 3–6 mm long, canaliculate adaxially, glabrous or rarely pubescent with short appressed hairs. Blades obovate or elliptic or narrowly so (5.5–)7–13.5 × (1.5–)2.5–4.7 cm, coriaceous, drying brown or brownish green above and paler below, glabrous on both surfaces; tip acuminate, acumen 4–25 mm long; base cuneate to attenuate; five to eight pairs of secondary nerves; ciliate pit domatia few to several. Stipules with sheath 0.5–1.5 mm high, at least partly sparsely to moderately pubescent with short appressed hairs outside; awn 0.5–2 mm long. Inflorescences (1–)3–9-flowered, shortly pedunculate [peduncle 1–2(–3) mm long], compact, all parts moderately or densely pubescent with short, appressed, whitish hairs; axes ≤ 1 mm long, pedicels 0(–1) mm long; bracts and bracteoles fused into calyculi, 1(–2) per flower; calyculi cupular, foliar awns ≤ 1 mm long or absent, stipular awns inconspicuous or absent. Flowers six-merous; bud shortly acuminate; calyx drying brown, completely or at least the upper half moderately to densely covered with short, appressed, whitish hairs outside, densely pubescent and with few scattered collectors inside; calyx tube 0.75–1.5 mm long; calyx lobes (5–)6(–7), triangular, ≤ 0.5 mm long; corolla tube 2–3(–3.5) mm long, c. 2 mm wide at the

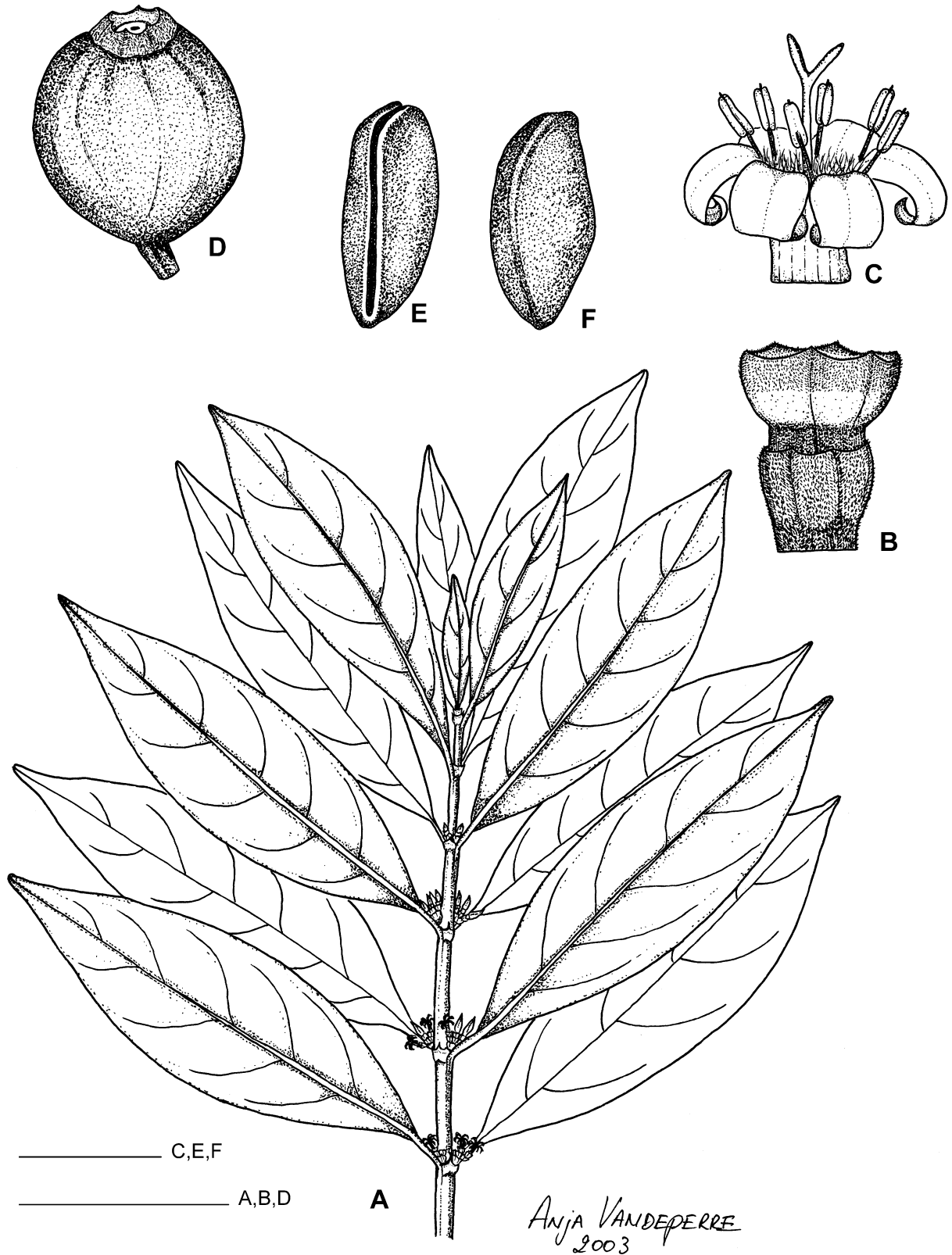


Figure 13. *Tricalysia boiviniana* (Baill.) Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, calyx and calyculus $\times 8$; C, corolla $\times 6$; D, fruit $\times 4$; E, F, seed $\times 6$. A, Hildebrandt 2895; B, C, coll. ignot. 9298 -SF; D-F, Hildebrandt 3138.

base and 2.5–3 mm wide at the throat, glabrous outside, glabrous inside except for a dense ring of long white hairs just below the throat; corolla lobes (3–)4–4.5(–5) mm long, glabrous but sparsely ciliate or with at least a few hairs on the margin near the tip; anthers 1–2.2 mm long, glabrous, apical sterile appendix minute, filaments 1(–1.5) mm long; ovary 1–1.5 mm high, glabrous, usually dark brown to blackish when dry and strongly contrasting with the paler calyx and the other inflorescence parts; style and stigma 5.5–7.5 mm long, glabrous, stigmatic lobes 1.2–2 mm long; functionally female flowers: anthers not opening and/or not containing well-developed pollen, six to eight ovules loosely impressed in a large placenta; functionally male flowers: ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas. Fruits spherical, 7–9 × 7–8.5 mm, red when mature, drying brown, glabrous. Seeds (6–)8–16 per fruit, 3.5–5 × 2–2.75 mm.

Distribution: North-west Madagascar: occurring in Antsiranana (on Nossi-Be and in the region of Ambilobe and Ambanja) and Mahajanga (in the region of the Baie du Mahajamba and Antsohihy) Provinces (Fig. 11C: one specimen, Richard 78, was not included in the distribution map; its locality, Vohemar, may be faulty or imprecise).

Ecology: In lowland, humid, evergreen forest on sandstone or sandy substrate; altitude: 0–400 m.

Phenology: Flowering: February–July; fruiting: (February–)May–October.

Vernacular names: kafeala; djarandrapilifa; taolagnosy; taolankenavaviny (Sakalava).

Note: Palacky (1906: 55) listed *Tricalysia acuminata* Vatke in the fourth volume of his *Catalogus Plantarum Madagascariensium*. The specimen he cited (*Hildebrandt 3138*, LE and P), together with duplicates of this collection and *Hildebrandt 2895*, are often annotated as *Tricalysia acuminata* Vatke, but not in Vatke's own handwriting. As was the case with many names listed in Palacky's catalogue, the name *Tricalysia acuminata* seems not to have been validly published.

Material studied: MADAGASCAR. Antsiranana Province: Nossi-Be, RNI 6, Lokobe, iv.1994 (fl), *Antilahimena 102* (BR, MO, P); along river Bevoay, trail to Ankarefo, Ambato classified forest, Ambanja, v.1998 (fr), *Antilahimena*, *Rabenantoandro & Tsitra 368* (BR, MO, P); Ambobaka, fiv. Ambanja, iv.2000 (fl), *Antilahimena*, *Ravelonarivo & Ratovoson 456* (K, MO);

Nossi-Be, bord de la mer, au dessous du plateau de Hell-Ville, iii.1851 (fr), *Boivin 2069* (P); Nossi-Be, Lokobe, iii.1964 (fl), *Capuron 23453-SF* (BR, P, TEF); à la base d'Ambohibe, E de Marivorahona, Ambilobe, v.1966 (fl), *Capuron 24738-SF* (BR, P, TEF); Mahilakakolana, Ambanja, iv.1951 (fl), *coll. ignot. 3242-SF* (P, TEF); Nossi-Be, RNI 6, Lokobe, x.1952 (fr), *coll. ignot. 4335-RN* (P); W du village Ankatatafa, Ambanja, iii.1954 (fl), *coll. ignot. 9289-SF* (BR, P, TEF); Anaborano, Ifasy, canton Ambilobe, vii.1962 (fl), *coll. ignot. 12148-RN* (BR, P, TEF); district d'Ambanja, Ampasindava, viii.1957 (st), *Cours 5230* (P); district d'Ambilobe, Village d'Ankatoko, Montagne d'Ambohipiraka, ii.1960 (fl), *Cours & Humbert 5646* (P); district d'Ambilobe, village d'Ambilomagodro, montagne d'Ambohibe, ii.1960 (fl), *Cours & Humbert 5686* (P); Nossi-Be, iv.1872 (fl), *Hildebrandt 2895* (K, LE, P, WU); Nossi-Be, Lokobe, vii.1872 (fr), *Hildebrandt 3138* (K, LE, P); collines et plateaux calcaires de l'Ankarana, i–ii.1960 (fl), *Humbert 32772* (P); collines et plateaux calcaires de l'Ankarana, i–ii.1960 (fl), *Humbert 32791* (P); Mont Ambohipiraka, NE d'Ambilobe, vallée du Mananjeba, ii.1960 (fl), *Humbert & Cours 32887* (P); Antsatsaka, Ambanja, v.1998 (fr), *Rabenantoandro & Antilahimena 28* (BR, MO); Vohemar, 1840 (fr), *Richard 78* (P); Nossi-Be, without date (fr), *Richard 309* (P); Nossi-Be, 1840 (fr), *Richard 360* (P); Nossi-Be, without date (fr), *Richard 647* (P). Mahajanga Province: environs de la Baie du Mahajamba, Boina, v.1907 (fl), *Perrier de la Bâthie 3715* (P); Antsohihy, Ankerika, Andohanakerika, vi.2000 (fr), *Rakotonasolo 207* (BR, K, TAN).

TRICALYSIA CRYPTOCALYX BAKER (FIG. 14)

Tricalysia cryptocalyx Baker, *Journ. Bot.* **20**: 138 (1882). *Type:* MADAGASCAR. Forests of West Betsileo, *Baron 159* (holo-: K; iso-: P).

Webera axillaris, nomen in herb. (Lyll 394).

Description: Dioecious shrubs or, rarely, small trees, up to 8 m high; flowering branches slender, flattened, and bisulcate; youngest internodes brown, densely pubescent with very fine, short, appressed hairs; older internodes fawnish, greyish, or brown to reddish brown, often flaking. Leaves with petioles 2–4 mm long, canaliculate adaxially, usually densely pubescent with short appressed hairs. Blades lanceolate (narrowly elliptic) or rarely elliptic or somewhat obovate or ovate (2–)2.5–8.5(–10) × (0.5–)0.8–3 cm, coriaceous, drying brownish, somewhat paler below, glabrous on both surfaces but midrib often pubescent on lower or both surfaces (at least in the basal half of the blade) and leaf base usually sparsely pubescent in the region of the petiole; tip obtuse, acute, or rarely very weakly acuminate; base attenuate or cuneate;

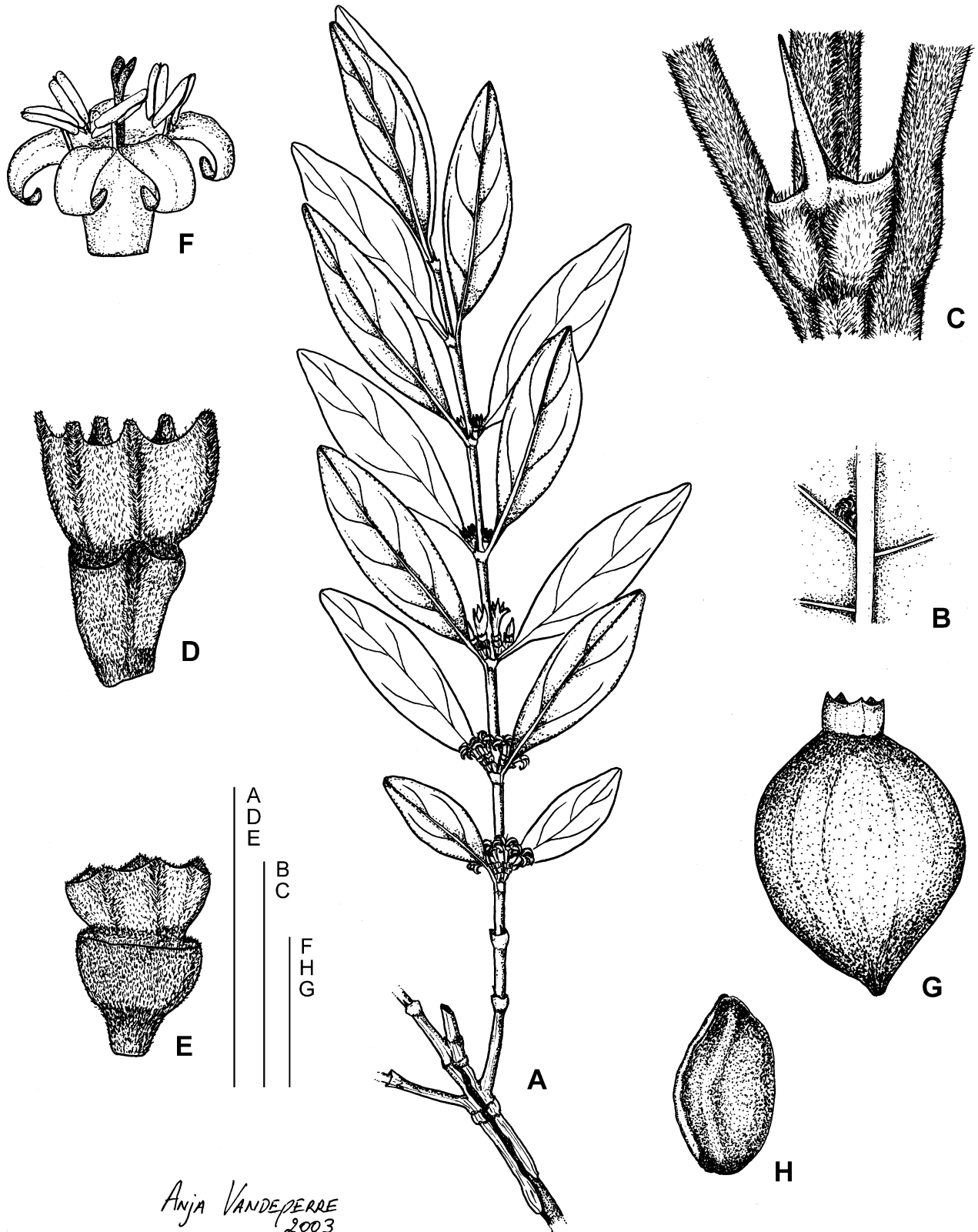


Figure 14. *Tricalysia cryptocalyx* Baker. A, Flowering branch $\times 0.8$; B, domatia $\times 12$; C, stipules $\times 12$; D, E, calyx and calyculus $\times 8$; F, corolla $\times 4$; G, fruit $\times 4$; H, seed $\times 4$. A–C, *De Block et al.* 527; D, F, *De Block et al.* 726; E, *Rakotonasolo* 43; G, H, *coll. ignot.* 11992-RN.

five to nine pairs of secondary nerves; ciliate pit or tuft domatia conspicuous. Stipules with sheath 1–1.5 mm high, densely pubescent with short appressed hairs outside; awn (0.5–)1–2(–2.5) mm long. Inflorescences one- to five-flowered, subsessile or shortly pedunculate (peduncle 0.5–2 mm long), compact, all parts densely pubescent with appressed hairs; axes 0–1.5 mm long; pedicels 0–1.5 mm long; bracts and bracteoles fused into calyculi, one to two per flower; calyculi cupular, foliar appendages awn-like (up to 3 mm long) or subfoliaceous [4–10(–25) mm long] in calyculi supporting inflorescence branches, awn-like (up to 1 mm long) in others, stipular awns inconspicuous or absent. Flowers five- to six-merous; bud acute to acuminate; calyx densely to moderately pubescent with short appressed hairs in the upper half or all over outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1.25–2 mm long; calyx lobes narrowly triangular to linear, \leq 0.5 mm long; corolla tube 2–4 mm long, 1.5–2 mm wide at the base, and *c.* 2.5–3.5 mm wide at the throat, glabrous outside, upper half densely pubescent inside; corolla lobes 3.5–4.75 mm long, glabrous but often sparsely ciliate; anthers 1.5–2.5 mm long, glabrous, apical sterile appendix minute, filaments 0.5–1.25 mm long; ovary 0.8–1.5 mm high, glabrous; style and stigma 4–6.5 mm long, glabrous, stigmatic lobes 0.75–1.5(–2) mm long; functionally male flowers: corolla tube (2.5–)3–4 mm long, corolla lobes (3.5–)4–4.75 mm long, anthers 2–2.5 mm long, filaments 0.75–1.25 mm long, ovary 0.8–1 mm high, ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas, style and stigma (5.5–)6–6.5 mm long; functionally female flowers: corolla tube 2–3.5 mm long, corolla lobes 3–4 mm long, anthers not opening and/or not containing well-developed pollen, 1.5–1.8 mm long, filaments 0.5–0.75(–1) mm long, ovary 0.9–1.5 mm long, (2–)3–4(–5) ovules loosely immersed in each placenta, style and stigma 4–5(–5.5) mm long. Fruits spherical or slightly longer than wide, 6–9.5 \times 5–8 mm, red when ripe, drying brown or rarely orange-brown, glabrous. Seeds 4–8 per fruit, 3.5–6.5 \times 2–4.5 mm.

Distribution: High plateau species. Occurs in Antananarivo and Fianarantsoa Provinces, from the Tampoketsa d'Ankazobe in the north to Ranotsara-Sud in the south (Fig. 11D).

Ecology: In high plateau forest, gallery forest, remnant forest patches in degraded vegetation, or cultivated landscape on different soil types (rocky, granitic, quartzite, clay, etc.), but not often on sand; altitude: 700–1700 m.

Phenology: Flowering: November–March with peak in January–February; fruiting: throughout the year, especially from March to August.

Vernacular names: fatsikahitra; fatsikala; kafeala; kafealamadinidravina; pitsikahitra; ramalefaka; randrompody vavy; tavaza; tsavaza; velomizy (Tanala); velonizy; zavaza (Betsileo).

Uses: Firewood; wood for construction (poles for huts or enclosures); an infusion of the leaves is used as a gargle against inflammation of the throat.

Material studied: MADAGASCAR. Antananarivo Province: Massif Andringitra, N d'Ivato, Antananarivo, vii.1957 (fr), *Capuron 18039-SF* (BR, P, TEF); Tampoketsa, Ankazobe, km 176 on route Tana-Majunga, i.1949 (fl), *coll. ignot. 214-SF* (P, TEF); Sarobaratra, pays Sihanaka, viii.1937 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 2915* (P); Manankazo, Tampoketsa d'Ankazobe, i.1942 (fl), *coll. ignot. 17161-RN* (BR, P); Tampoketsa d'Ankazobe, proche d'Ankazobe, vi.1961 (fr), *coll. ignot. 19956-SF* (BR, P, TEF); district d'Ankazobe, plateau du Tampoketsa, vi.1957 (fr), *Cours 5229* (P); RN4, road Antananarivo–Majunga, PK 180, ii.1999 (fl), *De Block, Rakotonasolo & Randraamboavonjy 762* (BR, G, K, MO, P, TAN, WAG); Manankazo, Tampoketsa d'Ankazobe, i.1942 (fl), *Decary 17161* (BR, P); Manankazo, Tampoketsa d'Ankazobe, i.1942 (fl), *Decary 17181* (BR, P); Bongolava, E d'Ankavandra, vii.1930 (fl), *Decary 7975* (BR, P); route de Majunga, PK 181, Tampoketsa, i.1972 (fl), *Jacquemin 894* (P); Manohilahy, 20 km W d'Anjozorobe, vii.1962 (fr), *Leroy 98* (K, P); Manohilahy, 20 km W d'Anjozorobe, vii.1962 (st), *Leroy 99* (K, P); Ibity Massif, northern sector, ridge above cement factory, just above Tapia woodland, ii.1997 (fr), *Lowry & Schatz 4835* (BR, K, MO, P); Antongona, iii.1960 (fr), *Peltier J. & M. 1981* (P, TAN); Tampoketsa d'Ankazobe, vii.1966 (fr), *Peltier J. & M. 5972* (BR, P); Tampoketsa d'Ankazobe, S du Mahatsinjo, vii.1925 (fr), *Perrier de la Bâthie 17330* (P); Mount Ibity, iii.1928 (fr), *Perrier de la Bâthie 18475* (P); district Anjozorobe, Ampilanonana, xii.1998 (fl), *Rakotonasolo 43* (BR, K, TAN); Ibity Massif, ii.2003 (fr), *Schatz, Lowry, Andriamihajarivo, Hong Wa, Rabevohitra & S. Lowry 4026* (MO, P). Fianarantsoa Province: Fort-Carnot, x.1988 (fr), *Beaujard 405* (K, P); Tanala, 1994 (fr), *Beaujard 542* (P); haute vallée de la Sahambano, iv.1970 (fr), *Boiteau 2049* (P); à la base de l'Andrambaky (as Iandrambaky), SW d'Iarintsena, Ambalavao, v.1965 (fr), *Capuron 24108-SF* (BR, P, TEF); NE d'Ithosy, ii.1949 (fr), *coll. ignot. 280-SF* (P); Iarintsena, Ambalavao, without date (fl), *coll. ignot. 2700-SF* (P, TAN); Ampamaherana, Fianarantsoa, without date (fr), *coll. ignot. 2764-SF* (P); forêt

d'Analamazaha, Ihosy, vi.1951 (fr), *coll. ignot. 4737-SF* (BR, P, TEF); Soarano, canton Vohitsaoka, district Ambalavao, v.1955 (fr), *coll. ignot. 7189-RN* (P, TEF); Ambalavao, Sendrisoa, iii.1956 (fl), *coll. ignot. 8107-RN* (P, TAN, TEF); Safadavaka, canton de Mahajoany, district d'Ambalavao, iii.1957 (fr), *coll. ignot. 9194-RN* (P); canton de Vohitsaoka, district d'Ambalavao, ii.1961 (fl), *coll. ignot. 11678-RN* (BR, P); Ivohibe, Antambohobe, iv.1962 (fr), *coll. ignot. 11969-RN* (P); canton Vohitsaoka, district Ambalavao, iii.1962 (fr), *coll. ignot. 11992-RN* (BR, P, TEF); Massif de l'Ingaro, Fenoarivo, Ambalavao, ii.1955 (fl), *coll. ignot. 13745-SF* (BR, P, TEF); Ampamaherana, Fianarantsoa, v.1954 (fr), *coll. ignot. 14459-SF* (P, TEF); village Ampamaherana, canton Fandrandava, district Fianarantsoa, vi.1955 (fr), *coll. ignot. 14627-SF* (BR, P, TEF); Ankarongana, canton Mahasoabe, district Fianarantsoa, v.1955 (fr), *coll. ignot. 14847-SF* (BR, P, TEF); 500 m E du village Antsolaitra, xi.1963 (fl), *coll. ignot. 21480-SF* (P, TEF); district d'Ihosy, canton et poste de Ranohira, entre Tametsoa et Sahanafa au N d'Isalo, i.1955 (fr), *Cours 5047* (BR, P); Antamboara, canton de Ranotsara-Sud, district de Midongy du Sud, massif de l'Ivakoany, montagne Analanavelo, without date (fr), *Cours 5211* (P); RN7, 39 km N of Ambositra, i.1975 (fr), *Croat 29429* (K, TAN); inselbergs W of Ambalavao, PK 475, i.1975 (fl), *Croat 30196* (MO, P, TAN); inselbergs near PK 475, W of Ambalavao, ii.1975 (fl), *Croat 30299* (K, MO, P, TAN); vicinity of Zazafotsy, on RN7 between Ambalavao and Ihosy, ii.1975 (fl), *Croat 30433* (MO, P, TAN); 5 km NE of Ihosy, xi.1998 (fl), *Davis, Rakotonasolo & De Block 2173* (BR, K); 12 km SW of Ihosy, adjacent to RN 7, xi.1998 (fr), *Davis, Rakotonasolo & De Block 2191* (BR, K); road Antananarivo–Ambositra (RN7), last village before Ambositra, Tatezambato, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 527* (BR, K, MO, P, TAN); S of Ambalavao, on RN7, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 533* (BR, K, MO, TAN); PK 474 on road RN7 from Tuléar to Fianarantsoa, 6 km before reaching Ambalavao, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 600* (BR, K, MO, P, TAN); PK 474 on road RN7 from Tuléar to Fianarantsoa, 6 km before reaching Ambalavao, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 604* (BR, MO, P, TAN); on RN7, 38 km from Fianarantsoa, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 625* (BR, K, MO, TAN); vallée du Sakaleona, vi.1939 (fr), *Decary 14249* (P); environs d'Ihosy, ii.1957 (fl), *Descoings 2214* (P, TAN); RN7, c. 10 km S of Ambalavao and 33.2 km N of Zomandao River, iii.1985 (fr), *Dorr, Bamett, Rakotozafy, Creek & Razafimalala 3919* (BR, K, P, TAN); Massif de l'Ivakoany, xii.1928 (fl), *Humbert 6983* (BR, P); environs d'Ihosy, iii.1934 (fl), *Humbert 14432* (BR, P); Montagnes W d'Itremo, W Betsileo, i–ii.1955 (fl),

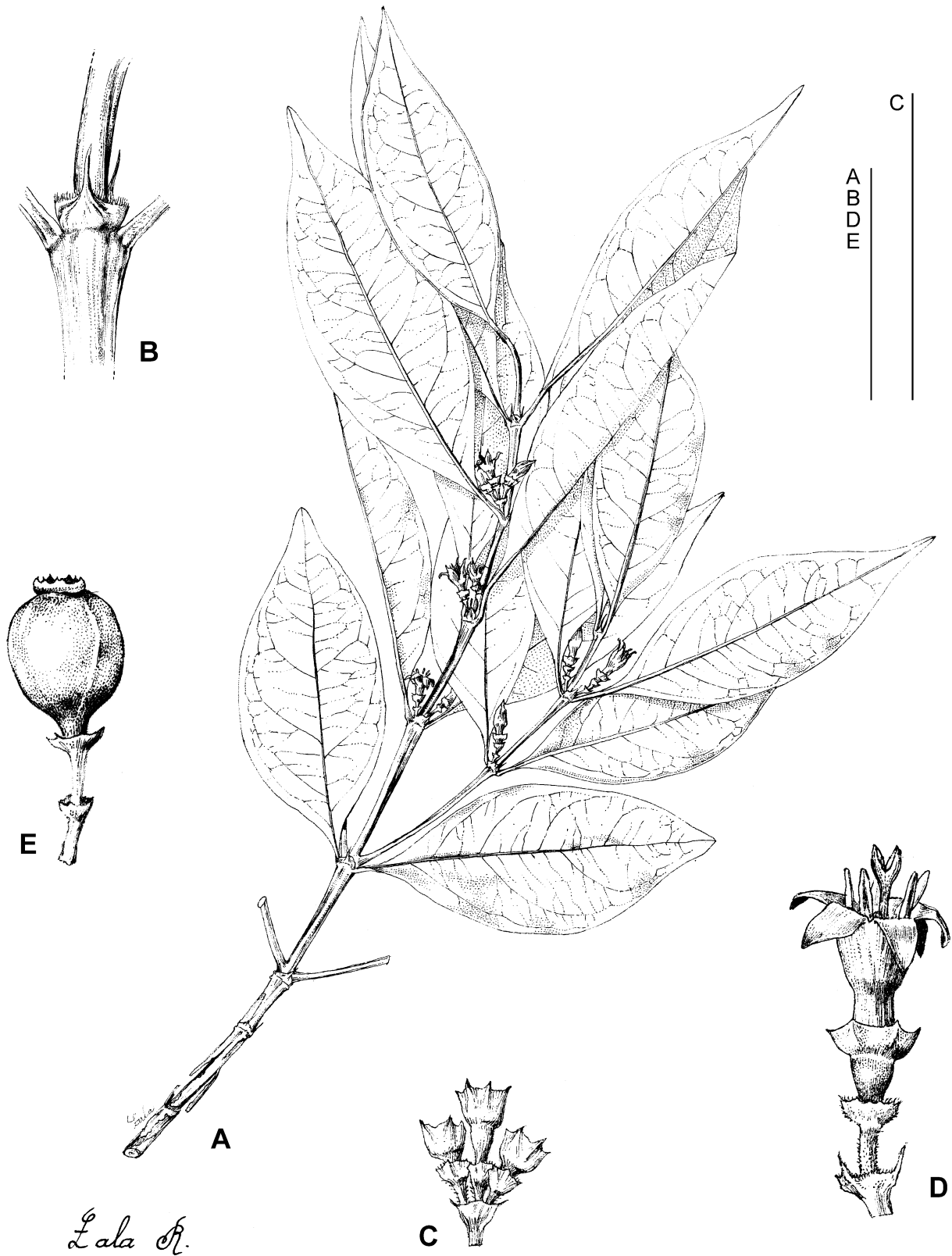
Humbert 28336 (P); plateaux et vallées de l'Isalo, W de Ranohira, 1955 (fl, fr), *Humbert 28722* (BR, P); Ikalamavony, district d'Ambohimahasoana, 1955 (fr), *Humbert 30246* (BR, P); Ihosy, base de la montée sur l'Horombe, vers le PK 620, ii.1973 (fl), *Jacquemin 1257* (P); PK 590, 18 km d'Ihosy, x.1966 (fl), *Leroy 20* (P); Ampantsakambe, PK 474, RN 7, Ambalavao, Ihosy, iv.1971 (fr), *Mabberley 1014* (K, TEF); 12 km S of Ihosy on RN7, stream on the north edge of the Horombe Plateau, iv.1991 (fl), *Miller & Randrianasolo 6238* (K, P, TAN); premier pont sur la Saonjo, après Fenoarivo, v.1964 (fr), *Morat 1131* (P, TAN); Ihosy, montée vers l'Horombe, ii.1961 (fl), *Peltier 2765* (BR, P, TAN); environs d'Ihosy, vi.1933 (fr), *Perrier de la Bâthie 19276* (P); près de la confluence de la Mania et de l'Ivato, vi.1912 (fl, fr), *Perrier de la Bâthie 3913* (P); 22 km NE of Ihosy on RN7, iii.1992 (fl, fr), *Phillipson, Clement & Rafamantanantsoa 3926* (K, TAN); Ranomafana National Park, Ifanadiana, viii.1998 (fr), *Razafimandimbison 390* (BR, K, MO). Not located: forests of West Betsilea, without date (fl), *Baron 159* (K, P); chûte de Manamontana, ii.1945 (fl, fr), *Cours 2673* (BR, P, TAN); Ankafana, 1880 (fl), *Cowan s.n.* (P); route de Vohidiabe, without date (fr), *Dequaire 27780* (P). Without locality or date: *Baron 164* (K) (fl); *Baron 967* (K, P) (fr); *Baron 4637* (K) (fl); *Baron 4794* (K) (fl); *Grevé 153* (P) (fr); *Homolle 1802* (BR, P) (fr); *Lyll 394* (K) (fl).

TRICALYSIA DAUPHINENSIS RANDRIAMB. & DE BLOCK, **SP. NOV.** (FIG. 15)

Type: MADAGASCAR. Toliara Province, north-east of town in Mandena coastal forest, east and beyond QIT camp, *McPherson & Dumetz 14661* (holo-: MO; iso-: K, P, TAN).

Diagnosis: *T. cryptocalycis* similis a qua foliorum laminis papyraceis apice acuminatis differt; ob stantum verisimiliter gynodioecium etiamque distinguitur.

Description: Gynodioecious shrubs or, rarely, small trees, up to 8 m high; flowering branches slender, flattened, and bisulcate; youngest internodes brown, glabrous or densely pubescent with short, appressed to spreading hairs; older internodes brown or reddish brown, usually not turning fawnish, flaking. Leaves with petioles 2–7 mm long, canaliculate adaxially, glabrous or densely pubescent with short appressed hairs. Blades elliptic, somewhat obovate or ovate or rarely narrowly so, 3–10 × 1–4 cm, papyraceous, drying brown or green and somewhat glossy above, discolorous or not, glabrous on both surfaces but midrib often pubescent on both sides (at least in the basal half of the blade); tip acuminate, rarely weakly



Lala R.

Figure 15. *Tricalysia dauphinensis* Randriamb. & De Block. A, flowering branch $\times 2/3$; B, stipules $\times 2.5$; C, inflorescence $\times 3$; D, calyculus, calyx and corolla $\times 4$; E, fruit $\times 2$. A-D, McPherson & Dumetz 14661; E, Gereau 3339.

acuminate (acumen 6–15 mm long); base attenuate or cuneate; six to ten pairs of secondary nerves; ciliate pit or rarely tuft domatia conspicuous. Stipules with sheath 1–2 mm high, glabrous or densely pubescent with short appressed hairs outside; awn (0.5–)1–2(–3) mm long. Inflorescences 1- or 3(–5)-flowered, subsessile or shortly pedunculate (peduncle 0.5–4 mm long), lax, all parts glabrous or moderately to densely pubescent with short appressed hairs; pedicels 0–3 mm long; bracts and bracteoles fused into calyculi, one to two per flower; calyculi cupular, foliar awns up to 1 mm long or inconspicuous (rarely foliar appendages subfoliaceous, up to 5 mm long), stipular awns inconspicuous or absent. Flowers (4–)5(–7)-merous; bud shortly acuminate; calyx glabrous or sparsely to moderately pubescent with short appressed hairs, densely covered with appressed hairs and scattered colleters inside; calyx tube 1–1.5 mm long; calyx lobes \leq 0.5 mm long; corolla tube (2–)2.5–3.5 mm long, c. 1.5 mm wide at the base and c. 2 mm wide at the throat, glabrous outside, glabrous inside except for a dense ring of hairs at the throat; corolla lobes 3–4.5 mm long, glabrous but sometimes sparsely ciliate; anthers 1.25–2 mm long, glabrous, apical sterile appendix minute, filaments 0.5–1 mm long; ovary 0.75–1.5 mm high, glabrous, (2–)3(–4) ovules loosely immersed in each placenta; style and stigma 5–7 mm long, glabrous, stigmatic lobes 1–2 mm long; functionally female flowers: anthers not opening and/or not containing well-developed pollen. Fruits spherical or slightly longer than wide, 6–9.5 \times 5–8 mm, red when mature, drying brown or rarely orange–brown, glabrous. Seeds 4–8 per fruit, 3.5–6.5 \times 2–4.5 mm.

Distribution: Restricted to south-eastern Madagascar in the Taolagnaro region (Toliara Province) (Fig. 11E).

Ecology: In littoral, coastal, or lowland humid forest on sandy soil; altitude: 700–1700 m.

Phenology: Flowering: December–February; fruiting: (January–)March–September.

Vernacular names: hazongalala; hazombalala fotsy.

Uses: Firewood; wood for construction (poles for huts or enclosures).

Material studied: MADAGASCAR. Toliara Province: forêt de Mandena, N de Taolagnaro, xii.1969 (fl), *Capuron 29016-SF* (BR, P, TEF); Andohahela, RNI 11, iii.1953 (fr), *coll. ignot. 5162-RN* (BR, P, TEF); RNI 11, Andohahela, iii.1953 (fr), *coll. ignot. 6162-RN* (BR, P); Ampandrandava, without date (fl, fr), *coll. ignot. (Herb. Jard. Bot. Tan.) 6297* (BR, P); forêt d'Haramy,

Mahareno, canton Ranomafana, district Taolagnaro, v.1954 (fr), *coll. ignot. 10092-SF* (BR, P, TEF); Mandena, Taolagnaro, xii.1954 (fl), *coll. ignot. 15619-SF* (BR, P, TEF); above St. Jacques, 5.9 km NNW of Taolagnaro, above the waterfall, xii.1997 (fl), *Davis, Andriantiana & Gower 1211* (K, P); Mandena forest, forest parcel M15, ii.2001 (fl), *Davis & Rakotonasolo 2718* (K, TAN, TEF); Mandena, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 669* (BR, K, MO, P, TAN); Taolagnaro, Mandena, i.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 670* (BR, K, MO, P, TAN); Andohahela, parcelle 1, col de Manangotry, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 689* (BR, K, MO, P, TAN); Andohahela, parcelle 1, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 693* (BR, K, MO, P, TAN); Andohahela, parcelle 1, i.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 694* (BR, K, MO, P, WAG); Andohahela, parcelle 1, i.1999 (fl), *De Block, Rakotonasolo & Randriamboavonjy 698* (BR, K, MO, P, TAN); Andohahela, parcelle 3, Tsimelaha, i.1999 (fr), *De Block, Rakotonasolo & Randriamboavonjy 731* (BR, K, MO, TAN); forêt de Petriky, xii.1989 (fl), *Dumetz & McPherson 1120* (K, MO, P); Mandena, iv.1989 (fr), *Dumetz, Gereau & Rabevohitra 697* (K, MO, P, TAN); fok. Mandena, fir. Ampasy, Fort-Dauphin, xii.2000 (fl), *Falinina, Rabenantoandro & Ramisy 92* (BR, MO); 22 km N d'Ifarantosoa, RNI 11, bords de la piste Ranomafana-Sud, iv.1988 (fr), *Floret, Lowry, Leeuwenberg & Rajemisa 1972* (K); canton Manambaro, préfecture Taolagnaro, Petriky forest, S of large dune near NE corner of Lake Andranany, iv.1989 (fr), *Gereau 3339* (BR, K, P, TAN); bassin de réception de la Mananara, affluent du Mandrare, pentes occidentelles des montagnes entre l'Andohahela et l'Elakelaka au Vatazo, S d'Imonty, ii.1934 (fl), *Humbert 14056* (P); bassin de réception de la Mananara, affluent du Mandrare, col d'Ambato et pentes occidentelles du Vohipaly, ii.1934 (fl), *Humbert 14139* (BR, P); Baie des Galions, Ranofotsy, SW de Fort-Dauphin, ii.1955 (fl), *Humbert & Capuron 28972* (BR, P); Mont Ankazovandamena, près de la Baie des Galions, Ranofotsy, SW de Fort-Dauphin, ii.1955 (fl), *Humbert 29048* (BR, P); plot de suivi Antseva, Ihazofotsy, RNI d'Andohahela, vii.1996 (fr), *Laha 293* (K); Taolagnaro, NE of town in coastal forest called Mandena, road side forest E and beyond QIT camp, xii.1989 (fl), *McPherson & Dumetz 14661* (K, P, TAN); private Forest Reserve owned by Heanlure family, ix.1968 (fr), *McWhirter 142* (P, K); 5 km S of Manambaro, 23 km W of Taolagnaro, iii.1991 (fr), *Miller & Randrianasolo 6193* (K, MO, P, TAN); Berenty, vii.1985 (fr), *O'Connor 19* (BR, K, P); forêt d'Ambatorongorongo, Amboavola, Sarisambo, Taolagnaro, vi.1999 (fr), *Rabenantoandro, Randrihasipara & Ramisy 114* (BR, K, MO, P); Station Forestière de

Mandena, c. 7.5 km N de Taolagnaro, iii.1989 (fr), *Rabevohitra*, Dumetz & Gereau 1768 (BR, K, MO, P, TAN); près de la rivière d'Antorendrika, avant Belavenona, près du radier, c. 22 km NE de Taolagnaro, iii.1989 (fl), *Rabevohitra*, Dumetz & Gereau 1775 (K, MO, P); préfecture Taolagnaro, Petriky, i.1990 (fl), *Rabevohitra* 2115 (K, MO, P, TAN); Mandena Forest, forest parcel M. 13, Oxford transect RA4, tree number 56, ii.2001 (fr), *Rakotonasolo*, Ranaivojaona, Ralimanana & Davis OKTAN 68 (K, TAN, TEF); RNI 11, Andohahela, parcelle 1, Isaka Ivondro, iii.1993 (fr), *Randriamampionona* 250 (BR, K, MO, P); RNI 11, Andohahela, parcelle 1, Isaka Ivondro, vi.1993 (fr), *Randriamampionona* 442 (BR, K, MO, P); Etsilisy, Ampanasa-vaovao, parcelle 1 d'Andohahela, vii.1994 (fr), *Randriamampionona* 816 (BR, K, MO); woods near Fort Dauphin, without date (fr), *Scott Elliot* 2489 (K, P); Fort-Dauphin, without date (fl), *Scott-Elliot* 2746 (K); SE d'Ampandrandava, entre Bekily et Tsivory, iv.1943 (fl, fr), *Seyrig* 686 (P). Without locality: xii.1971 (fl), *Guillaumet* 888 J (P).

TRICALYSIA HUBERTII RANDRIAMB. & DE BLOCK,
SP. NOV. (FIG. 16)

Type: MADAGASCAR. Antsiranana Province, collines et plateaux de l'Ankarana, colline sud du Jardin Botanique, *Humbert* 32625 (holo-: P).

Diagnosis: Inter speciebus 4-meris bene diagnoscenda propter foliorum laminas papyraceas, stipulas solummodo breviter aristatas et calyculorum appendices calycis lobos nullos vel minutos.

Description: Shrub or, rarely, small tree, up to 4 m high. Flowering branches slender, flattened, and bisulcate or quadrangular, glabrous or densely pubescent with short spreading or erect hairs; young internodes brown to reddish brown, not turning fawnish, often flaking. Leaves with petioles 2–6(–10) mm long, canaliculate adaxially, glabrous or densely pubescent with short spreading or erect hairs. Blades elliptic, ovate, or obovate, 3.5–9(–13.5) × 1.5–4(–5) cm, papyraceous, drying brownish or greenish above and paler below, glabrous on both surfaces but commonly midrib and rarely secondary nerves pubescent; tip acuminate, acumen 3–15 mm long; base cuneate to acute; five to ten pairs of secondary nerves; ciliate pit domatia present. Stipules with sheath 1–1.5(–2) mm high, glabrous or sparsely to densely pubescent with short hairs outside; awn 0.1–1(–1.5) mm long. Inflorescences one- to five-flowered (coaxillary inflorescences common in some specimens), shortly pedunculate (peduncle 0–2 mm long), compact in flowering stage, lax in fruiting stage, inflorescence parts glabrous or sparsely to densely pubescent with

appressed hairs; pedicels 0.5–3 mm long; bracts and bracteoles fused into calyculi, usually one per flower; calyculi cupular, foliar awns up to 1 mm long or inconspicuous, stipular awns inconspicuous or absent. Species hermaphroditic. Flowers 4(–5)-merous; bud acuminate; calyx glabrous or moderately pubescent with short appressed hairs, densely covered with appressed hairs and with scattered colleters inside; calyx c. 1 mm long, with 4(–5) minute teeth or almost truncate; corolla tube (2–)3–3.5 mm long, c. 1 mm wide at the base and 1.25–1.75 mm wide at the throat, glabrous outside, glabrous inside except for a dense ring of hairs at the throat; corolla lobes (2.5–)3–4 mm long, glabrous but sometimes sparsely ciliate; anthers sessile, the base included in the corolla tube, erect at anthesis, 1.25–2 mm long, glabrous, apical sterile appendix minute; ovary c. 1 mm high, glabrous, two to four ovules loosely impressed in each placenta; style and stigma 4–6 mm long, glabrous; stigmatic lobes 0.75–1.25 mm long. Fruits spherical when mature, slightly longer than wide when immature, 5–8 × 5–7 mm, red when mature, drying brown, glabrous. Seeds 2–6 per fruit, 4–6 × 3–4 mm.

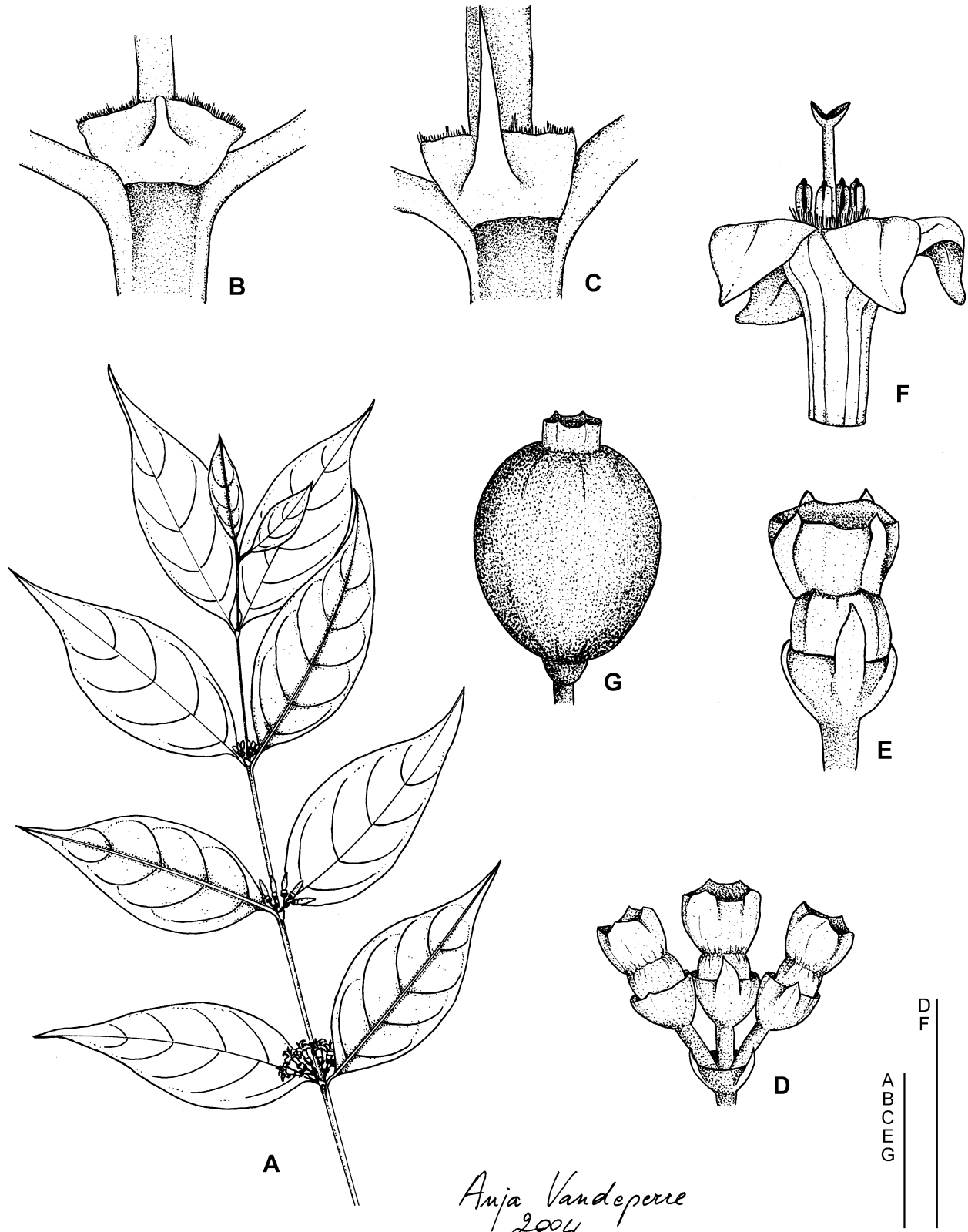
Distribution: Northern Madagascar, Antsiranana Province, in the region of Ankarana, Analamera, and along the Saharaina (= Saharenena) river north of Analamera (Fig. 11F).

Ecology: In lowland forest on calcareous soil; altitude: 30–350 m.

Phenology: Flowering: January–February; fruiting: January–October.

Vernacular names: kafeala.

Material studied: MADAGASCAR. Antsiranana Province: fiv. Ambilobe, Réserve Spéciale d'Ankarana, 108 km S d'Antsiranana par RN6, 12 km W du village Mahamasina, iv.1996 (fr), *Andrianantoanina* & *Bezara* 959 (MO, K, P); plateau calcaire de l'Ankarana, vi.1990 (fr), *Bardot-Vaucoulon* 3535 (K); forêt de Sahafary, bassin de la Saharaina, ii.1962 (fl), *Capuron* 20989-SF (BR, P, TEF); forêt de Sahafary, bassin de Saharaina, iv.1963 (fr), *Capuron* 22710-SF (BR, P, TEF); forêt de Sahafary, bassin de Saharaina, ii.1964 (fr), *Capuron* 23321-SF (BR, P, TEF); forêt d'Analafondro, au pied SE du plateau de Sahafary, bassin inférieur du Rodo, ii.1966 (fl), *Capuron* 24519-SF (BR, P, TEF); Massif de l'Ankitekona, S du baie d'Ambararata, iv.1966 (fr), *Capuron* 24672-SF (BR, P, TEF); forêt de Sahafary, bassin de Saharaina, vi.1970 (fr), *Capuron* 29203-SF (BR, P, TEF); district d'Ambilobe, forêt d'Andranonakoho, calcaires de



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Figure 16. *Tricalysia humbertii* Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, C, stipules $\times 8$; D, inflorescence $\times 6$; E, calyx and calyculus $\times 8$; F, corolla $\times 6$; G, fruit $\times 4$. A, B, *Humbert 32432*; C, *Humbert 32814*; D, E, *Humbert 32625*; F, *Capuron 24519-SF*; G, *Capuron 23321-SF*.

l'Ankarana, km 103 sur la route de Diego à Ambilobe, i.1960 (fl), *Cours & Humbert 5535* (BR, P); district d'Ambilobe, Montagne d'Andavakafanihy, calcaires de l'Ankarana, km 105 sur la route d'Ambilobe, ii.1960 (fl), *Cours & Humbert 5628* (BR, P); Massif de l'Ankarana, x.1939 (fr), *Decary 14546* (BR, P); Analamera, vallée de l'Analabe, sous-affluent du Rodo, i.1938 (fr), *Humbert 19228* (BR, P); collines et plateaux calcaires de l'Ankarana, lisière de calcaire S d'Anivorano, i–ii.1960 (fl), *Humbert 32432* (BR, P); collines et plateaux calcaires de l'Ankarana, i–ii.1960 (fl), *Humbert 32469* (BR, P); collines et plateaux de l'Ankarana, colline S du JB8 (Jardin Botanique), i–ii.1960 (fl), *Humbert 32625* (P); collines et plateaux calcaires de l'Ankarana, W de la route, vers la grotte du Fanihy, i–ii.1960 (fl), *Humbert 32737* (BR, P); collines et plateaux calcaires de l'Ankarana, i–ii.1960 (fr), *Humbert 32771* (P); collines et plateaux calcaires de l'Ankarana, Ambilomagadro, i–ii.1960 (fl), *Humbert 32814* (BR, P); forêt de Sahafary, S de Diego, iii.1962 (fr), *Keraudren 1661* (P).

TRICALYSIA LEUCOCARPA (BAILL.) RANDRIAMB. & DE BLOCK, **COMB. NOV.** (FIG. 17)

Hypobathrum leucocarpum Baill., *Adansonia* **12**: 225 (1878). *Type*: MADAGASCAR. Antsiranana Province, Nossi-Be, *Boivin 2056* (holo-: P; iso-: P).

Description: Dioecious shrubs or small trees, up to 4.5 m high; flowering branches stout, flattened, and bisulcate or quadrangular and canaliculate on all sides, sparsely to moderately pubescent with short appressed hairs or glabrous; young internodes brown or reddish brown, smooth, not turning fawnish. Leaves with petioles 3–8 mm long, canaliculate adaxially, glabrous or sparsely to moderately pubescent with short appressed hairs. Blades elliptic to obovate or narrowly so, rarely ovate, 9.5–19.5 × 3.5–7.5 cm, coriaceous, usually drying fawnish or pale green, not discoloured, glabrous on both surfaces; tip acuminate, acumen 7–30 mm long; base cuneate or acute; five to nine pairs of secondary nerves; ciliate pit or tuft domatia often present but inconspicuous. Stipules with sheath 1–2.5 mm high, moderately or sparsely pubescent with short appressed hairs outside (hairs sometimes only visible on youngest stipule pair); awn (0.5–)1–3 mm long. Inflorescences three- to nine-flowered, subsessile (but sometimes shortly pedunculate in fruit (peduncle ≤ 2 mm long), compact, all parts moderately to densely pubescent with appressed hairs; axes < 1 mm long (< 2 mm in fruit); pedicels 0–1 mm long; bracts and bracteoles fused into calyculi, usually one per flower; calyculi cupular, foliar awns up to 1.5 mm long in calyculi supporting inflorescence branches, inconspicuous in others,

stipular awns inconspicuous or absent. Flowers five- to six-merous; bud acuminate; calyx moderately to densely pubescent with short appressed hairs outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1–1.4 mm long; calyx lobes narrowly triangular to subulate, ≤ 0.5 mm long; corolla tube 2–5 mm long, 1–1.5 mm wide at the base and c. 2 mm wide at the throat, glabrous outside, glabrous inside except for a ring of hairs at the throat; corolla lobes 3.5–4 mm long, glabrous; anthers subsessile (filaments < 0.5 mm long), 1.25–2.5 mm long, glabrous, apical sterile appendix minute; ovary 0.75–1 mm high, glabrous; style and stigma 5–8 mm long, glabrous, stigmatic lobes 1–1.25 mm long; functionally male flowers: corolla tube 3.5–5 mm long, anthers 2–2.5 mm long, ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas, style and stigma 7–8 mm long; functionally female flowers: corolla tube 2–2.5 mm long, anthers not opening and/or not containing well-developed pollen, c. 1.5 mm long, ovary with three to four ovules per locule, style and stigma c. 5 mm long. Fruits spherical or slightly longer than wide, (7–)8–12 × 7–11 mm, red when mature, drying orange-brown, glabrous. Seeds 3–6 per fruit, 4.5–8 × 3–4 mm.

Distribution: Northern Madagascar, Antsiranana Province, from Nossi-Be to Antalaha (Fig. 18A).

Ecology: In lowland or mid-altitudinal humid forest; altitude: 0–1000 m.

Phenology: Flowering: December–January; fruiting: (December–)February–July.

Vernacular names: kafeala; sakainala; tsifo; tsifofotsy; tsimahamasatsokina.

Notes: (1) The type specimen of *T. leucocarpa* was collected on Nossi-Be, but the material is very poor with only a single flower and fruits available. All other specimens from this island are also collected in fruit. Flowering specimens are only known from other localities in Antsiranana Province. They, together with fruiting material from the same region, are included in *T. leucocarpa* on the basis of similar leaves, stipules, and stems, and because they possess, as does the type specimen of *T. leucocarpa*, compact, pubescent inflorescences and relatively short pubescent calyces. Moreover, all specimens occur in the same forest types (lowland or mid-altitudinal humid forest). (2) The specimen *Capuron 24863-SF* from the region of Vohemar has smaller leaves (up to 9 × 4.5 cm) and is tentatively included.

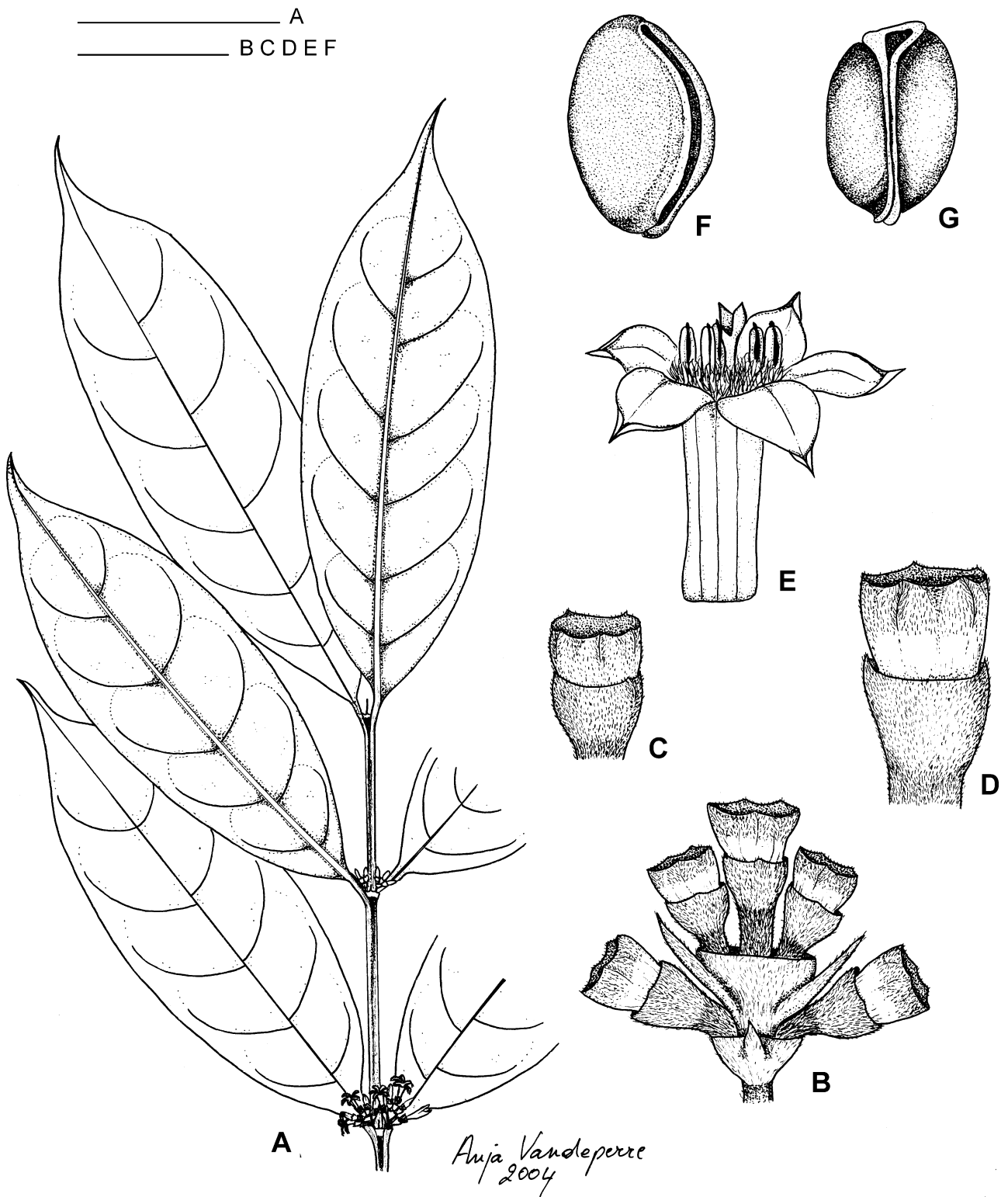


Figure 17. *Tricalysia leucocarpa* (Baill.) Randriamb. & De Block. A, Flowering branch $\times 1/2$; B, inflorescence $\times 4$; C, D, calyx and calyculus $\times 8$; E, corolla $\times 9$; F, G, seed $\times 4$. A, C, E, *Humbert 22414*; B, D, *coll. ignot. 11729-RN*; F, G, *coll. ignot. 10743-RN*.

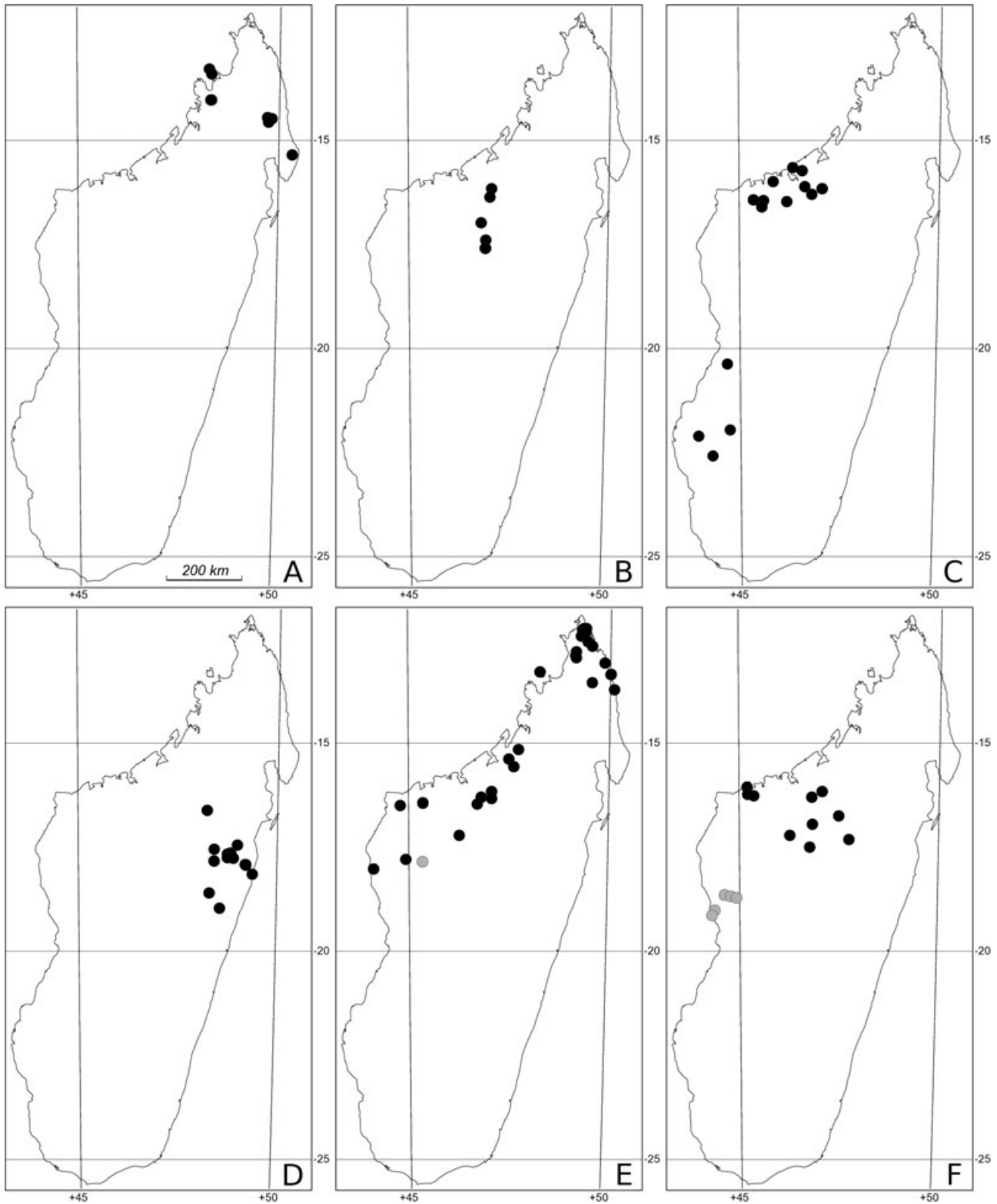


Figure 18. Distribution maps of *Tricalysia*. A, *T. leucocarpa*; B, *T. madagascariensis*; C, *T. majungensis*; D, *T. orientalis*; E, *T. ovalifolia* var. *ovalifolia* (black circles) and var. *glabrata* (grey circles); F, *T. perrieri* ssp. *perrieri* (black circles) and ssp. *antsalovensensis* (grey circles).

Material studied: MADAGASCAR. Antsiranana Province: Nossi-Be, RNI de Lokobe, iv.1994 (fr), *Antalahimena* 87 (BR, K, MO, P); Nossi-Be, i.1850 (fr), *Boivin* 2056 (P); Nossi-Be, forêt de Lokobe, iii.1964 (fr), *Capuron* 23458-SF (BR, P, TEF); Nossi-Be, forêt de Lokobe, v.1966 (fr), *Capuron* 24755-SF (BR, P, TEF); canton Ambohitralanana, district Antalaha, iv.1960 (fr), *coll. ignot.* 10743-RN (BR, P, TEF); canton Maroambihy, district Sambava, xii.1961 (fl), *coll. ignot.* 11729-RN (BR, P, TEF); montagne d'Ambohimarangitra, xii.1948 (fl), *Cours* 3195 (BR, P, TAN); forêt de la montagne de Mainampango, E du village Ambalavoanio (= ?Ambalavonihio), i.1949 (fl), *Cours* 3206 (BR, P, TAN); Réserve Naturelle de Marojejy, xii.1972 (fr), *Guillaumet* 4217 (BR, P); pentes orientales du Massif de Marojejy (Nord-est), W de la rivière Manantenina, affluent de la Lokoho, xii.1948 (fl), *Humbert* 22414 (BR, P); Nossi-Be, forêt de Lokobe, iii.1962 (fr), *Keraudren* 1577 (P); Réserve Naturelle de Marojejy, along the trail to the summit of Marojejy Est, NW of Mandena, along Manantenina River, ii.1989 (fr), *Miller & Lowry* 4002 (K, MO, P); Manongarivo, W slopes of peak E of Beraty, vii.1987 (fr), *Phillipson* 2040 (MO, P, TAN); Lokobe, SE d'Hellville, Ambanoro, Nossi-Be, v.1998 (fr), *Rabenantoandro, Birkinshaw & Antilahimena* 12 (MO, P).

Tentatively included material: S de Vohemar, x.1966 (fr), *Capuron* 24863-SF (P, TEF).

TRICALYSIA MADAGASCARIENSIS (DRAKE EX DUBARD)
A.CHEV. (FIG. 19)

Tricalysia madagascariensis (Drake ex Dubard) A.Chev., *Rev. Bot. Appl.* **18**: 414 (1938), *Encycl. Biol.* **22**: 36, Pl. 153 (1942) (see note 1) & *Encycl. Biol.* **28**: 245 (1947), p.p., excluding *Richard* 78.

Coffea madagascariensis Drake ex Dubard, *Bull. Mus. Hist. Nat. Paris* **13**: 281 (1907); Mariani, *Les Caféiers*: 118, Figs. 36–37 (1908); Jumelle & Perrier de la Bâthie, *Ann. Mus. col. Marseille sér. 2*, **8**: 464 (1910) (see note 2); Jumelle, *Ann. Mus. col. Marseille, sér. 5*, **1**: 6 (1933); Gaffier, *Ann. Mus. col. Marseille, sér. 5*, **1**: 22 (1933); De Wildeman, *Etude Coffea*: 427 (1941). *Type:* MADAGASCAR. Mahajanga Province, Firingalava, *Perrier de la Bâthie* 465 (holo-: P; iso-: P) (see note 3).

Description: Gynodioecious shrub or, rarely, small tree, 2–5 m high (see note 4); flowering branches moderately stout, flattened, and often bisulcate, glabrous or internodes sparsely and nodes moderately to densely pubescent with short appressed hairs; youngest internode brown, smooth; older internodes fawnish, flaking. Leaves with petioles 3–6 mm long, canaliculate adaxially, moderately to densely pubes-

cent with short appressed hairs (hairs often restricted to adaxial side). Blades elliptic or somewhat obovate, 6.5–12 × 3.4–5.8 cm, coriaceous, drying green or brown above and paler below, glabrous on both surfaces; tip acuminate, acumen 3–10 mm long; base cuneate to acute; (5–)6–8 pairs of secondary nerves; large ciliate pit domatia conspicuous. Stipules with sheath 1–2 mm high, glabrous to densely pubescent with short appressed hairs outside; awn 1.5–4.5 mm long. Inflorescences three- to five-flowered, sessile or subsessile (peduncle ≤ 1 mm long), compact, all parts densely pubescent with short, appressed, whitish hairs; axes ≤ 1 mm long; pedicels 0(–)1 mm long; bracts and bracteoles fused into calyculi, one to two per flower; calyculi cupular, foliar appendages awn-like (≤ 1 mm long) or rarely subfoliaceous (≤ 5 mm long), stipular awns inconspicuous or absent. Flowers five- to seven-merous; bud shortly acuminate; calyx drying pale brown, densely pubescent with short appressed hairs outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1.5–2.5 mm long, faintly ridged longitudinally; calyx lobes narrowly triangular to subulate, keeled, ≤ 0.5 mm long; corolla tube 5–7.5 mm long, 0.9–1.3 mm wide at the base and 1.5–2 mm wide at the throat, moderately to densely pubescent with short spreading hairs from the middle upwards or all over outside, densely covered with long spreading hairs in the upper half or upper two-thirds inside; corolla lobes 4.5–6 mm long, ciliate and moderately to densely pubescent with short spreading hairs outside, glabrous inside; anthers 3.5–4.5 mm long, glabrous, apical sterile appendix minute, filaments 1.2–2 mm long; ovary 0.5–1 mm high, glabrous (1–)2 ovules loosely immersed in each placenta; style and stigma 8.5–11.5 mm long, all but base moderately to densely pubescent, stigmatic lobes 2–3.5 mm long; functionally female flowers: anthers not opening and/or not containing well-developed pollen. Fruits spherical, 4–6.5 × 4–7.5 mm diameter, red, drying brown to blackish, glabrous. Seeds 2–4 per fruit, 3.5–5 × 2.5–4.5 mm.

Distribution: Central west Madagascar (Mahajanga Province), from Ankarafantsika to Firingalava (Fig. 18B).

Ecology: In lowland deciduous or semi-deciduous dry forest on sandy soil.

Phenology: Flowering: April–June; fruiting: July–September.

Vernacular names: kafeala.

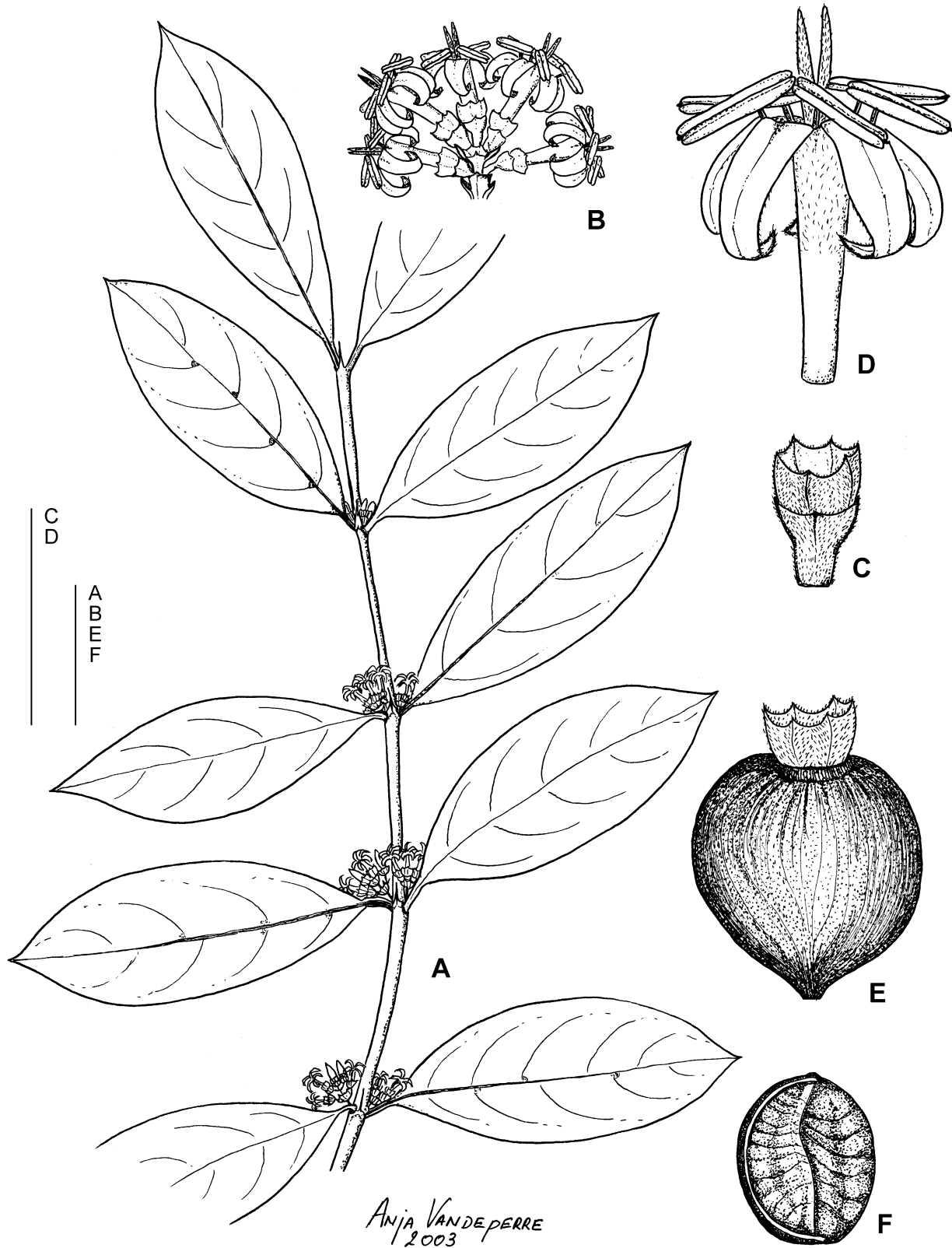


Figure 19. *Tricalysia madagascariensis* (Drake ex Dubard.) A.Chev. A, Flowering branch $\times 2/3$; B, inflorescence $\times 2$; C, calyx and calyculus $\times 6$; D, corolla $\times 6$; E, fruit $\times 4$; F, seed $\times 4$. A–D, Hildebrandt 3464; E, F, Boiteau 1020.

Notes: (1) Chevalier (1942: 36) wrongfully cited *Perrier de la Bâthie 3464* as type. (2) As already indicated by Jumelle & Perrier de la Bâthie (1910), the specimens collected as *Perrier de la Bâthie 465* belong to two species: *Tricalysia madagascariensis* and *Coffea perrieri* Drake ex Jumelle & Perrier. All specimens belonging to *T. madagascariensis* have the number 465; those belonging to *C. perrieri* are numbered 465 and 465 bis, ter, and tes. The collections were made over several years by collectors sent out by Perrier de la Bâthie to gather more material of the original collection (A. P. Davis, Royal Botanic Gardens, Kew, pers. comm.). (3) In P, several duplicates of the type collection *Perrier de la Bâthie 465* are available, mostly from the Drake herbarium. Most of these are annotated as *Coffea madagascariensis* Drake or *Coffea madagascariensis* Drake ex Dubard. The handwriting is the same on all specimens, but is neither Drake's nor Dubard's. The only specimen annotated by Dubard which formerly belonged to the Drake herbarium is now kept at P. This specimen, cited here as Drake s.n., is most probably a duplicate of *Perrier de la Bâthie 465*, but the label only reads 'échantillon provenant de l'herbier Drake, ou l'espèce est représenté plusieurs fois avec étiquette de provenance', without mentioning the collector's name and number. The printed locality information (Ankarafantsika) is probably a mistake. From the protologue, it is clear that Dubard based his description on the entirety of the *Perrier de la Bâthie 465* specimens. It seems impossible to decide which one of the duplicates should be considered as the holotype. (4) In the protologue of *Coffea madagascariensis*, Dubard (1907: 283) repeated the plant description given by Drake Del Castillo (1902: 144–145): tree reaching a height of 10 m and a stem diameter of 40 cm with greenish brown fruits and seeds giving a somewhat bitter-tasting coffee with a nice aroma. This description, however, pertains to *Coffea perrieri* Drake ex Jumelle & Perrier, not *T. (Coffea) madagascariensis* (Jumelle & Perrier de la Bâthie, 1910: 464, footnote 1; Jumelle, 1933: 6).

Material studied: MADAGASCAR. Mahajanga Province: Station forestière de Tsaramandroso, viii.1968 (fr), *Boiteau 1020* (BR, P); Ankarafantsika, without date (fl), *coll. ignot. 10-SF* (P); Ankarafantsika, RNI 7, canton Tsaramandroso, district Ambato-Boeni, ix.1951 (fr), *coll. ignot. 2977-RN* (BR, P, TAN); ?Ankarafantsika, without date (fl), *Drake s.n.* (P); Uferwald des Marokoloi, vi.1880 (fl), *Hildebrandt 3464* (K, LE, P, WU); Firingalava, iv.1898 (fl), *Perrier de la Bâthie 465* (P); Belambo, environs de Maevatanana, vii.1900 (fr), *Perrier de la Bâthie 591-bis* (P); environs d'Andriba, iv.1922 (fl), *Perrier de la Bâthie 14640* (P). Without locality: vii.1898 (fr), *Perrier de la Bâthie 591* (P).

***TRICALYSIA MAJUNGENSIS* RANDRIAMB. & DE BLOCK, SP. NOV. (FIG. 20)**

Type: MADAGASCAR. Mahajanga Province, Réserve Naturelle Intégrale 8, Tsingy de Namoroka, Andranomavo, Soalala, *coll. ignot. 6143-RN* (holo.: P; iso-BR, TEF).

Diagnosis: *T. boiviniana* similis propter inflorescentiarum et florum fabricam, sed ab illa differt foliorum laminis angustioribus papyraceisque et ramis floriferis tenuibus.

Description: Dioecious large shrubs or small trees, up to 10 m high; flowering branches slender, somewhat flattened and bisulcate, glabrous or densely pubescent with short appressed hairs (Toliara specimens, see note); youngest internodes brown to reddish brown, smooth; older internodes greyish or brownish, rough, with numerous fissures and flaking. Leaves with petioles 4–8 mm long, canaliculate adaxially, glabrous. Blades narrowly elliptic, 5.5–11 × 1–3(–3.5) cm, papyraceous to subcoriaceous, drying green or brown above and paler below, glabrous on both surfaces; tip acuminate or rarely obtuse to weakly acuminate (Toliara specimens, see note), acumen 3–15 mm long; base attenuate; five to seven pairs of secondary nerves; ciliate pit domatia few to several, obscure to conspicuous. Stipules with sheath 0.5–1.5 mm high, sparsely to moderately covered with short appressed hairs outside, hairs often few and restricted to lateral sides of the sheath; awn 0.5–2 mm long. Inflorescences one- to nine-flowered, subsessile (peduncle < 1 mm long), compact, all parts densely covered with short appressed hairs; axes ≤ 1.5 mm long; pedicels 0–1 mm long; bracts and bracteoles fused into calyculi, one to three per flower; calyculi cupular, foliar appendages awn-like [≤ 1(–1.5) mm long] or rarely subfoliaceous (≤ 15 mm long; in Toliara specimens, see note), stipular awns inconspicuous or absent. Flowers (5–)6-merous; bud acuminate; calyx drying brown, at least upper half moderately to densely covered with short appressed hairs outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1–1.5 mm long; calyx lobes (5–)6(–7), triangular, keeled, ≤ 0.5 mm long; corolla tube 2.7–4 mm long, c. 1.2 mm wide at the base and c. 2 mm wide at the throat, glabrous outside, densely covered with long spreading hairs in the upper half inside; corolla lobes 4–5 mm long, glabrous on both surfaces, but usually sparsely ciliate, especially near the tip; anthers 2–2.5 mm long, glabrous, apical sterile appendix minute, filaments 0.75–1.5 mm long; ovary 1–1.5 mm high, glabrous; style and stigma 6.5–8 mm long, glabrous, stigmatic lobes 1.5–2(–2.5) mm long; functionally female flowers not seen; functionally

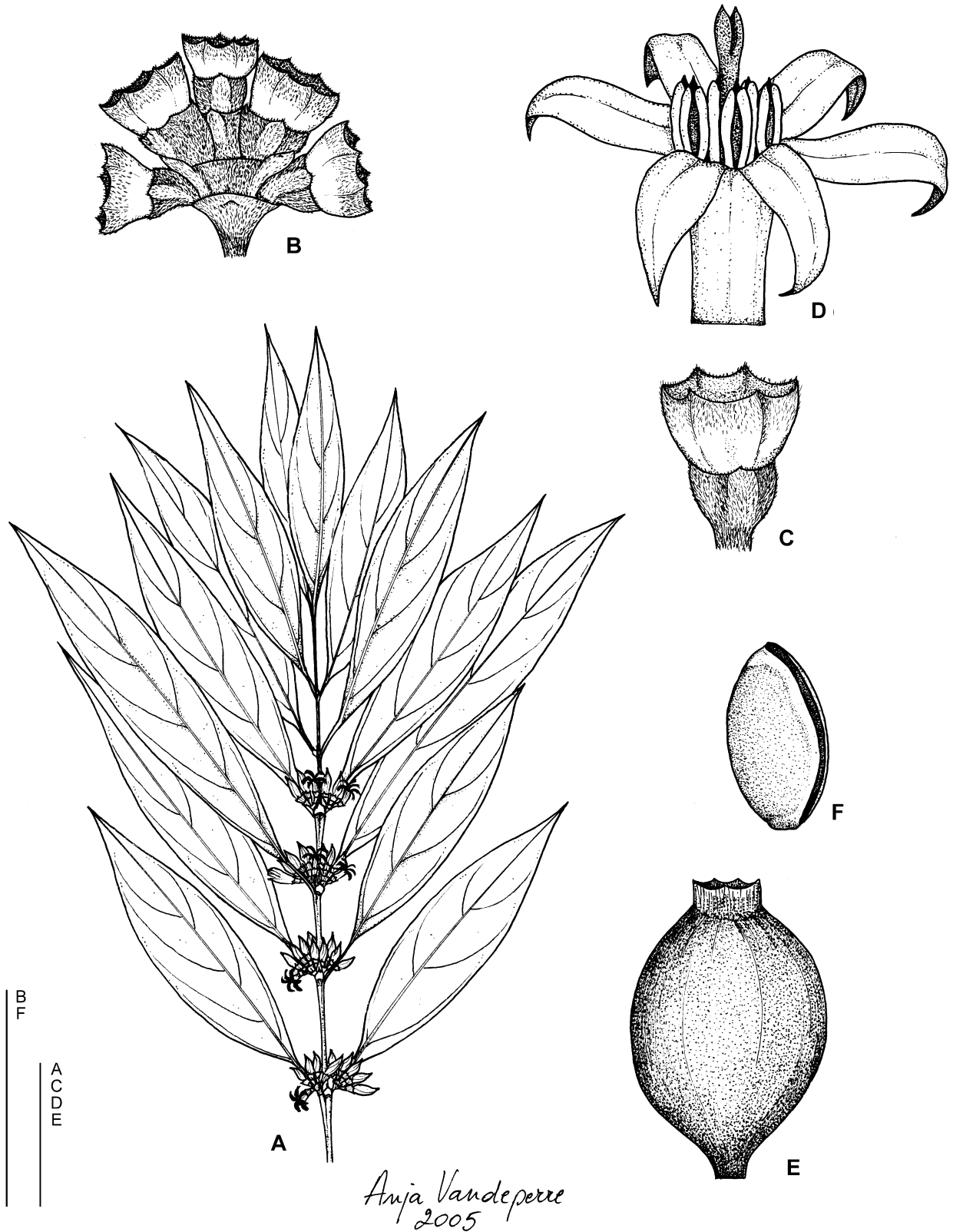


Figure 20. *Tricalysia majungensis* Homolle ex Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, inflorescence $\times 6$; C, calyx and calyculus $\times 9$; D, corolla $\times 9$; E, fruit $\times 4$; F, seed $\times 6$. A–D, coll. ignot. 6143-RN; E, F, Rakotomalaza et al. 391.

male flowers: ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas. Fruits spherical, 6–9 × 5.5–8 mm, red when mature, drying orange–brown or brown, glabrous. Seeds 6–10 per fruit, 4–5 × 2.5–3 mm.

Distribution: Western Madagascar. Disjunct distribution with glabrous specimens in Mahajanga Province (from the Baie du Mahajamba to the region of Soalala, especially well collected in the reserves of Ankarafantsika and Namoroka) and pubescent specimens (tentatively included: see note) in Toliara Province (region of Befandriana-Sud and Morombe) (Fig. 18C).

Ecology: In dry deciduous or semi-deciduous forest on sandy substrates; altitude: 0–300 m.

Phenology: Flowering: February–June; fruiting: June–August.

Vernacular names: hazotsikorovana or hazotsikovana; kafeala; mantsaka (Bara); nofotrakoho (Sakalava); taolankena; tsilanivoana; voantsokorova.

Uses: Wood used as firewood and for construction.

Note: The specimens from Toliara Province differ from those from the region of Majunga in several characters. Their flowering branches, stipules, and petioles are densely pubescent with short appressed hairs, their leaves are small (5.5–9 × 1–2.5 cm) with obtuse to weakly acuminate tips, and the foliar appendages of the calyculi are often subfoliaceous (up to 15 mm long). They are tentatively included in *T. majungensis*, but are also reminiscent of *T. cryptocalyx*, from which they differ by the coarser pubescence on the vegetative parts, the texture of the leaves, the shape of the leaf acumen, etc. More material from this region is needed to ascertain the affinity of these Toliara specimens.

Material studied: MADAGASCAR. Mahajanga Province: Majunga, Amborovy, v.1912 (fl), *Afzelius s.n.* (P); forêt d'Ankarafantsika, viii.1968 (fr), *Boiteau 1050* (BR, P); table calcaire de Begidro, sur rebord du plateau de Berivotra, iv.1965 (fl), *Capuron 24081-SF* (BR, P, TEF); RNI 8, tsingy de Namoroka, without date (fr), *coll. ignot. 33-SF* (BR, P); RNI 7, Ankarafantsika, vii.1951 (fr), *coll. ignot. 2937-RN* (P); RNI 7, Ankarafantsika, vii.1951 (fr), *coll. ignot. 3320-RN* (BR, P, TAN); Komihevitsy, Soalala, viii.1951 (fr), *coll. ignot. 4014-SF* (P, TAN, TEF); RNI 8, tsingy de Namoroka, vii.1952 (fr), *coll. ignot. 4204-RN* (P, TAN); Ankazambo, Befandriana-Nord, vii.1942 (fl), *coll. ignot. (Herb. Jard. Bot. Tana) 5194* (P); RNI 8, tsingy

de Namoroka, iii.1954 (fl), *coll. ignot. 6143-RN* (BR, P, TEF); RNI 8, tsingy de Namoroka, Ambatolafia, vii.1954 (fr), *coll. ignot. 6285-RN* (BR, P, TEF); RNI 8, tsingy de Namoroka, v.1954 (fl), *coll. ignot. 6372-RN* (BR, P, TEF); Andranomavo, Soalala, vii.1956 (fr), *coll. ignot. 8005-RN* (P, TAN); Andranomavo, Soalala, iii.1956 (fl), *coll. ignot. 8567-RN* (BR, P, TAN); Andranomavo, Soalala, vii.1959 (fr), *coll. ignot. 11626-RN* (BR, P); Ampijoroa, Ankarafantsika, vii.1966 (fr), *Peltier J. & M. 5985* (P); plateau de l'Antanimena, Boina, vi.1906 (fr), *Perrier de la Bâthie 3700* (P); environs de la Baie du Mahajamba, Boina, v.1907 (fl), *Perrier de la Bâthie 3715* (P); Mahevarano, près de Majunga, vi.1908 (fl), *Perrier de la Bâthie 3764* (P); route vers la forêt de Mangabe, vii.1995 (fr), *Rakotomalaza, Raharilala, Vognono, Rasolomanana, Randrianasolo & Rakotomamonjy 391* (BR, MO). Toliara Province: Ankazoabo, Befandriana, vii.1942 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 5194* (P); route E du station forestière vers Ankara, Befandriana-Sud, district Morombe, iii.1955 (fl), *coll. ignot. 13353-SF* (P, TEF); Mitia, canton Mahaboboka, district Toliara, xii.1955 (fl), *coll. ignot. 15342-SF* (BR, P, TEF); Morombe, ii.1943 (fl), *coll. ignot. 18724-RN* (BR, P). Not located: ferme de Mahabo, without date (fl), *Dequaire 27272* (P, TAN).

TRICALYSIA ORIENTALIS RANDRIAMB. & DE BLOCK,
SP. NOV. (FIG. 21)

Type: MADAGASCAR. Toamasina Province, canton Manakambahiny-Est, district Ambatondrazaka, *coll. ignot. 12435-RN* (holo-: P; iso-: BR, TEF).

Diagnosis: Inter speciebus 4-meris ob partes vegetativas glabras, foliorum laminas coriaceas vel subcoriaceas ellipticas-obovatas apice saepium longe acuminatas atque stipularum aristam comparate longam notabilis.

Description: Shrub, 1–2 m high, or rarely small tree, up to 4 m high; dioecious. Flowering branches moderately stout, flattened, and bisulcate, glabrous; youngest internodes brown, smooth; older internodes fawnish. Leaves with petioles 3–6 mm long, canaliculate adaxially, glabrous. Blades elliptic or obovate, 5.5–13 × 2.5–5 cm, coriaceous or subcoriaceous, drying brown above and paler below, glabrous on both surfaces; tip acuminate, acumen (7–)10–25 mm long; base cuneate to attenuate; (6–)7–10 pairs of secondary nerves; domatia absent or present (tuft or ciliate pit). Stipules with sheath 1–2 mm high, glabrous outside; awn (1–)2–5 mm long. Inflorescences usually three-flowered, shortly pedunculate [peduncle 0.5–1.5(–2) mm long], moderately compact, all parts sparsely to moderately pubescent with short

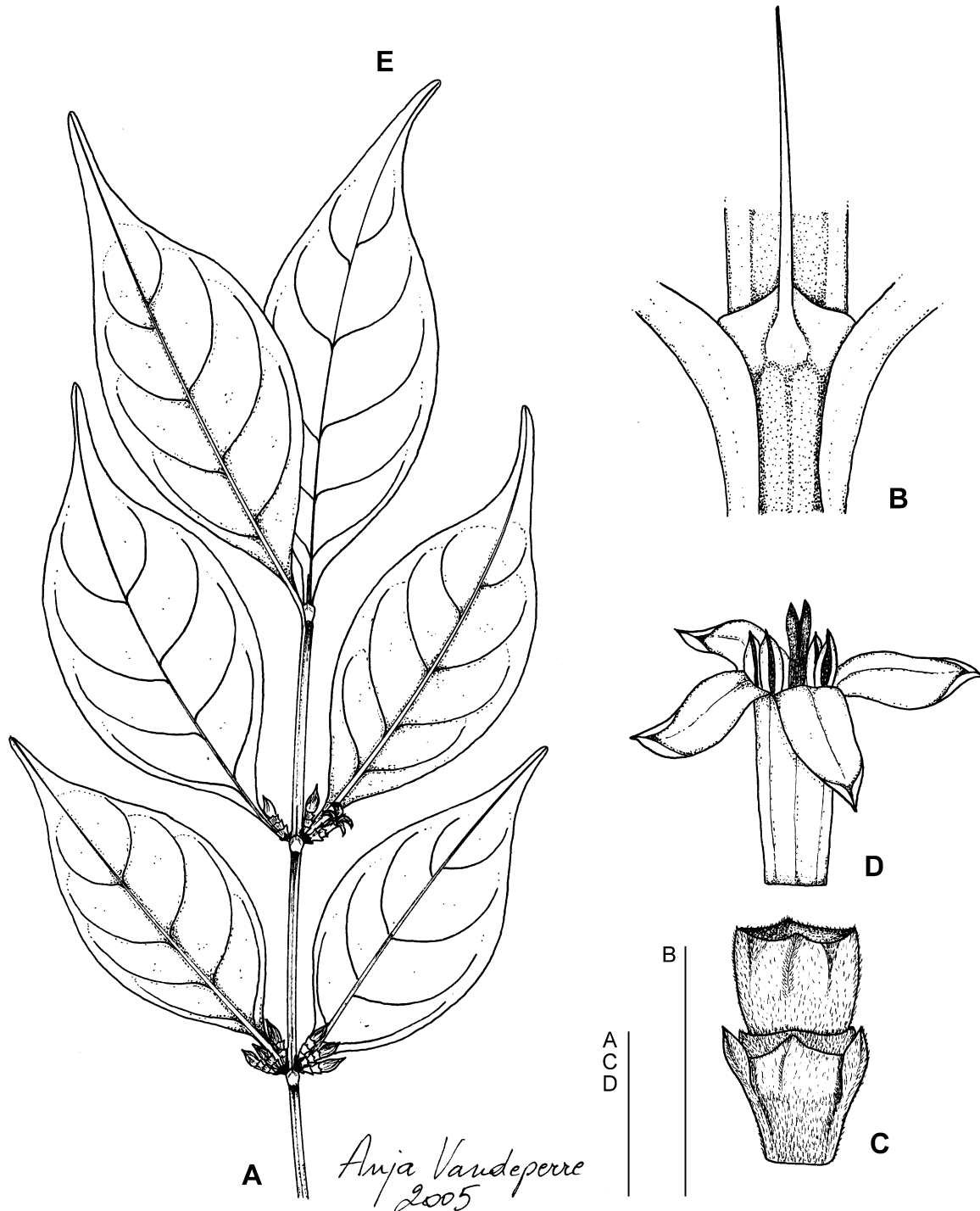


Figure 21. *Tricalysia orientalis* Homolle ex Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, stipule $\times 6$; C, calyx and calyculus $\times 9$; D, corolla $\times 9$. A–C, coll. ignot. 12435-RN; D, coll. ignot. 10586-RN.

appressed hairs; axes 0–1.5 mm long, pedicels 0–1.5 mm long; bracts and bracteoles fused into calyculi, usually two per flower; calyculi cupular, basalmost calyculi with foliar appendages (awns or

minute leaves) up to 3 mm long, stipular awns up to 1 mm long; calyculi higher up with foliar awns inconspicuous or up to 1 mm long, stipular awns inconspicuous or absent. Flowers 4(–5)-merous; bud

acuminate; calyx moderately to densely covered with short appressed hairs outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1.5–2 mm long, truncate or with four to seven minute teeth; corolla tube 4–5.5 mm long, 1.25–1.5 mm wide at the base and 1.5–2 mm wide at the throat, glabrous outside, upper half or upper third densely pubescent inside; corolla lobes 2.5–3.5 mm long, glabrous; anthers sessile, basal part included in corolla tube at anthesis (1.5–)2–2.5 mm long, glabrous, apical sterile appendix minute; ovary 0.5–1 mm high, glabrous; style and stigma 6–8 mm long, glabrous, stigmatic lobes 1–1.5 mm long; functionally female flowers not seen; functionally male flowers: ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas. Fruits spherical, 8–10 × 7–10 mm, red when ripe, drying orange brown, glabrous. Seeds (3–)4–(5) per fruit, 5.5–8 × 3–5 mm.

Distribution: Eastern Madagascar, between 19° and 16°30'S, especially well collected in the region of Ambatondrazaka (Fig. 18D).

Ecology: In humid evergreen forest; altitude: 450–1200 m.

Phenology: Flowering: December–January; fruiting: (March–)July–November.

Vernacular names: andraretra; arongampanihy; kafeala; voandraretra.

Uses: The fruits of this species are said to be edible (*coll. ignot. 10513-RN*).

Material studied: MADAGASCAR. Toamasina Province: forêt d'Angodronava?, S du poste de RNI 1, Betampona, vii.1949 (fr), *coll. ignot. 4-RN* (P); Vohimarantina, dans la RNI 1, N du poste de Rendrirendry, canton d'Ambodiriana, district de Tamatave, vii.1962 (fr), *coll. ignot. 103-RN* (BR, P); Varahina, aux confins du pays Sihanaka, viii.1937 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 2719* (P); Nonokambo, aux confins du pays Sihanaka, viii.1937 (fr), *coll. ignot. (Herb. Jard. Bot. Tana) 2792* (P); chute de l'Onibe, entre Fotsialonana et Mitanonoka, ix.1948 (st), *coll. ignot. (Herb. Institute. Sc. Mada.) 3158* (P); Lac Alaotra, without date (fl), *coll. ignot. (Herb. Jard. Bot. Tan.) 3846* (P); Rendrirendry, Tamatave, vii.1955 (st), *coll. ignot. 7244-RN* (BR, P); Nonokambo, canton Manakambahiny-Est, iv.1954 (fr), *coll. ignot. 9777-SF* (P, TEF); Ambodiantakhitra, village Ambodimanga II, canton Sahatavy, district Vavatenina, x.1959 (fr), *coll. ignot. 10513-RN* (P, TEF); Manakambahiny-Est, Androrangabe, district Ambatondrazaka, i.1960

(fl), *coll. ignot. 10586-RN* (P, TEF); canton Manakambahiny-Est, district Ambatondrazaka, vi.1961 (fr), *coll. ignot. 11898-RN* (P); canton Ambodiriana, district Toamasina, xi.1961 (fr), *coll. ignot. 12017-RN* (P); canton Manakambahiny-Est, district Ambatondrazaka, iii.1962 (fr), *coll. ignot. 12052-RN* (P); canton Sahatavy, district Vavatenina, iv.1962 (fr), *coll. ignot. 12433-RN* (BR, P); canton Manakambahiny-Est, district Ambatondrazaka, i.1963 (fl), *coll. ignot. 12435-RN* (BR, P, TEF); forêt d'Ankarana, Marofinaritra, Miarinarivo, Vavatenina, viii.1964 (fr), *coll. ignot. 21805-SF* (P, TEF); Ambodiriana, rive droite du fleuve, xii.1944 (fl), *Cours 1915* (BR, P); de Manakambahiny à Nonokambo, i.1945 (fl), *Cours 2366* (BR, P); forêt d'Ankiribiri au N d'Ambodiriana, i.1945 (fl), *Cours 2619* (P); Ambohidray, without date (fl), *Cours 4843* (P); Beforona, vii.1942 (fr), *Decary 18006* (BR, P); Sahamalaza, without date (fr), *Dequaire 27890* (P); c. 50 km NW of Toamasina, trail from Fotsimavo to RNI de Betampona, iv.1974 (fr), *Genetry 11309* (MO, P, TAN); Massif de l'Andrangovallo, SE du Lac Alaotra, RNI 3, Zahamema, bassin de l'Onibe, x.1937 (fr), *Humbert & Cours 17667* (BR, P); piste de Sahasomangana à Mitanonoka, x.1966 (fr), *Jacquemin H200J* (P); Vavatenina, commune Miarinarivo, fok. Anaborano, Savaharina, limite du Parc National Zahamena, à côté de la rivière Ihofika, vi.2001 (fr), *Rakotonandrasana, Ratovoson, Rasolohery, Randriamanarivo, Randrianjanaka, Rakotozafy, Bemalaza & Tataina 478* (K, MO). Not located: entre Ambodivoangy et les chûtes, xii.1944 (st), *Cours 1860* (BR, P); forêt d'Analamihilana, xii.1944 (fl), *Cours 2020* (BR, P, TAN); Mont Andriambavibe, vii.1942 (fr), *Decary 18116* (BR, P). Without locality or date: *Homolle 056* (P) (fr); *Homolle 531* (P) (fr); *Homolle 1860* (P) (fr); *Homolle 2366* (P) (fl).

TRICALYSIA OVALIFOLIA HIERN (FIG. 22)

Tricalysia ovalifolia Hiern [var. *ovalifolia*], in Oliv., *Fl. Trop. Afr.* **3**: 119 (1877); Brenan, *Kew Bull.* **1947**: 57 (1947); Robbrecht, *Bull. Jard. Bot. Nat. Belg.* **49**: 279 (1979); Robbrecht, in Bridson & Verdcourt, *Fl. East Trop. Afr., Rubiaceae (part 2)*: 561, Fig. 93; Friedmann, *Flore des Seychelles: dicotylédones*: 597, Pl. 189 (1994); Schatz, *Generic Tree Flora of Madagascar*: 345, Fig. 397 (2001). *Types:* Zanzibar, Kirk s.n. (flowering) (syn-: K), Kirk s.n. (fruiting) (lecto-: K), Hildebrandt 1177 (syn-: BM).

Eriostoma albicaulis Boivin [in Baillon, *Adansonia* **12**: 208 (1978)], nomen nudum (see note 1 in Robbrecht, 1979a: 281).

Hypobathrum albicaule Baillon, *Adansonia* **12**: 209 (1878); Drake del Castillo in Granddidier, *Hist. Phys. Nat. Pol. Madagascar* **36** (Hist. Nat. Pl. 6, Atlas 4):



Figure 22. *Tricalysia ovalifolia* Hiern. Reprinted from: Drake del Castillo in Grandidier, *Hist. Phys. Nat. Pol. Madagascar* 36 (*Hist. Nat. Pl.* 6, Atlas 4): tab. 445 (1897). A, Flowering branch; B, fruiting branch; C, opening flower; D, flower at anthesis; E, calyx; F, longitudinal section through calyx; G, inside of corolla; H, anther; I, fruit; J, transverse section through fruit; K, seed.

tab. 445 (1897). *Types*: Madagascar, *Boivin 2421* (syn-: P); Vohemar, *Richard 120* (syn-: P) & *650* (syn-: P); Nosy Be, *Boivin 2059* (syn-: P; isosyn-: K) & *Pervillé s.n.* (syn-: P); Comores, Moheli, *Boivin s.n.* (syn-: P), *Richard 264* (lecto-: P) & *655* (syn-: P).

Hypobathrum comorense Baillon, *Adansonia* **12**: 210 (1878), ubi sphalm. *Boivin 3776*. *Type*: Mayotte, Pamanzi Island, *Boivin 3176* (flowering) (holo-: P; iso-: BR, P) (type erroneously cited as *Boivin 3776* in protologue: see note 2 in Robbrecht, 1979a: 281).

Tricalysia cuneifolia Baker, *Kew Bull.* **1894**: 148 (1894); Schinz, *Abhandl. Senckenb. Naturforsch. Gesellsch.* **21**: 91 (solummodo quoad Abbott s.n.) (1897); Hemsley, *Journ. Bot. (Lond.)* **54**, suppl. 2: 18 (1916) & *Kew Bull.* **1919**: 123 (1919). *Type*: Abbott s.n. (partly, see note 3 in Robbrecht, 1979a: 282) (lecto-: K).

Tricalysia sonderiana auct. non Hiern [*Fl. Trop. Afr.* **3**: 119 (1877)]: Fosberg, *Phytologia* **41**: 360 (1979); Fosberg & Renvoize, *Flora of Aldabra*: 165 (1980).

Description: Hermaphroditic shrubs or, rarely, small trees, 2–6 m high, evergreen or rarely deciduous (see note 2); flowering branches moderately stout, somewhat flattened, and often bisulcate; youngest internodes brown, smooth, glabrous or sparsely to moderately pubescent with short appressed hairs; older internodes fawnish, glabrous, often flaking. Leaves with petioles 1–4(–5) mm long, canaliculate adaxially, glabrous or pubescent with short appressed hairs (pubescence usually restricted to adaxial side). Blades elliptic, obovate, ovate or rarely narrowly so, 3.5–12.5 × 1–5 cm, coriaceous, drying green or brown and glossy above, paler below, glabrous on both surfaces; tip subacute to shortly acuminate (acumen ≤ 7 mm) or rarely obtuse; base cuneate to acute; 7–11 pairs of secondary nerves; domatia absent (but see note 3). Stipules with sheath 1–2 mm high, glabrous or rarely pubescent with short appressed hairs outside; awn 2–6 mm long. Inflorescences (1–)3–5(–6)-flowered, sessile or subsessile (peduncle ≤ 1 mm), lax, all parts glabrous; axes ≤ 1(–2) mm; pedicels (1.5–)3–16 mm long; bracts fused into calyculi but bracteoles free; calyculi cupular, foliar awns ≤ 1.5 mm long, stipular awns inconspicuous or absent; bracteoles occurring on the pedicel (usually halfway up), subopposite or alternate, broadly triangular, 1–1.5 mm long. Flowers five-merous, sweet-scented; bud subacute; calyx glabrous outside, glabrous and without colleters inside; calyx tube 0.5–0.7 mm long; calyx lobes (4–)5(–6), broadly triangular, 0.3–0.6 mm long, tip subacute, obtuse, or rounded; corolla tube 4–5 mm long, 1.5–2 mm wide at the base and 2.5–3 mm wide at the throat, glabrous outside, glabrous inside except for a dense ring of hairs at the throat (extending along the base of the corolla lobes and projecting

above the throat); corolla lobes (4.5–)5–7 mm long, glabrous (except the base inside); anthers fully exerted and reflexed, 4–6 mm long, glabrous, sterile apical appendix 1–2 mm long, filaments 1–1.5 mm long; ovary c. 1 mm high, glabrous; two to five ovules immersed in each placenta; style and stigma 7–10 mm long, glabrous, stigmatic lobes 2–3 mm long. Fruits spherical or slightly wider than high, 5–8 × 5–9 mm, black when ripe, drying dark brown to black, glabrous. Seeds (2–)3–7(–9) per fruit, 3–4 × 3.5–5.5 mm.

Distribution: North and north-west Madagascar (Antsiranana and Mahajanga Provinces) (Fig. 18E). Also occurring in continental Africa, in Kenya (K7), Tanzania (T3 & T6), Zanzibar, Aldabra, Assumption, and the Comores (see Robbrecht, 1979b: map 535).

Ecology: In littoral formations (open or more closed scrub or thicket) and deciduous or semi-deciduous dry forest on sandy soil (white sand, red sand, sandy loam, alluvial or dune sand) or in calcareous regions (red sand on limestone); occurring high on the beach as well as further inland; altitude: 0–450 m.

Phenology: Flowering: October–January; fruiting: January–December.

Vernacular names: malainarety; nofotrakoho; sanirambavy; taindahitsy; taolankena; tsimahamasasokina; valanira.

Uses: Wood used as firewood or for building cattle fences.

Notes: (1) Baillon (1878: 209) used the unpublished combination *Hypobathrum ovalifolium* while discussing the differences between *T. ovalifolia* and *Hypobathrum albicaule*. (2) This species is evergreen, but occasionally loses its leaves in very dry periods. This was observed during fieldwork in January 2002 when no rain had yet fallen in the area around Antsiranana. Plants from drier habitats, such as the dry forest of Ivovo, possessed young inflorescences and/or flower buds and small new leaves (e.g. *De Block et al.* 1072). (3) Robbrecht (1979a: 282, note 6) already mentioned teratological developments of hairs found on a number of specimens from Aldabra, the Comores, and Madagascar. These patches of pubescence occur along the midrib and/or irregularly distributed on the lower leaf surface (e.g. *Baron 6190*, *Boivin 2421*, *Cours 5458*, *Decary 14600*) or on the upper leaf surface (e.g. *Bernier 279*). Furthermore, dense patches of pubescence sometimes occur on young branches, stipules, pedicels, or flowers (e.g. *Cours 5458*, *Capuron 22955*).

Material studied: MADAGASCAR. Antsiranana Province: Nossi-Be, 1849–1850 (fr), *Boivin 2059* (P); Baie de Diego-Suarez, x.1848 (fr), *Boivin 2421* (P); PK 10 de la route Diego–Suarez–Orangea, xii.1963 (fl), *Capuron 22955-SF* (BR, P); Analanandriana, station forestière de Sakaramy, vi.1956 (fr), *coll. ignot. 15861-SF* (P, TEF); forêt d’Orangea, i.1960 (fr), *Cours & Humbert 5400* (BR, P), see note under var. *glabrata*; canton d’Anivorano-Nord, village de Marovato-Anketrabe, forêt de Misoromalalana, i.1960 (fr), *Cours & Humbert 5458* (BR, P); district d’Ambilobe, forêt d’Andranakoho, PK 103 de la route de Diego à Ambilobe, i.1960 (fr), *Cours & Humbert 5554* (P); forêt d’Ivovo, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1072* (BR, K, MO, P, TAN, UPS, WAG); Analamera, along Ambatabe River, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1090* (BR, K, MO, P, TAN, UPS); Analamera, along Ambatabe River, i.2002 (fr), *De Block, Rakotonasolo & Randriamboavonjy 1126* (BR, K, MO, TAN, UPS); Analamera, bank of Irodo River, to the right of Irodo camp, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1144* (BR, K, MO, P, TAN, WAG); Baie de Sakalava, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1292* (BR, G, K, MO, P, TAN, WAG); Baie de Sakalava, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1292-bis* (BR, K, MO, P, TAN); Montagne des Français, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1361* (BR, K, MO, P, TAN); Forêt d’Orangea, i.2002 (fl), *De Block, Rakotonasolo & Randriamboavonjy 1379* (BR, K, MO, TAN); Vohemar, vii.1939 (fr), *Decary 14600* (BR, P); collines et plateaux de l’Ankarana, partie Nord, i.1937 (fl), *Humbert 18919* (P); forêt de Sahafary, S de Diego, iii.1962 (fr), *Keraudren 1662* (P); Nossi-Be, 1893 (fl), *Pervillé s.n.* (P); fiv. Vohemar, commune rurale Tsarabaria, fok. Manakana, x.2002 (fr), *Rabevohitra, McPherson, Rabenantoandro & Ranarivelo 4424* (MO, P); fiv. Vohemar, commune rurale Nossi-Be, près du village d’Anaborano et du Lac Sahaka, ii.2003 (fr), *Rabevohitra, Rabenantoandro & Razakamalala 4457* (MO, P); Vohemar, Fanambana, remnant forest near Anteraserabe, W of Fanambana, xi.2000 (fl), *Rakotonasolo 257* (BR, K, TAN); Analamera, i.2002 (fl), *Razafimandimbison, Andriambolonerana & Andriana-toanina 419* (BR, UPS); Vohemar, without date (fr), *Richard 54* (P); Vohemar, 1837 (fr), *Richard 120* (P); Vohemar, 1840 (fr), *Richard 650* (P). Mahajanga Province: Bongolava Hills, Port-Bergé, xi.1987 (fl), *Bisset 1442* (K); Ankarafantsika, RNI 7, alluvions Bepilo, without date (fl), *coll. ignot. 4-SF* (BR, P); tsingy de Namoroka, RNI 8, without date (fr), *coll. ignot. 13-SF* (BR, P), see note under var. *glabrata*; Bevezaha, canton Tsaramandroso, district Ambato-Boeni, x.1948 (fl), *coll. ignot. 1681-RN* (BR, P); Ankarafantsika, canton Tsaramandroso, district Ambato-Boeni,

xi.1950 (fl), *coll. ignot. 2055-RN* (BR, P); Ankarafantsika, RNI 7, canton Tsaramandroso, district Ambato-Boeni, xi.1950 (fl), *coll. ignot. 2556-RN* (P); district Ambato-Boeni, iv.1951 (fr), *coll. ignot. 3479-SF* (BR, P, TEF); Ankarafantsika, Ampijoroa, v.1952 (fr), *coll. ignot. 4951-SF* (P, TEF); Mangatsiaka, canton Andranomavo, Soalala, xii.1955 (fl), *coll. ignot. 7754-RN* (P, TEF); Jardin Botanique B, station Ampijoroa, Marovoay, xi.1953 (fl), *coll. ignot. 7941-SF* (BR, P, TEF); Jardin Botanique, sect. B, Ampijoroa, Marovoay, iii.1954 (fr), *coll. ignot. 9840-SF* (BR, P); Ampijoroa, district de Marovoy, iv.1954 (fr), *coll. ignot. 9867-SF* (BR, P, TEF); N du fleuve de Manambato, village Morafenobe, canton & district Morafenobe, v.1955 (fr), *coll. ignot. 14120-SF* (BR, P, TEF); Amboloando, canton & district Maintirano, v.1956 (fr), *coll. ignot. 16325-SF* (BR, P, TEF); forêt d’Amboloando, village Amboloando, canton & district Maintirano, ii.1956 (fr), *coll. ignot. 16360-SF* (BR, P, TEF); forêt d’Andranomafana, village d’Andranomafana, canton d’Andribavontsona, district d’Analalava, v.1958 (fr), *coll. ignot. 19112-SF* (P, TEF); Ampijoroa Forestry Station, Jardin Botanique B, ii.1999 (fr), *De Block, Luckow & Rakotonasolo 765* (BR, K, MO, P, TAN); Ankarafantsika, Ampijoroa, iv.1999 (fr), *Gentry & Schatz 62032* (K, MO); Manasamody, Port Bergé, iv.1974 (fr), *Morat 4548* (P, TAN); Kapiloza, Ambongo, xi.1904 (fl), *Perrier de la Bâthie 3865* (P); Ankaladina, sur le Betsiboka, Boina, x.1901 (fl), *Perrier de la Bâthie 3866* (P); station forestière d’Ampijoroa, rive NE du lac Ravelobe, vii.1995 (fr), *Rakotomalaza, Raharilala, Vognono, Rasolomanana, Randrianasolo & Rakotomamonjy 361* (BR, MO); Réserve d’Ankarafantsika à Bedo, près du village de Manarimavo, iii.1996 (fr), *Rakotomalaza, Sikes, Rasolomanana, Andrianasolo & Andriantsiferana 652* (BR, MO); Antsohihy, Anjimangirana, Analanambe, Andraffiborizina, v.2000 (fr), *Rakotonasolo 182* (BR, K, TAN). Not located: Andravine, 1839 (fr), *Bernier 279* (P); Ankoriko, xii.1916 (fl), *Decary 75* (P); Nossi Mitsiori, xii.1932 (st), *Perrier de la Bâthie 18803* (P). Without locality or date: *Baron 6190* (K) (fr); *Bernier s.n.* (K) (fr); *Douillot s.n.* (P) (fr); *Homolle 421* (BR, P); *Richard 127* (K) (fr).

TRICALYSIA OVALIFOLIA VAR. GLABRATA (OLIV.)

BRENAN

Tricalysia ovalifolia var. *glabrata* (Oliv.) Brenan, *Kew Bull.* **1947**: 58 (1947); Robbrecht, *Bull. Jard. Bot. Nat. Belg.* **49**: 283 (1979); Robbrecht, in Bridson & Verdcourt, *Fl. East Trop. Afr., Rubiaceae (part 2)*: 563. Type: *Johnston s.n.* (Kilimanjaro Expedition) (holo-: K).

Empogona kirkii Hook.f. var.? *glabrata* Oliv. [in Johnston, *Kilima-Njaro Exp.* 341 (1886), nomen

nudum], *Trans. Linn. Soc., Bot., ser. 2*, **2**: 336 (1887). *Type: Johnston s.n.* (Kilimanjaro Expedition) (holo-: K). *Tricalysia ovalifolia* Hiern var. *acutifolia* Brenan, *Kew Bull.* **1947**: 58 (1947). *Type: Tanzania, East Usambaras, Bombo-Daluni, Greenway 4103* (holo-: K).

Description: Differs from var. *ovalifolia* as follows: stems more densely and persistently pubescent; leaves with petioles pubescent all around; blades with midrib puberulous on both surfaces, especially near the leaf base; pedicels, bracteoles, and sometimes also the ovary pubescent.

Distribution: In Madagascar, only known from specimen cited below from Maintirano (Fig. 18E). Also occurring in continental Africa, in Kenya (K7) and Tanzania (T3, T6, T8) (see Robbrecht, 1979b: map 536).

Note: Two other Madagascan specimens are somewhat similar to *T. ovalifolia* var. *glabrata*, in that the pubescence on their stems is denser than in var. *ovalifolia*. This is the case for *coll. ignot. 13-SF* and *Cours 5400*. In *coll. ignot. 13-SF*, all plant parts, except for the stem, are glabrous. In *Cours 5400*, the stems, stipules, petioles, and midrib on both leaf surfaces are densely pubescent. The pedicels, calyx lobes, and bracteoles are, however, glabrous.

Material studied: MADAGASCAR. Mahajanga Province: Ambararatakely, Maintirano, canton & district Maintirano, i.1957 (fr), *coll. ignot. 16691-SF* (P, TEF).

TRICALYSIA PERRIERI HOMOLLE EX RANDRIAMB. & DE BLOCK, **SP. NOV.** (FIG. 23)

Type: MADAGASCAR. Mahajanga Province, Morataitra, rive droite de Betsiboka en amont de son confluent au l'Ikopa, *Perrier de la Bâthie 845* (holo-: P; iso-: P).

Diagnosis: Inter speciebus 4-meris dioeciis propter corollarum, antherarum stylorumque pubescentiam bene distinguitur.

Description: Dioecious shrubs or, rarely, small trees, 1.5–7 m high; flowering branches slender to moderately stout, somewhat flattened and often bisulcate; young internodes pale brown to reddish brown, densely pubescent with moderately long erect hairs. Leaves with petioles 3–7 mm long, canaliculate adaxially, densely pubescent. Blades elliptic, 5–10(–13) × 2.3–4.8 cm, papyraceous or rarely subcoriaceous, drying brownish or greenish above and paler below, both leaf surfaces densely to moderately pubescent (hairs moderately long and erect below, shorter and erect or appressed above) or rarely glabrous (but

then at least midrib and often also secondary nerves sparsely to densely pubescent); tip shortly acuminate to subacute, acumen 3–9(–11) mm long; base cuneate to acute; (4–)5–7 pairs of secondary nerves; tuft domatia obscure to conspicuous. Stipules densely pubescent abaxially; sheath 1–1.75(–2) mm high; awn 0.75–2 mm long. Inflorescences (1–)3–5-flowered, sometimes two to three per axil, sessile (peduncle ≤ 1 mm long) but shortly pedunculate in axillary inflorescences (≤ 3 mm long), compact, all parts densely pubescent; axes ≤ 1.5 mm long; pedicels 0(–1) mm long; bracts and bracteoles fused into calyculi, 1(–3) per flower; calyculi cupular, foliar awns up to 1.5 mm long or rarely subfoliaceous and then up to 5 mm long, stipular awns inconspicuous or absent. Flowers 4(–5)-merous; bud long acuminate; calyx densely covered with appressed hairs outside, densely covered with appressed hairs and scattered colleters inside; calyx tube 1–1.5 mm long; calyx lobes triangular to subulate, keeled, 0.4–0.75 mm long; corolla tube 3–4.25 mm long, 0.8–1.25 mm wide at the base and 1.5–2.25 mm wide at the throat, moderately to densely covered with spreading hairs from c. the middle upwards outside, densely covered with long hairs in the upper half inside; corolla lobes 3.5–4 mm long, ciliate and moderately to densely covered with spreading hairs outside, glabrous inside; anthers 1.5–2 mm long, thecae sparsely pubescent with long spreading hairs, apical sterile appendix minute, filaments ≤ 0.5 mm long; ovary 0.9–1.25 mm high, moderately to densely covered with long appressed hairs; style and stigma 4.5–7 mm long, upper half or upper third moderately pubescent (hairs often continuing on the abaxial side of the stigmatic lobes); stigmatic lobes 1–1.75 mm long; functionally female flowers not seen; functionally male flowers: ovary with locular cavities absent or, if present, then reduced and empty or with rudimentary placentas. Fruits spherical or slightly longer than wide, 5.5–11 × 5–10 mm, red when mature, drying brown to blackish, sparsely to moderately pubescent with long appressed hairs (rarely hairs only remaining at the base of the fruit or below the calyx). Seeds (3–)4–5(–9) per fruit, 4–6 × 2–4 mm.

Distribution: Central west Madagascar, Mahajanga Province, in the region of Ambongo, Ankarafantsika, and the Tampoketsa de Tsaratanana (Fig. 18F).

Ecology: In lowland deciduous or semi-deciduous dry forest or gallery forest on sandy or lateritic soil.

Phenology: Flowering: February–March, July*; fruiting: January*, April–May (*these dates from specimens collected by Perrier de la Bâthie may be erroneous).

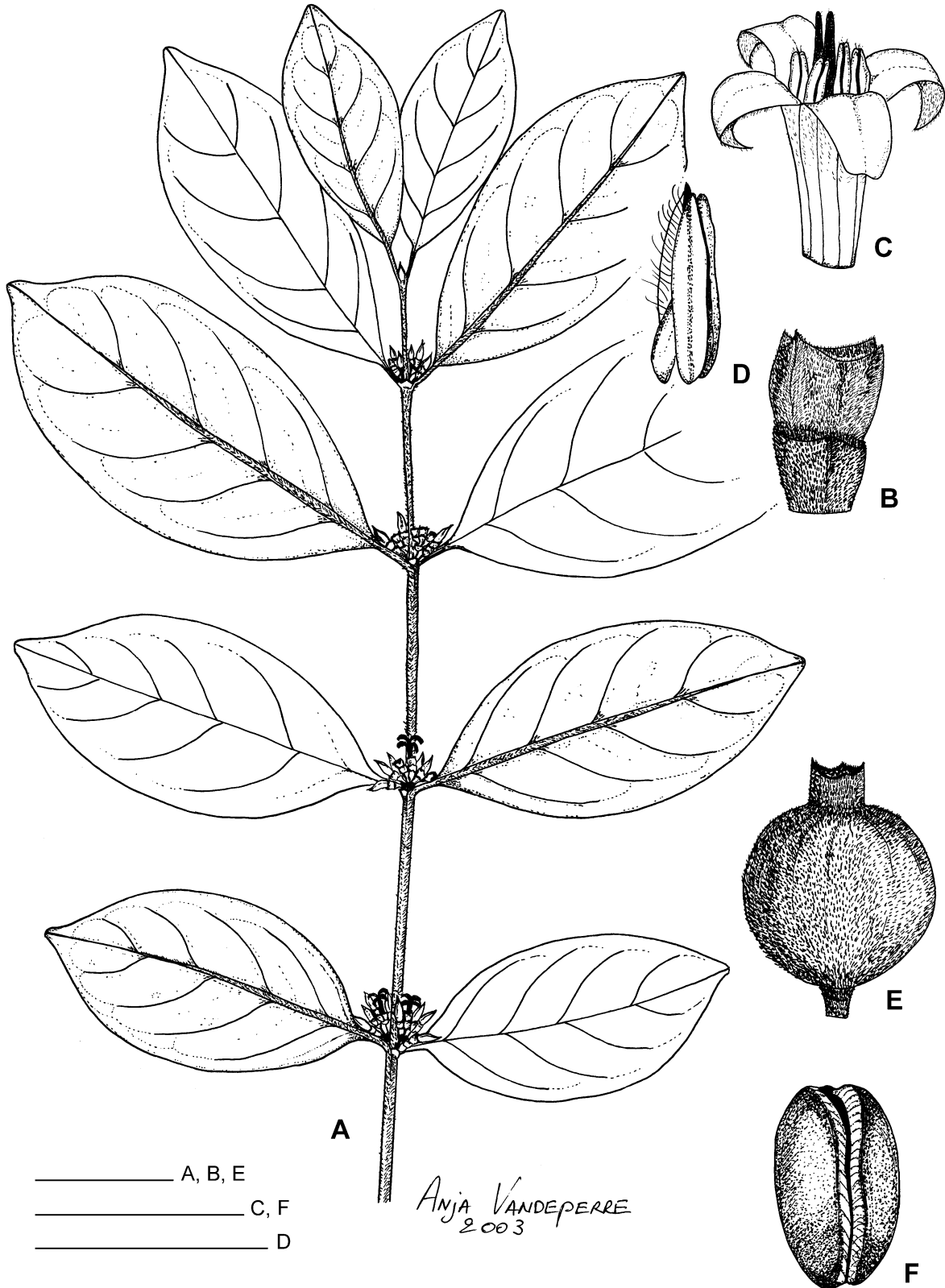


Figure 23. *Tricalysia perrieri* Homolle ex Randriamb. & De Block. A, Flowering branch $\times 2/3$; B, calyx and calyx tube $\times 8$; C, corolla $\times 6$; D, anther $\times 16$; E, fruit $\times 4$; F, seed $\times 6$. A–D, De Block et al. 824; E, F, Perrier de la Bâthie 3608.

Vernacular names: kafeala.

Uses: Wood used for construction.

Notes: (1) *T. perrieri* is one of three Malagasy species with four-merous flowers and can easily be distinguished from the other two. It differs from *T. orientalis* in the texture and pubescence of the leaves: papyraceous or rarely subcoriaceous and blades or at least midrib pubescent in *T. perrieri* vs. coriaceous and completely glabrous in *T. orientalis*. It differs from *T. humbertii* by its densely pubescent calyx and the well-developed calyx tube (1–1.5 mm long) and lobes (0.4–0.75 mm long). The calyx is shorter, usually glabrous, and almost truncate in *T. humbertii*. The latter species never has pubescent leaf blades (but the midrib is commonly pubescent). (2) *T. perrieri* shows a large variation in the pubescence of the leaf blades, from densely pubescent on both surfaces (unique within the Malagasy *Tricalysia*) to glabrous except for the midrib. (3) The specimens from the region of Antsalova were found to differ significantly from the majority of the material. Their leaf blades are glabrous (except for the midrib) and they lack the typical pubescence on the outside of the corolla, style, thecae, and fruits. However, they possess densely pubescent and well-developed calyx tubes and are therefore better placed as a subspecies than a separate species.

Material studied: MADAGASCAR. Mahajanga Province: Ankarafantsika, without date (fr), *coll. ignot. 10 SF-bis* (P); bord de rivière Manankasina, village Manankasina, canton Betandraka, district Tsaratanana, v.1958 (fr), *coll. ignot. 19149-SF* (BR, P, TEF); forêt d'Ampasindava, village d'Ambanjabe, canton et district Tsaratanana, ii.1959 (fl), *coll. ignot. 19462-SF* (BR, P, TEF); Ampijoroa Forestry Station, Jardin Botanique B, road towards lake, ii.1999 (fl), *De Block, Luckow & Rakotonasolo 766* (BR, K, MO, P, TAN); along RN 4, PK 340 from Antananarivo, ii.1999 (fl), *De Block & Rakotonasolo 824* (BR, G, K, MO, P, TAN, UPS, WAG); vicinity of Lac Ampijoroa, 30 km N of Tsaramandroso on highway to Mahajanga, region of Ankarafantsika, v.1974 (fr), *Gentry 11459* (K, P, TAN); Morataitra, rive droite de Betsiboka en amont de son confluent au l'Ikopa, iii.1899 (fl, fr), *Perrier de la Bâthie 845* (P); Haute-Bemarivo, Boina, vii.1907 (fl), *Perrier de la Bâthie 3608* (BR, P); Ankarafantsika, près Marovoay, i.1908 (fr), *Perrier de la Bâthie 3756* (P); Manongarivo, Ambongo, i.1904 (fr), *Perrier de la Bâthie 3857* (P); Kapiloza, Ambongo, iv.1903 (fr), *Perrier de la Bâthie 3858* (P); Belambo, vii.1900 (fl), *Perrier de la Bâthie 3864* (P).

TRICALYSIA PERRIERI HOMOLLE EX RANDRIAMB. & DE BLOCK **ssp. ANTALOVENSIS** RANDRIAMB. & DE BLOCK, **ssp. nov.**

Type: MADAGASCAR. Mahajanga Province, Antsingy, vers Andobo, E d'Antsalova, chemin vers Tsiandro, *Leandri & Saboureau 3000* (holo-: P: iso-: BR, P).

Diagnosis: Propter flores 4-meros atque calycem comparate bene effectum ad *Tricalysiam perrieri* pertinet, sed florum pubescentiam subspeciei *perrieri* deest.

Description: Differs from ssp. *perrieri* as follows. Flowering branches sparsely to moderately pubescent (hairs short and appressed or rarely spreading); blades glabrous except for midrib on both sides (in basal half of the leaf); calyx tube and lobes often in the lower range of the values for the species; corolla glabrous (but corolla lobes ciliate) outside; style and stigma glabrous; thecae glabrous.

Distribution: Only known from the region of Antsalova (Mahajanga Province) (Fig. 18F).

Ecology: In lowland deciduous or semi-deciduous dry forest, probably on calcareous soil; altitude: 0–300 m.

Phenology: Flowering: February; fruiting: February, May.

Vernacular names: hazopasy; kafeala; taolankena (Sakalava).

Material studied: MADAGASCAR. Mahajanga Province: Antsalova, v.1955 (fr), *coll. ignot 7201-RN* (BR, P); canton Bekopaka, district Antsalova, ii.1959 (fl), *coll. ignot. 10332-RN* (P, TEF); canton et district Antsalova, ii.1960 (fr), *coll. ignot. 11094-RN* (BR, P, TEF); canton et district Antsalova, ii.1960 (fl), *coll. ignot. 11114-RN* (P, TAN); canton et district Antsalova, ii.1962 (fl), *coll. ignot. 12465-RN* (BR, K, P, TEF); forêt de Tsimembo, canton Trangahy, district Antsalova, ii.1961 (fr), *coll. ignot. 19834-SF* (P, TEF); originally from Antsalova but cultivated at Coffee Research Centre at Kianjavato (FOFIFA), 25 km E of Ifanadiana, district Ifanadiana, xi.1999 (st), *Davis & Rakotonasolo 2325* (BR, K); Antsingy, vers Andobo, E d'Antsalova, chemin vers Tsiandro, ii.1960 (fl), *Leandri & Saboureau 3000* (BR, P).

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REFERENCES

- Ali SJ, Robbrecht E. 1991.** Remarks on the tropical Asian and Australian taxa included in *Diplospora* or *Tricalysia* (Rubiaceae – Ixoroideae – Gardenieae). *Blumea* **35**: 279–305.
- Andreasen K, Bremer B. 2000.** Combined phylogenetic analysis in the Rubiaceae-Ixoroideae: morphology, nuclear and chloroplast DNA data. *American Journal of Botany* **87**: 1731–1748.
- Baillon H. 1878.** Mémoire sur les genres *Canthium* et *Hypobathrum*. *Adansonia* **12**: 179–213.
- Beille L. 1939.** Structure anatomique des *Lemyrea*. *Revue Internationale de Botanique Appliquée et d'Agriculture Tropicale* **19**: 250–255.
- Bridson DM. 2003.** *Tricalysia* DC. In: Pope GV, ed. *Flora Zambesiaca*, Vol. 5(3). Kew: Royal Botanic Gardens Kew, 463–505.
- Capuron R. 1973.** Révision des Rubiacées de Madagascar et des Comores. Notes regroupées et mises en forme par J. Bosser, dactylographiées de F. Chauvet. Paris: Laboratoire de Phanérogamie.
- Chevalier A. 1942.** Les caféiers du globe. 2. Iconographie des caféiers sauvages et cultivés. *Encyclopédie Biologique* **22**: 1–158.
- Chevalier A. 1947.** Les caféiers du globe 3. Systématique des caféiers, maladies et insectes nuisibles. *Encyclopédie Biologique* **28**: 1–357.
- Dorr LJ. 1997.** *Plant collectors in Madagascar and the Comoro Islands*. Kew: Royal Botanic Gardens Kew.
- Drake Del Castillo E. 1902.** Botanique. In: Blanchard RAE, ed. *Madagascar au début du XXe siècle*. Paris: De Rudeval.
- Dubard M. 1907.** Les caféiers sauvages de Madagascar. *Bulletin du Muséum d'Histoire Naturelle Paris* **13**: 279–283.
- Hooker JD. 1873.** Rubiaceae. In: Bentham G, Hooker JD, eds. *Genera Plantarum*, Vol. 2(1). London: L. Reeve & Co., 7–151.
- Humbert H. 1955.** Les territoires phytogéographiques de Madagascar. Leur cartographie. *Colloques Internationaux du Centre National de la Recherche Scientifique* **59**: 195–204.
- Jumelle MH. 1933.** Caféiers sauvages de Madagascar. *Annales du Musée Colonial de Marseille, Séries* **5** (1): 1–14.
- Jumelle MH, Perrier de la Bâthie H. 1910.** Fragments biologiques de la flore de Madagascar (*Dioscorea*, *Adansonia*, *Coffea*, etc.). *Annales du Musée Colonial de Marseille, Séries* **2** (8): 373–468.
- Palacky J. 1906.** Rubiaceae. In: *Catalogus Plantarum Madagascariensium*, Vol. 4. Prague: J. Palacky, 50–60.
- Puff C, Igersheim A. 1994.** Intra-ovarian trichomes in *Jackiopsis ornata* (Wallich) Ridsdale (Rubiaceae – Jackieae). *Botanical Journal of the Linnean Society* **115**: 29–33.
- Randriamboavonjy T. 2000.** Contribution à l'étude systématique des espèces malgaches de *Tricalysia* A.Rich. (Rubiaceae – Ixoroideae – Gardenieae – Diplosporinae). Masters Thesis, Mémoire de Diplôme d'Etudes Approfondies (D.E.A.), Université d'Antananarivo.
- Richard A. 1830.** *Mémoire sur la familles des Rubiacées*. Paris: J. Tastu.
- Richard A. 1834.** *Mémoire sur la familles des Rubiacées*. *Mémoires de la Société d'Histoire Naturelle de Paris* **5**: 81–305.
- Robbrecht E. 1978.** *Sericanthe*, a new African genus of Rubiaceae (Coffeae). *Bulletin du Jardin Botanique National de Belgique* **48**: 3–78.
- Robbrecht E. 1979a.** The African genus *Tricalysia* A.Rich. (Rubiaceae-Coffeae). 1. A revision of the species of subgenus *Empogona*. *Bulletin du Jardin Botanique National de Belgique* **49**: 239–360.
- Robbrecht E. 1979b.** Rubiaceae: *Tricalysia*. *Distributiones Plantarum Africanarum* **16**: 531–562.
- Robbrecht E. 1980.** Bijdragen tot de classificatie van de Ixoroideae en tot de revisie van *Tricalysia* S.L. (Rubiaceae). DPhil Thesis, University of Gent.
- Robbrecht E. 1982.** The African genus *Tricalysia* A.Rich. (Rubiaceae-Coffeae) 2. *Ephedranthera*, a new section of subgenus *Tricalysia*. *Bulletin du Jardin Botanique National de Belgique* **52**: 311–329.
- Robbrecht E. 1983.** The African genus *Tricalysia* A.Rich. (Rubiaceae): 3. *Probletostemon* revived as a section of subgenus *Tricalysia*. *Bulletin du Jardin Botanique National de Belgique* **53**: 299–320.
- Robbrecht E. 1985.** The identity of *Diplospora africana* (Rubiaceae). *South African Journal of Botany* **5**: 331–334.
- Robbrecht E. 1987.** The African genus *Tricalysia* A.Rich. (Rubiaceae). 4. A revision of the species of section *Tricalysia*

and section *Rosea*. *Bulletin du Jardin Botanique National de Belgique* **57**: 39–208.

Robbrecht E. 1988. Tropical woody Rubiaceae: Characteristic features and progressions. Contributions to a new subfamilial classification. *Opera Botanic Belgica* **1**: 1–271.

Schumann K. 1891. Rubiaceae. In: Engler A, Prantl K, eds. *Die natürlichen pflanzenfamilien*, Vol. 4(4). Leipzig: Wilhelm Engelmann Verlag, 1–156.

White F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. *Natural Resources Research (UNESCO)* **20**: 1–356.

APPENDIX 1

ALPHABETICAL LIST OF TAXA

In the following list, all taxa recognized in Madagascar are cited. In parentheses, the mnemonic abbreviation, consisting of the first four letters of the name, is given. In the case of an infraspecific taxon, the mnemonic abbreviation consists of the four first letters of the specific epithet, followed by the first four letters of the subspecific name.

Tricalysia ambrensis Randriamb. & De Block ssp. *ambrensis* (**ambrambr**)

Tricalysia ambrensis Randriamb. & De Block ssp. *coriacea* Randriamb. & De Block (**ambrcori**)

Tricalysia analamazaotrensis Homolle ex Randriamb. & De Block (**anal**)

Tricalysia boiviniana (Baill.) Randriamb. & De Block (**boiv**)

Tricalysia cryptocalyx Baker (**cryp**)

Tricalysia dauphinensis Randriamb. & De Block (**daup**)

Tricalysia humbertii Randriamb. & De Block (**humb**)

Tricalysia leucocarpa (Baill.) Randriamb. & De Block (**leuc**)

Tricalysia madagascariensis (Drake ex Dubard.) A.Chev. (**mada**)

Tricalysia majungensis Homolle ex Randriamb. & De Block (**maju**)

Tricalysia orientalis Homolle ex Randriamb. & De Block (**orie**)

Tricalysia ovalifolia Hiern var. *ovalifolia* (**ovaloval**)

Tricalysia ovalifolia var. *glabrata* (Oliv.) Brenan (**ovalglab**)

Tricalysia perrieri Homolle ex Randriamb. & De Block ssp. *perrieri* (**perrperr**)

Tricalysia perrieri Homolle ex Randriamb. & De Block ssp. *antsalovensensis* Randriamb. & De Block (**perrants**)

APPENDIX 2

ALPHABETICAL LIST OF EXSICCATAE

Collections identified during the revision are listed, followed by the mnemonic abbreviation of the taxon to which they belong.

Abbott: sn (ovaloval);
 Afzelius: 267 (maju); sn (maju);
 Andrianantoanina & Bezara: 959 (humb);
 Andrianantoanina & Rocsceohclher: 304 (ambrambr);
 Andrianantoanina, Solotiana & Bezara Roch: 102 (ambrambr);
 Antilahimena: 87 (leuc); 102 (boiv);
 Antilahimena, Rabenantoandro & Tsitra: 368 (boiv);
 Antilahimena, Ravelonarivo & Ratovoson: 456 (boiv);
 Bardot-Vaucoulon: 3535 (humb);
 Baron: 159 (cryp); 164 (cryp); 967 (cryp); 1623 (anal);
 2314 (anal); 3069 (anal); 3070 (anal); 4637 (cryp);
 4794 (cryp); 6190 (ovaloval);
 Beaujard: 405 (cryp); 542 (cryp);
 Benoist: 1210 (anal);
 Bernier: 279 (ovaloval); sn (ovaloval);
 Bisset: 1442 (ovaloval);
 Boiteau: 1020 (mada); 1050 (maju); 2049 (cryp); 2069 (boiv); 2421 (ovaloval); 2056 (leuc); 2059 (ovaloval);
 Bosser 7709 (anal);
 Capuron: 18039-SF (cryp); 20989-SF (humb);
 22710-SF (humb); 22955-SF (ovaloval); 23321-SF (humb);
 23453-SF (boiv); 23458-SF (leuc); 24081-SF (maju);
 24108-SF (cryp); 24519-SF (humb); 24672-SF (humb);
 24738-SF (boiv); 24755-SF (leuc); 24863-SF (cf. leuc);
 27176-SF (ambrcori); 29016-SF (daup); 29203-SF (humb);
 Cours: 1860 (orie); 1915 (orie); 2016 (anal); 2020 (orie);
 2366 (orie); 2619 (orie); 2673 (cryp); 3195 (leuc); 3206 (leuc);
 3596 (ambrcori); 4843 (orie); 5047 (cryp); 5211 (cryp);
 5229 (cryp); 5230 (boiv);
 Cours & Humbert: 5373 (ambrambr); 5374 (ambrambr);
 5375 (ambrambr); 5376 (ambrambr); 5400 (ovaloval);
 5458 (ovaloval); 5535 (humb); 5554 (ovaloval);
 5628 (humb); 5646 (boiv); 5686 (boiv);
 Cowan: sn (cryp);
 CRN/CRNPNM: see RN-series
 Croat: 29429 (cryp); 30196 (cryp); 30299 (cryp); 30433 (cryp);
 Davis, Andriantiana & Gower: 1211 (daup);
 Davis & Rakotonasolo: 2325 (perrants); 2718 (daup);
 Davis, Rakotonasolo & De Block: 2173 (cryp); 2191 (cryp);
 De Block, Luckow & Rakotonasolo: 765 (ovaloval);
 766 (perrperr); De Block & Rakotonasolo: 824 (perrperr);
 836 (anal); 844 (anal); 861 (anal);
 De Block, Rakotonasolo & Randriamboavonjy: 527 (cryp);
 533 (cryp); 600 (cryp); 604 (cryp); 625 (cryp); 669 (daup);
 670 (daup); 689 (daup); 693 (daup); 694 (daup);
 698 (daup); 731 (daup); 762 (cryp); 915 (anal); 978 (ambrambr);
 979 (ambrambr); 1072 (ovaloval); 1090 (ovaloval);
 1126 (ovaloval); 1144 (ovaloval); 1292 (ovaloval);
 1292-bis (ovaloval); 1313 (ambrambr); 1361 (ovaloval);
 1379 (ovaloval);
 Decary: 75 (ovaloval); 7030 (anal); 7034 (anal); 7975 (cryp);
 14249 (cryp); 14546 (humb); 14600 (ovaloval);

- 17161 (cryp); 17181 (cryp); 17914 (anal); 18006 (orie); 18116 (orie);
 Dequaire: 27272 (maju); 27780 (cryp); 27890 (orie); sn (ambrcori);
 Descoings: 2214 (cryp);
 Dorr, Bamett, Rakotozafy, Creek & Razafimalala: 3919 (cryp);
 Douillot: sn (ovaloval);
 Drake: sn (mada);
 Dumetz, Gereau & Rabevohitra: 697 (daup);
 Dumetz & McPherson: 1120 (daup);
 Dupont: 3 (ovaloval); 132 (ovaloval);
 Evrard: 11223 (anal);
 Faliniaina, Rabenantoandro & Ramisy: 92 (daup);
 Floret, Lowry, Leeuwenberg & Rajemisa: 1972 (daup);
 Gautier: 2990 (leuc);
 Gautier, Chatelain & Derleth: 2442 (leuc);
 Geay: 8033 (cryp);
 Gentry: 11309 (orie); 11459 (perrperr);
 Gentry & Schatz: 62032 (ovaloval);
 Gereau: 3339 (daup);
 Grevé: 153 (cryp);
 Guillaumet 888 J (daup); 4217 (leuc);
 Herb. J. Bot. Tan.: 2155 (anal); 2719 (orie); 2792 (orie); 2915 (cryp); 3732 (anal); 3846 (orie); 5194 (maju); 6297 (daup);
 Hildebrandt: 2895 (boiv); 3138 (boiv); 3464 (mada);
 HISM: 3158 (orie);
 Homolle: 50 (ambrambr); 51 (ambrambr); 52 (ambrambr); 120 (ambrambr); 421 (ovaloval); 531 (orie); 1802 (cryp); 1860 (orie); 2015 (anal); 2366 (orie); E5 (anal); O56 (orie);
 Humbert: 6983 (cryp); 14056 (daup); 14139 (daup); 14432 (cryp); 18919 (ovaloval); 19228 (humb); 22414 (leuc); 28336 (cryp); 28722 (cryp); 29048 (daup); 30246 (cryp); 32088 (ambrambr); 32102 (ambrambr); 32119 (ambrambr); 32132 (ambrambr); 32133 (ambrambr); 32135 (ambrambr); 32137 (ambrambr); 32432 (humb); 32469 (humb); 32625 (humb); 32737 (humb); 32771 (humb); 32772 (boiv); 32791 (boiv); 32814 (humb);
 Humbert & Capuron: 24845 (ambrcori); 25006 (ambrcori); 28972 (daup);
 Humbert & Cours: 17667 (orie); 22802 (ambrcori); 32887 (boiv);
 Jacquemin: 894 (cryp); 1257 (cryp); H200J (orie);
 Keraudren: 1577 (leuc); 1661 (humb); 1662 (ovaloval);
 Laha: 293 (daup);
 Leandri & Capuron: 1518 (anal);
 Leandri & Saboureaux: 3000 (perrants);
 Leroy: 20 (cryp); 98 (cryp); 99 (cryp);
 Lowry & Schatz: 4835 (cryp);
 Lyaill: 394 (cryp);
 Mabblerley: 1014 (cryp);
 McPherson & Dumetz: 14661 (daup);
 McWhirter: 142 (daup);
 Miller: 4213 (ambrcori);
 Miller & Lowry: 4002 (leuc);
 Miller & Randrianasolo: 6193 (daup); 6238 (cryp);
 Morat: 1131 (cryp); 4548 (ovaloval);
 O'Connor: 19 (daup);
 Peltier J. & M.: 1981 (cryp); 2765 (cryp); 5972 (cryp); 5985 (maju);
 Perrier de la Bâthie: 465 (mada); 591 (mada); 591-bis (mada); 845 (perrperr); 3608 (perrperr); 3700 (maju); 3715 (boiv); 3756 (perrperr); 3764 (maju); 3857 (perrperr); 3858 (perrperr); 3864 (perrperr); 3865 (ovaloval); 3866 (ovaloval); 3913 (cryp); 4002 (anal); 6904 (anal); 14640 (mada); 17330 (cryp); 18271 (anal); 18475 (cryp); 18803 (ovaloval); 19276 (cryp);
 Pervillé: sn (ovaloval);
 Phillipson: 2040 (leuc);
 Phillipson, Clement & Rafamantanantsoa: 3926 (cryp);
 Rabenantoandro & Antilahimena: 28 (boiv);
 Rabenantoandro, Birkinshaw & Antilahimena: 12 (leuc);
 Rabenantoandro, Randrihasipara & Ramisy: 114 (daup);
 Rabevohitra: 2115 (daup);
 Rabevohitra, Dumetz & Gereau: 1768 (daup); 1775 (daup);
 Rabevohitra, McPherson, Rabenantoandro & Ranavelo: 4424 (ovaloval);
 Rabevohitra, Rabenantoandro & Razakamalala: 4457 (ovaloval);
 Rakotomalaza, Raharilala, Vognono, Rasolomanana, Randrianasolo & Rakotomamonjy: 361 (ovaloval); 391 (maju);
 Rakotomalaza, Sikes, Rasolomanana, Andrianasolo & Andriantsiferana: 652 (ovaloval);
 Rakotonandrasana, Ratovoson, Rasolohery, Randriamanarivo, Randrianjanaka, Rakotozafy, Bemalaza & Tataina: 478 (orie);
 Rakotonasolo: 43 (cryp); 182 (ovaloval); 207 (boiv); 257 (ovaloval);
 Rakotonasolo, Ranaivojaona, Ralimanana & Davis: OKTAN68 (daup);
 Randriamampionona: 250 (daup); 442 (daup); 816 (daup);
 Randrianasolo: 208 (anal);
 Randrianjanaka & Zafy: 204 (anal);
 Rasoavimbahoaka: 635 (ambrcori); 701 (ambrcori);
 Ravelonarivo & Rabesonina: 724 (ambrcori); 738 (ambrcori); 770 (ambrcori);
 Ravelonarivo, Rabesonina & Ramainty: 368 (ambrcori);
 Ravelonarivo, Raymond & Bekamisy: 180 (ambrcori);
 Richard: 54 (ovaloval); 78 (boiv); 120 (ovaloval); 127 (ovaloval); 309 (boiv); 360 (boiv); 647 (boiv); 650 (ovaloval);
 RN-series: sn (Ecole forestière) (anal); 4-RN (orie); 103-RN (orie); 2055-RN (ovaloval); 2556-RN

(ovaloval); 2937-RN (maju); 2977-RN (mada); 3320-RN; (maju); 4204-RN (maju); 4335-RN (boiv); 5162-RN (daup); 6143-RN (maju); 6162-RN (daup); 6285-RN (maju); 6372-RN (maju); 7189-RN (cryp); 7201-RN (perrants); 7244-RN (orie); 7754-RN (ovaloval); 7989-RN (ambrcori); 8005-RN (maju); 8107-RN (cryp); 8220-RN (ambrcori); 8250-RN (ambrcori); 8567-RN (maju); 9011-RN (ambrcori); 9194-RN (cryp); 10332-RN (perrants); 10513-RN (orie); 10586-RN (orie); 10743-RN (leuc); 11094-RN (perrants); 11114-RN (perrants); 11626-RN (maju); 11678-RN (cryp); 11729-RN (leuc); 11898-RN (orie); 11969-RN (cryp); 11992-RN (cryp); 12017-RN (orie); 12052-RN (orie); 12148-RN (boiv); 12433-RN (orie); 12435-RN (orie); 12465-RN (perrants); 1681-RN (ovaloval); 17161-RN (cryp); 18724-RN (maju); 19956-RN (cryp);
 Schatz, Lowry, Andriamihajarivo, Hong Wa, Rabevohitra & S. Lowry: 4026 (cryp);
 Scott Elliot: 2489 (daup); 2746 (daup);
 SEFM: see SF series;
 SF: 4-SF (ovaloval); 10-SF (mada); 10-SF-bis (perrperr); 13-SF (ovaloval); 33-SF (maju); 214-SF (cryp); 280-SF (cryp); 1408-SF (anal); 1815-SF (anal); 2179-SF (anal); 2700-SF (cryp); 2764-SF (cryp); 3242-SF (boiv); 3479-SF (ovaloval); 3519-SF (anal); 4014-SF (maju); 4737-SF (cryp); 4951-SF (ovaloval); 5076-SF (anal); 7195 (ambrambr); 7941-SF (ovaloval); 9289-SF (boiv); 9777-SF (orie); 9840-SF (ovaloval); 9867-SF (ovaloval); 9957-SF (ambrambr); 10092-SF (daup); 13353-SF (maju); 13745-SF (cryp); 14120-SF (ovaloval); 14459-SF (cryp); 14627-SF (cryp); 14847-SF (cryp); 15342-SF (maju); 15619-SF (daup); 15861-SF (ovaloval); 16325-SF (ovaloval); 16360-SF (ovaloval); 16691-SF (ovalglab); 17073-SF (maju); 19112-SF (ovaloval); 19149-SF (perrperr); 19462-SF (perrperr); 19834-SF (perrants); 21230-SF (anal); 21480-SF (cryp); 21805-SF (orie); 21879-SF (anal); 21941-SF (anal); 29190 bis-SF (orie); 25156-SF (anal); Seyrig: 686 (daup);
 Stoddart: 1037 (ovaloval);
 Thomasset: sn (ovaloval);
 Ursch: 38 (anal);
 Wood: 1614 (ovaloval).