

**RE-SHAPING MALLOTUS [PART 1]:
EXPANDED CIRCUMSCRIPTION AND REVISION
OF THE GENUS CORDEMOYA (EUPHORBIACEAE)**

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SUMMARY

A recent phylogenetic study based on DNA sequence data detected a well-supported clade of a number of *Mallotus* species together with the genus *Cordemoya*. This clade is distinct from the large *Mallotus* s.s. clade. In this paper, *Cordemoya* (formerly monotypic with *C. integrifolia* from the Mascarene Islands) is expanded with sixteen additional species previously assigned to *Mallotus*. Taxa transferred to *Cordemoya* are: *Mallotus* sections *Hancea* and *Oliganthae* from Asia and *M. baillonianus*, *M. capuronii*, and *M. spinulosus* from Madagascar. The genus *Cordemoya* can be distinguished from *Mallotus* s.s. by the presence of pollen with areolate ornamentation with scabrae (perforate/micro-reticulate ornamentation with scabrae in the sample of *Mallotus* s.s. studied up to now) and of capitate glandular hairs with multicellular stalks and sessile peltate-stellate hairs with a central cell (spherical to disc-shaped multicellular glandular hairs in *Mallotus*). In the new circumscription of *Cordemoya* two subgenera are recognized: *Cordemoya* from Madagascar and Mascarenes and *Diplochlamys* from Asia. The latter is divided into two sections: *Diplochlamys* (former sect. *Hancea*), and *Oliganthae*. A taxonomic revision of part of these taxa is provided (excl. section *Diplochlamys*); descriptions, distribution maps, habit drawings and a key are included.

Key words: Euphorbiaceae, *Cordemoya*, *Deuteromallotus*, *Mallotus*, Malesia, Madagascar, Mauritius, Réunion.

INTRODUCTION

In the last classification of *Mallotus* Lour. by Airy Shaw (1968), the genus was subdivided into eight sections based on few morphological characters. However, two phylogenetic studies have recently contributed to the knowledge of the boundaries of the genus *Mallotus* and its relationships with related genera, namely with the members of subtribe Rottlerinae Meisn. (Webster, 1994) and the genus *Macaranga* Thouars. An analysis of morphological data (Slik & Van Welzen, 2001b) indicated that the Asian sections *Hancea* (Seem.) Pax & K. Hoffm. (12 spp.) and *Oliganthae* Airy Shaw (monotypic) might not belong to the same clade as the other *Mallotus* sections and the genus *Macaranga*. A study of DNA sequence data with a more extensive taxon sampling (Kulju et al., in prep.) confirmed this result, grouping these two sections together with three *Mallotus* species (= *Deuteromallotus*) endemic to Madagascar (*M. baillonianus* Müll.Arg., *M. capuronii* (Léandri) McPherson, and *M. spinulosus* McPherson), and

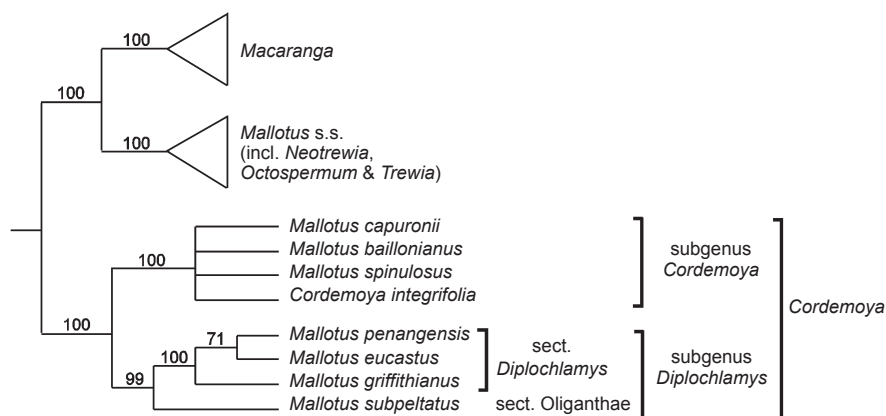


Fig. 1. A tree summarizing the phylogenetic relationships of *Macaranga*, *Mallotus* and related small genera (adapted from Fig. 2 & 3 in Kulju et al., in prep.). Maximum parsimony bootstrap values are given above branches. On the right the new circumscription and classification of the genus *Cordemoya*.

monotypic *Cordemoya* from Mauritius and Réunion. This clade is in a basal position compared to the *Mallotus* s.s. clade (with monotypic *Neotrewia* Pax & K. Hoffm., *Octospermum* Airy Shaw, and *Trewia* L.) and the *Macaranga* clade (Fig. 1). All these three clades have strong bootstrap support.

Consequently, the circumscription of *Mallotus* has to be changed to make the genus monophyletic. The inclusion of *Neotrewia*, *Octospermum*, and *Trewia* is discussed separately (Kulju & Van Welzen, in prep.). In this paper, *Mallotus* sections *Hancea* and *Oliganthae*, and three endemic Madagascan *Mallotus* species are transferred to the genus *Cordemoya*, which now consists of seventeen species: *C. acuminata* (Baill.) Baill., *C. capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen, *C. cordatifolia* (Slik) S.E.C. Sierra, Kulju & Welzen, *C. eucausta* (Airy Shaw) S.E.C. Sierra, Kulju & Welzen, *C. grandistipularis* (Slik) S.E.C. Sierra, Kulju & Welzen, *C. griffithiana* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen, *C. hirsuta* (Elmer) S.E.C. Sierra, Kulju & Welzen, *C. hookeriana* (Seem.) S.E.C. Sierra, Kulju & Welzen, *C. integrifolia* (Willd.) Baill., *C. kingii* (Hook. f.) S.E.C. Sierra, Kulju & Welzen, *C. longistyla* (Merr.) S.E.C. Sierra, Kulju & Welzen, *C. papuana* (J.J. Sm.) S.E.C. Sierra, Kulju & Welzen, *C. penangensis* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen, *C. spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen, *C. stipularis* (Meijer ex Airy Shaw) S.E.C. Sierra, Kulju & Welzen, *C. subpeltata* (Blume) M. Aparicio, and *C. wenzeliana* (Slik) S.E.C. Sierra, Kulju & Welzen. The morphological characters typical for *Cordemoya* and its morphological differences with *Mallotus* s.s. are discussed. An infrageneric classification with two subgenera and two sections is also proposed. Finally, a revision of *Cordemoya* with a key, descriptions, distribution maps and drawings is given (excluding section *Diplochlamys*).

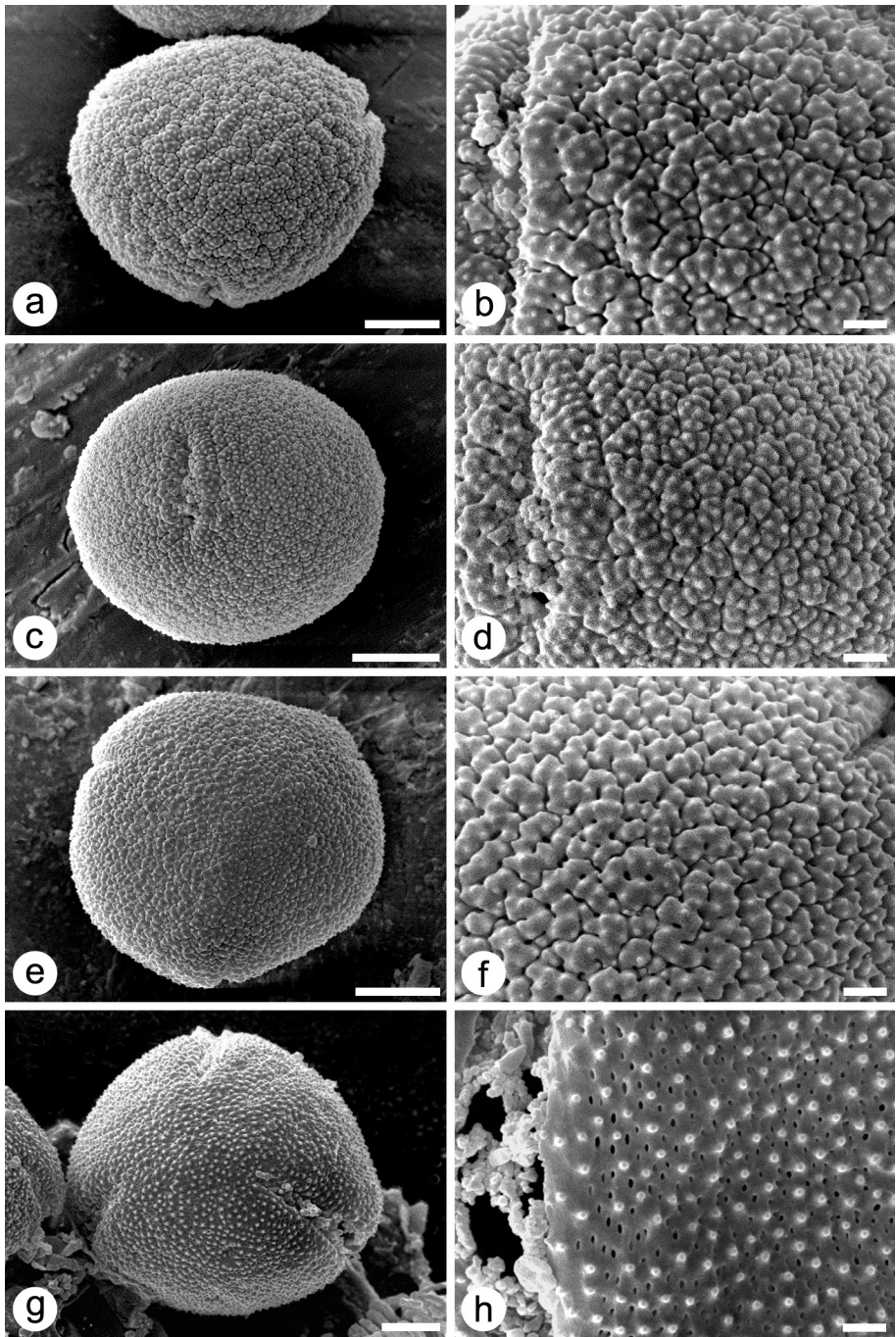
MORPHOLOGICAL AND ANATOMICAL CHARACTERS OF
MALLOWUS AND CORDEMOYA

The molecular support for the new circumscription of *Mallotus* and *Cordemoya* is strong; however, there are only few uniquely distinguishing morphological characters separating them. One distinct character is in the pollen ornamentation (Fig. 2): the genus *Cordemoya* has pollen with areolate ornamentation with scabrae instead of perforate/microreticulate ornamentation with scabrae as found in *Mallotus* s.s. [N.B. the genus has largely been sampled so far, but not completely, therefore other kinds of ornamentation could be present, including areolate]. Leaf anatomical studies have revealed the presence of capitate glandular hairs with multicellular stalks (in subg. *Diplochlamys* and *C. capuronii*, Fig. 3c) and of sessile peltate-stellate hairs with a central cell (in subg. *Cordemoya*, Fig. 3a, b), instead of spherical to disc-shaped multicellular glandular hairs found in *Mallotus* (Fig. 3d–f; Fišer et al., in prep.). Macromorphological differences also exist, but many of them overlap, often because of a few deviating *Mallotus* s.s. species. The main typical characters of *Cordemoya* are: extrafloral nectaries on the upper leaf surface absent or inconspicuous when present (always present and conspicuous in *Mallotus*); staminate inflorescences with 1–3 flowers per node (1–15 in *Mallotus*); pistillate inflorescences racemes or developing one terminal flower (racemes, panicles, spikes or umbels in *Mallotus*, with the exception of *Trewia nudiflora* L. (to be transferred to *Mallotus* together with *T. polycarpa* Benth., Kulju, in prep.), which sometimes develops only one terminal flower); stigmas erect and long, 5–22 mm (mostly reflexed and short, 0.7–11 mm in *Mallotus*, with the exception of *M. khasianus* Hook.f., 5–14 mm, *T. polycarpa* 10–12 mm, and *T. nudiflora*, 12–24 mm); and spiny fruits (spiny or not in *Mallotus*).

INFRAGENERIC CLASSIFICATION

The rank of subgenus was assigned to the two strongly supported and geographically distinct *Cordemoya* clades present in the phylogeny of Kulju et al. (in prep.; Fig. 1): subgenus *Cordemoya* consisting of four species from Madagascar and Mascarenes and subgenus *Diplochlamys* consisting of the Asian species. Furthermore, the subgenus *Diplochlamys* was subdivided into sections *Diplochlamys* and *Oliganthae*, corresponding to the former sections *Hancea* and *Oliganthae* in *Mallotus* s.l., respectively (Fig. 1).

Morphologically, these three taxa can be distinguished by leaf arrangement. In subg. *Cordemoya* the leaves are predominantly opposite and similar in shape, but one only slightly smaller than the other (sometimes the leaves are alternate). Additionally, it is the only subgenus which has sessile peltate-stellate hairs with a central cell. The members of section *Diplochlamys* also have opposite leaves, but the smaller leaf of each pair is reduced and dissimilar, resembling a stipule. Section *Oliganthae* always has alternate leaves. Sections *Diplochlamys* and *Oliganthae* have capitate glandular hairs with multicellular stalks, which are also present in *C. capuronii* of subgenus *Cordemoya*. Further characters separating section *Diplochlamys* from section *Oliganthae* are branches with conspicuously swollen nodes (slender in *Oliganthae*), interpetiolar stipules (axillary in *Oliganthae*), leaf blade not peltate (subpeltate in *Oliganthae*), axillary inflorescences (ramiflorous and axillary in *Oliganthae*), and fruits opening septicidally-loculicidally (loculicidally-septicidally in *Oliganthae*).



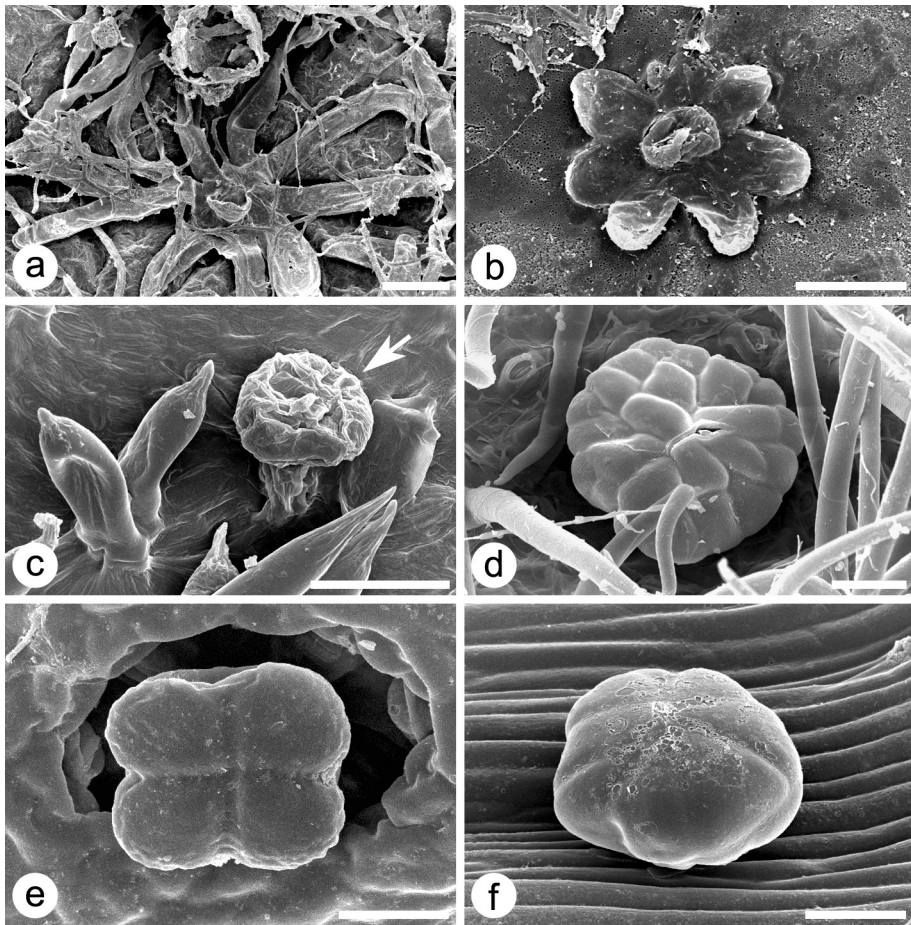


Fig. 3. *Cordemoya* and *Mallotus* hairs and glandular hairs. — a. *Cordemoya capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen. Sessile peltate-stellate hair with a central cell. — b. *Cordemoya spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen. Sessile peltate-stellate hair with a central cell. — c. *Cordemoya subpeltata* (Blume) M. Aparicio. Capitulate glandular hair with multicellular stalks. — d. *Mallotus repandus* (Rottler) Müll. Arg. Spherical multicellular glandular hair. — e. *Mallotus resinus* (Blanco) Merr. Disk-shaped multicellular glandular hairs. — f. *Mallotus lackeyi* Elmer. Spherical multicellular glandular hair (a: Messmer & Andriatsiferana 698, G; b: Totozafy Be 520, WAG; c: Prawiroatmodjo 361, L; d: Stocks s.n., L; e: Craven & Schodde 999, L; f: Ambriansyah & Abriansyah B805, L). — Scale bars: a–f = 25 μ m.

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Fig. 2. *Cordemoya* and *Mallotus* pollen micrographs. — a, b: *Cordemoya capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen. a. Polar view of 3-colporate grain; b. detail of ornamentation. — c, d: *Cordemoya subpeltata* (Blume) M. Aparicio. c. Equatorial view; d. detail of ornamentation. — e, f: *Cordemoya papuana* (J.J. Sm.) S.E.C. Sierra, Kulju & Welzen. e. Polar view of 3-colporate grain; f. detail of ornamentation. — g, h: *Mallotus hymenophyllus* Airy Shaw. g. Polar view of 3-colporate grain; h. detail of ornamentation (a, b: Labat & Andrianjafy 3399, G; c, d: Maxwell 86-133, L; e, f: Lam 7805, L; g, h: Larsen et al. 31247, L). — Scale bars: a, c, e, g = 5 μ m; b, d, f, h = 1 μ m.

TAXONOMIC HISTORY

The first generic name for the basal (*Cordemoya*) clade is *Boutonia* Bojer (1837), but this name was invalidly described, the only descriptive ‘character’ casually mentioned is ‘shrub’. The validation in 1846 by Bojer created a later homonym, because De Candolle (1838) had used *Boutonia* for an Acanthaceae.

The earliest legitimate generic name is *Cordemoya* Baill. (1861), which therefore is adopted here. It was proposed for *Ricinus integrifolius* Willd. from Mauritius. Baillon (1861) transferred the latter species to his new genus *Cordemoya* and added *C. acuminata* Baill. from Madagascar. Several years later Baillon (1891a) moved these two species to *Echinus* Lour. as sect. *Cordemoya*.

Müller Argoviensis (1865) transferred them to *Mallotus* sect. *Cordemoya* Müll. Arg., in which he also included *M. penangensis* Müll. Arg., a Southeast Asian species. This concept already anticipated the recent phylogenetic results (Kulju et al., in prep.) by grouping these geographically distinct species together. Airy Shaw (1968) placed *M. penangensis* in sect. *Hancea* and neither discussed the African species nor *Cordemoya* in literature (though he had his own ideas about the circumscription of *Cordemoya*, which was mainly based on fruit, flower and leaf morphology; see Coode, 1982).

Diplochlamys Müll. Arg. (1864) was monotypic (*D. griffithianus* Müll. Arg.). Bentham (1880) reduced it to *Mallotus*, while Pax (1890) regarded it as a section of *Mallotus* and added *M. subpeltatus* (Blume) Müll. Arg. However, Airy Shaw (1968) included the first species in sect. *Hancea* and the second in his new sect. *Oliganthae*. The section name *Hancea* dates from 1914 (Pax & Hoffmann), is younger than *Diplochlamys* and should therefore be regarded as a synonym. Most systematists either missed the fact that the name *Diplochlamys* was used on sectional level (e.g., Airy Shaw, 1968) or they failed to notice that *Diplochlamys* is an older name (e.g., Slik & Van Welzen, 2001a).

Deuteromallotus Pax & K. Hoffm. (1914) was described to accommodate *Boutonia acuminata* Baill. (1858). The classification of this species has varied much through time. Baillon (1861) placed it in *Cordemoya*, Müller Argoviensis (1865) put it in *Mallotus* sect. *Cordemoya* and, because of the already existing *M. acuminatus* (Blume) Müll. Arg. (1865), he renamed the species *M. baillonianus* Müll. Arg. Baillon (1891a) moved *M. baillonianus* to *Echinus* Lour. Finally, McPherson (1995) transferred it to *Mallotus*. Léandri (1957) added the compatriot *M. capuronii* to *Deuteromallotus*, which McPherson (1995) also placed in *Mallotus*.

CORDEMOYA Baill.

Cordemoya Baill. (1861) 255. — *Boutonia* Bojer (1837) 282, nom. nud.; (1846) 151, non DC. (1838). — *Mallotus* Lour. sect. *Cordemoya* (Baill.) Müll. Arg. (1865) 186. — *Echinus* Lour. sect. *Cordemoya* (Baill.) Baill. (1891a) 977. — Type: *Boutonia mascareinensis* Bojer [= *Cordemoya integrifolia* (Willd.) Baill.].

Hancea Seem. (1857) 409. — *Mallotus* Lour. sect. *Hancea* (Seem.) Pax & K. Hoffm. (1914) 199. — Type: *Hancea hookeriana* Seem. [= *Cordemoya hookeriana* (Seem.) S.E.C. Sierra, Kulju & Welzen].

Diplochlamys Müll. Arg. (1864) 539; (1866) 1023. — *Mallotus* Lour. sect. *Diplochlamys* (Müll. Arg.) Baill. ex T. Durand (1888) 370; Müll. Arg. ex Pax (1890) 55, isonym. — Type: *D. griffithianus* Müll. Arg. [= *Cordemoya griffithiana* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen].

Deuteromallotus Pax & K. Hoffm. (1914) 212. — Type: *Deuteromallotus acuminatus* (Baill.) Pax & K. Hoffm. [= *Cordemoya acuminata* (Baill.) Baill.].

Mallotus Lour. sect. *Oliganthae* Airy Shaw (1968) 389. — Type: *Mallotus subpeltatus* Blume [= *Cordemoya subpeltata* (Blume) M. Aparicio].

Shrubs to big trees, monoecious and/or dioecious. Branches with slender or conspicuously swollen nodes. *Indumentum* composed of simple hairs and sometimes capitate glandular hairs with multicellular stalks (subg. *Diplochlamys* and *C. capuronii*), or sessile peltate-stellate hairs with a central cell (subg. *Cordemoya*). *Resin* sometimes present (*C. integrifolia* and *C. spinulosa*). *Stipules* axillary or interpetiolar. *Leaves* simple, alternate or opposite (strongly unequal or not), (sub)coriaceous to chartaceous, adaxial extrafloral nectaries absent or when present inconspicuous, midrib, nerves and veins prominent, venation triplinerved, (rarely palminerved) or pinnate, veins scalariform, veinlets reticulate. *Inflorescences* ramiflorous, axillary, or terminal, unisexual to bisexual, with one bract per node; staminate ones with 1–3 flowers per bract, bracts persistent, bracteoles absent; pistillate ones with 1 flower per bract, bracts persistent to caducous, bracteoles rarely present. *Flowers* actinomorphic, not exceeding 1 cm diam.; sepals persistent; petals and disc absent. *Staminate flowers*: sepals 2–4, valvate, free to basally connate; stamens: thecae 2, parallel, opening extrorsely and lengthwise; pollen ornamentation areolate with scabrae; pistillode absent. *Pistillate flowers*: sepals (3 or 4–6 (or 7), valvate or imbricate, free; staminodes rarely present; ovary with 1 ovule per locule; style short, stigmas erect, inner surface densely covered with short papillae, outer surface hairy. *Fruits* dehiscent capsules, opening loculicidally-septicidally or septicidally-loculicidally, spiny, spines sometimes with terminal glands. *Seeds* (more or less) globose, somewhat trigonous in transverse section; caruncle or aril absent.

Distribution — Madagascar, Mauritius, Réunion, from South China throughout Southeast Asia and Malesia to New Guinea.

KEY TO THE SPECIES

- 1a. Leaves alternate or opposite with one leaf of a pair similar in shape and only slightly smaller than the other. Stipules axillary. 2
 b. Leaves opposite with one leaf of a pair stipuliform. Stipules interpetiolar.
 **Sect. *Diplochlamys***
 (see Slik & Van Welzen, 2001a, for key, descriptions, distributions, and figures)
- 2a. Leaves opposite or sometimes alternate, base not peltate, pinnately nerved. Stipules linear-triangular 3–20 by 0.2–1 mm, margin entire. Inflorescences axillary or terminal. Staminate inflorescences 2–10 cm long. — Madagascar, Mauritius and Réunion (Subg. *Cordemoya*). 3
 b. Leaves alternate, base subpeltate up to 2 mm, triplinerved. Stipules narrowly triangular 5–7 by 1.8–2 mm, margin serrate. Inflorescences ramiflorous or axillary. Staminate inflorescences 0.5–0.8 cm long. — Burma to Thailand, Peninsular Malaysia, Sumatra, Java, and Borneo (Sect. *Oliganthae*). **17. *C. subpeltata***
- 3a. Leaves ovate. Stipules 6.5–20 mm long. Stamens 200–250. — Mauritius and Réunion **3. *C. integrifolia***
 b. Leaves ovate, elliptic or obovate. Stipules 2–12 mm long. Stamens 70–150. — Madagascar 4

- 4a. Leaves obovate, apex emarginate, obtuse, rounded, to rarely acute or shortly acuminate **2. *C. capuronii***
 b. Leaves ovate to elliptic, apex acuminate to caudate 5
 5a. Young branches, petioles, leaf venation on lower surface and inflorescences densely to sparsely hairy with long and soft hairs. Stipules persistent to caducous, 5–12 mm. Leaf apex caudate. Fruit 15–25 by 30–35 mm, 2-locular, spines 80–100. **1. *C. acuminata***
 b. Young branches, petioles, leaf venation on lower surface and inflorescences (sub)glabrous. Stipules early caducous, 2–5 mm. Leaf apex acuminate. Fruit 5–6.5 by 8–9 mm, 2- or 3-locular, spines 4–6 **4. *C. spinulosa***

Subgenus *Cordemoya*

Cordemoya Baill. (1861) 255. — *Boutonia* Bojer (1837) 282, nom. nud.; (1846) 151, non DC. (1838). — *Mallotus* Lour. sect. *Cordemoya* (Baill.) Müll. Arg. (1865) 186. — *Mallotus* Lour. sect. *Boutonia* Benth. (1880) 319. — *Echinus* Lour. sect. *Cordemoya* (Baill.) Baill. (1891a) 977. — Type: *Boutonia mascareinensis* Bojer [= *Cordemoya integrifolia* (Willd.) Baill.].
Deuteromallotus Pax & K. Hoffm. (1914) 212. — Type: *Deuteromallotus acuminatus* (Baill.) Pax & K. Hoffm. [= *Cordemoya acuminata* (Baill.) Baill.].

Branches with slender nodes. *Indumentum* composed of simple and sessile peltate-stellate hairs with a central cell and capitate glandular hairs with multicellular stalks (*C. capuronii*). *Stipules* axillary, margin entire. *Leaves* opposite (in *C. capuronii*, *C. integrifolia*, and *C. spinulosa* sometimes alternate), unequal in size; blade not peltate, (sub)coriaceous, margin entire to crenate, extrafloral nectaries present or absent, venation pinnate with the lowest nerves undifferentiated and submarginal. *Inflorescences* axillary or terminal. *Staminate inflorescences* racemes (sometimes with 1–3 side branches), with 1–3 flowers per bract. *Male flowers*: sepals 2–4, valvate, basally connate; connective not widened. *Pistillate inflorescences* racemes and/or developing one flower terminally. *Pistillate flowers*: sepals 4–6; ovary 2- or 3-locular. *Fruits* opening septically-loculicidally, inside glabrous, spines without terminal glands.

Distribution — Madagascar, Mauritius, and Réunion.

1. *Cordemoya acuminata* (Baill.) Baill. — Fig. 4a–c; Map 1

Cordemoya acuminata (Baill.) Baill. (1861) 255. — *Boutonia acuminata* Baill. (1858) 401. — *Mallotus baillonianus* Müll. Arg. (1865) 186, non *M. acuminatus* (Blume) Müll. Arg. (1865) 187. — *Echinus baillonianus* (Müll. Arg.) Baill. (1891a) 977; (1891b) t. 175, nom. superfl. — *Deuteromallotus acuminatus* (Baill.) Pax & K. Hoffm. (1914) 212. — Lectotype (McPherson, 1995): *Chapelier s.n.* (P), Madagascar.

Small tree up to 15 m high, dbh up to 20 cm, dioecious. *Indumentum* composed of long and short simple hairs¹ and sessile peltate-stellate hairs with a central cell. *Stipules* linear-triangular, 5–12 by 0.5–1 mm, persistent to caducous, margin entire, apex acute, densely hairy on both sides. *Leaves*: petiole 10–45 by 0.5–1 mm, not grooved,

1) *Cordemoya acuminata* shares with subg. *Diplochlamys* the presence of simple, short and long (250–3000 μm) hairs, primarily found on the leaves (midrib and nerves) and sometimes on the fruits.

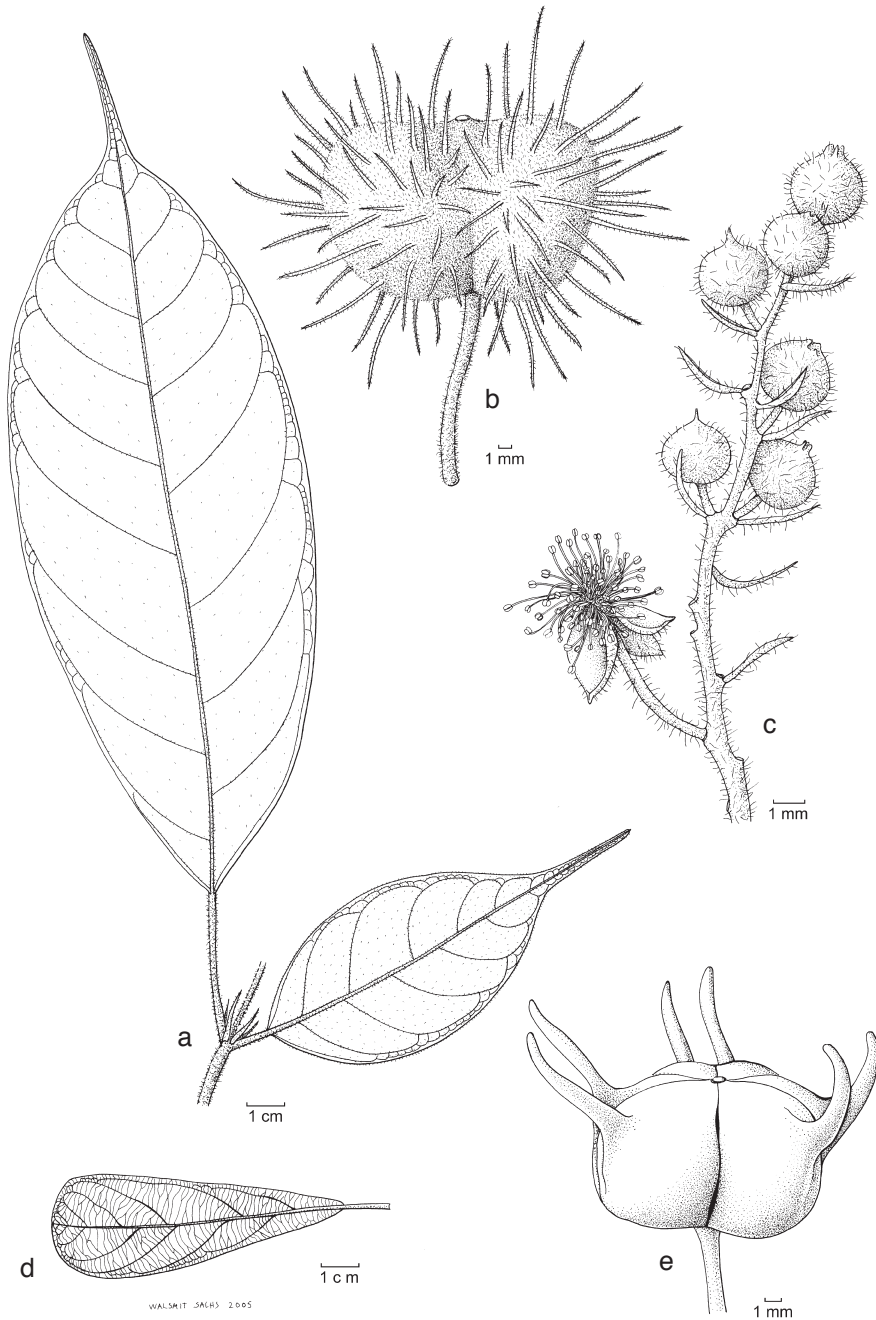


Fig. 4. a–c: *Cordemoya acuminata* (Baill.) Baill. a. Leaf pair with stipules; b. fruit; c. staminate inflorescence. — d, e: *Cordemoya capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen. d. Leaf; e. fruit (a, c: Aridy & Moise 184, MO; b: Randrianasolo & Bernardin 231, G; d: Labat & Andrianjafy 3399, G; e: Kotozafy 999, MO).

densely to sparsely hairy; blade elliptic, 8–20 by 2.8–5 cm, length/width ratio 2.8–4, subcoriaceous, base not peltate, acute, margin entire to crenate, apex caudate, upper surface sparsely hairy, lower surface densely to sparsely hairy, when young with sessile peltate-stellate hairs with a central cell on both sides, nerves 6–9 per side, looping close to the margin, with hair-tuft domatia. *Inflorescences* single, unisexual; peduncle 1–3 mm long; bracts linear-triangular, margin entire, apex acute, upper surface densely hairy, lower surface sparsely hairy. *Flowers*: pedicels densely hairy; sepals: margin entire, apex acute, sparsely hairy outside, subglabrous to glabrous inside. *Staminate inflorescences* racemes, 4.5–5 cm long, 1 or 2 flowers per node, nodes per branch 10–17; bracts 4–8 by 0.3–0.4 mm, bracteoles rarely present, linear-triangular, 0.5–0.8 by c. 0.1 mm, early caducous. *Staminate flowers* 4.5–5 mm diam.; pedicels 2–3 mm long; sepals 3 or 4, ovate to obovate, 2–2.5 by 1.8–2 mm, sparsely hairy outside, glabrous inside; stamens 120–150, glabrous, filaments 1–3 mm long, thecae ovoid, 0.2–0.3 by 0.2–0.25 mm, connective not widened. *Pistillate inflorescences* developing one flower terminally, 2.5–5 cm long; sterile bracts 2–5, 4–6 by 0.5–0.8 mm; bracteoles absent. *Pistillate flowers* 4–5 mm diam.; pedicels c. 1 mm long; sepals 5 or 6, 5–7 by 0.2–0.25 mm, valvate; ovary 2.5–3 by 3–4 mm, 2-locular, densely hairy; style 0.5–1 mm long; stigma 8–13 mm long; staminodes absent. *Fruits* 15–25 by 30–35 mm, green, outer surface sparsely hairy, spines 80–100, straight, 5–11 by 0.5–0.8 mm, sparsely hairy; wall 0.8–1.3 mm thick; column 6–6.5 by 8–8.5 mm. *Seeds* 11.5–12 by 11.5–12 by 10–10.5 mm, surface smooth, dull, light brown, striate.

Distribution — Endemic to Madagascar.

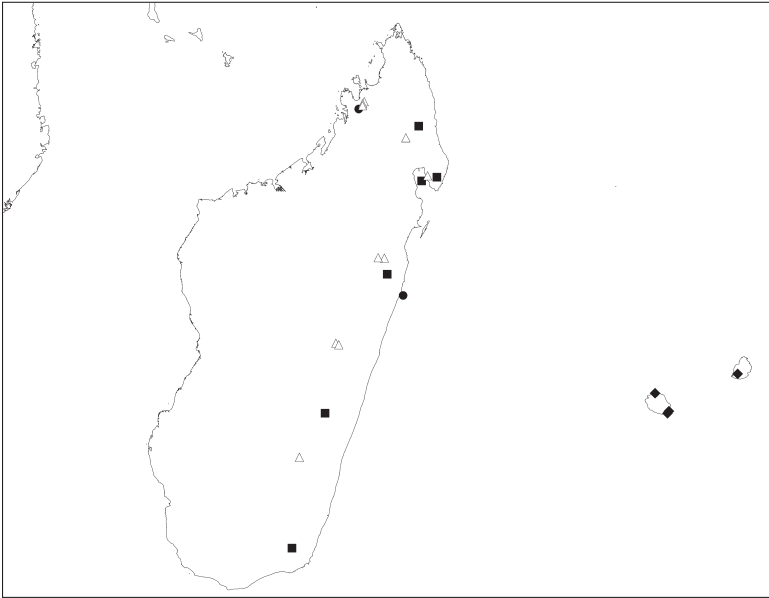
Habitat & Ecology — In evergreen forest. Altitude: sea level up to 1300 m. Flowering and fruiting: October to March.

Vernacular names — Madagascar: Hirondry, kinoronoro, sifidambo.

2. *Cordemoya capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen, *comb. nov.* — Fig. 4d, e; Map 1

Deuteromallotus capuronii Léandri, Bull. Soc. Bot. France 103 (1957, '1956') 605. — *Mallotus capuronii* (Léandri) McPherson (1995) 170. — Type: *SF (MAD)* [Capuron] 8713 (holo P; iso MO), Madagascar, Minombo, Amboditavolo.

Small to big trees up to 25 m high, dbh up to 35 cm, dioecious. *Indumentum* composed of short simple hairs, sessile peltate-stellate hairs with a central cell and capitate glandular hairs with multicellular stalks. *Resin* greenish. *Stipules* linear-triangular, 3–5 by 0.2–0.4 mm, early caducous, margin entire, apex acute, sparsely hairy on both sides. *Leaves*: petiole 3–24(–85) by 1–1.5(–2.5) mm, not grooved, scattered to sparsely hairy; blade obovate, 4.5–7(–22) by 1.3–3(–10) cm (see note 1), length/width ratio 2.3–2.5, coriaceous, base not peltate, acute, margin entire to crenate, apex emarginate to rounded to obtuse (to rarely acute or shortly acuminate), upper surface glabrous, lower surface sparsely hairy, glabrescent, nerves 4–10 per side, looping close to the margin, hair-tuft domatia present to absent. *Inflorescences* single, unisexual; peduncle 1–3.5 by 1–1.5 mm; bracts linear-triangular, margin entire, apex acute, upper surface densely hairy outside, lower surface densely hairy to subglabrous. *Flowers*: pedicels glabrous to sparsely hairy; sepals: margin entire, apex acute densely hairy to subglabrous outside,



Map 1. Distribution of *C. acuminata* (Baill.) Baill. (■), *C. capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen (Δ), *C. integrifolia* (Willd.) Baill. (◆), *C. spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen (●).

glabrous inside. *Staminate inflorescences* racemes, 2–5.2 cm long, 1 flower per node, nodes per branch 19–30; bracts 1.5–2(–3) by 0.3–0.4(–0.5) mm; bracteoles absent. *Staminate flowers* 3–4 mm diam.; pedicels 2.5–5 mm long; sepals 2 or 3, ovate to obovate, 2.5–4.5 by 2.5–3 mm, densely hairy outside, glabrous inside; stamens 80–130, glabrous, filaments 1–3 mm long, pale light yellow, thecae ovoid, 0.2–0.3 by 0.2–0.3 mm, brownish red, connective not widened. *Pistillate inflorescences* developing one flower terminally, 0.5–1.5 cm long; bracts 15–30, 2.8–3 by 0.2–0.3 mm; bracteoles 1–3 by 0.1–0.2 mm, early caducous. *Pistillate flowers* 2.5–3 mm diam.; pedicels 1 mm long; sepals 4 or 5, linear-triangular, 4–4.5 by 0.25–0.3 mm, valvate; staminodes absent; ovary 1.8–2 by 1.8–2 mm, 2- or 3-locular, densely hairy; style 0.5–1 mm long; stigma 8–15 mm long. *Fruits* 11–13 by 17–18 mm, green, outer surface subglabrous, spines 4 or 6 (to rarely 8, 12 or 20, see note 2), slightly curved, 14–17 by 0.8–1.2 mm, subglabrous to sparsely hairy; wall c. 0.3–0.5 mm thick; column 4–5 by 3.5–4 mm. *Seeds* 8–9 by 8–9 by 8–9 mm, surface smooth, dull, dark brown, striate.

Distribution — Endemic to Madagascar.

Habitat & Ecology — On edges of humid forest. Altitude 10–1700 m. Flowering and fruiting: September to March.

Vernacular names — Madagascar: Macarenana mavo.

Notes — 1. *Andrianjafy et al. 168* and *Ratovoson et al. 573* have bigger leaves and male inflorescences compared to the other collections studied.

2. *Ravelonarivo & Rabesonina 653* has 8, 12 or 20 fruit spines.

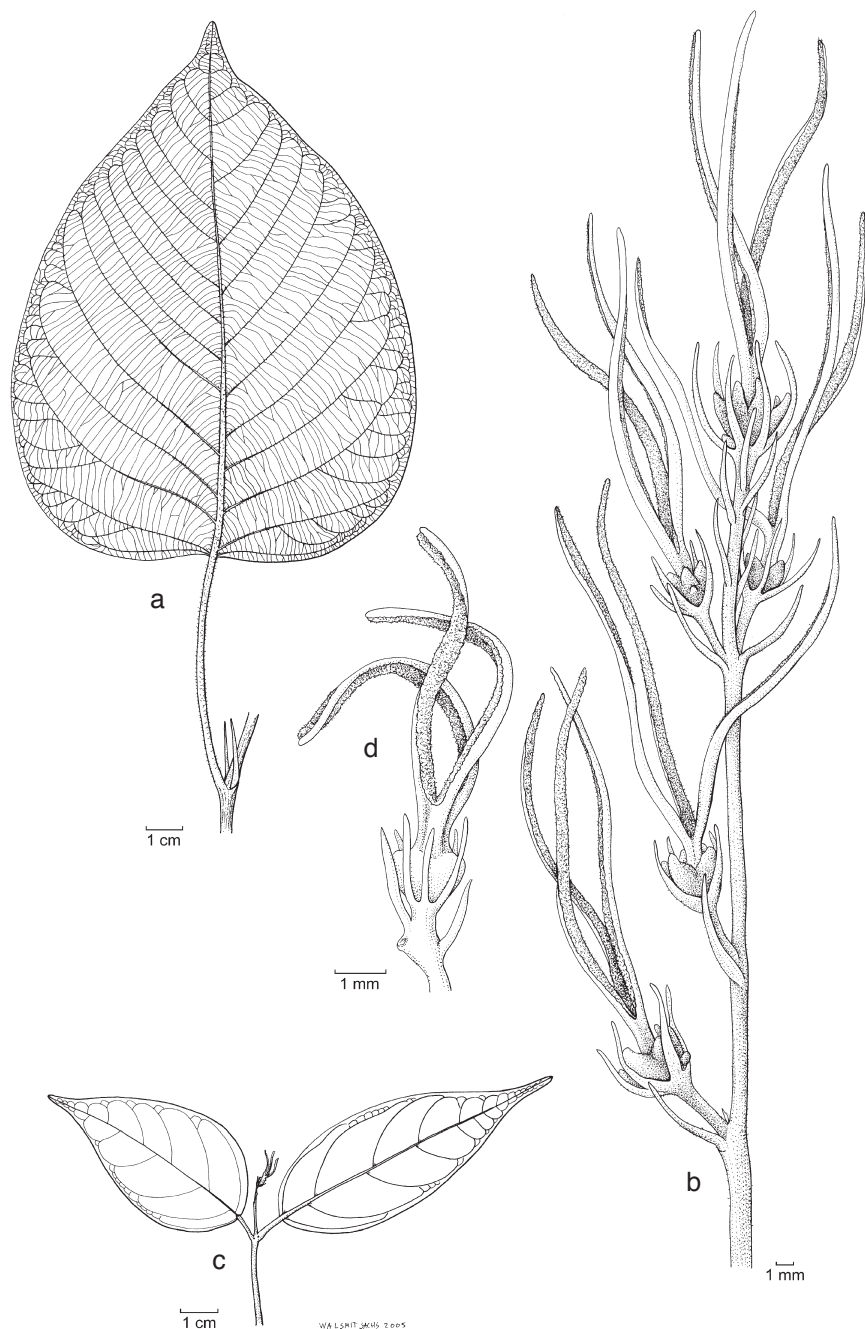


Fig. 5. a, b: *Cordemoya integrifolia* (Willd.) Baill. a. Leaf with stipules; b. pistillate inflorescence. — c, d: *Cordemoya spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen. c. Leaf pair with pistillate inflorescence; d. pistillate flower (a: Frappier 278, A; b: Blackburn s.n., A; c, d: Gautier & Totozafy Be 2910, G).

3. *Cordemoya integrifolia* (Willd.) Baill. — Fig. 5a, b; Map 1

- Cordemoya integrifolia* (Willd.) Baill. (1861) 255. — *Ricinus integrifolius* Willd. (1805) 567.
— *Boutonia mascariensis* Bojer (1837) 282, nom. superfl.; (1846) 151, nom. superfl. — *Mallotus integrifolius* (Willd.) Müll. Arg. (1865) 186. — *Echinus integrifolius* (Willd.) Baill. (1891a) 977.
— Lectotype (selected by Coode, 1982): *Unknown s.n.* (*Herb. Willd.* 17934, B, here limited to the sheet with Radlkofer's notes (IDC microfiche no. 1261)), Mauritius.
Ricinus dioicus Chev. ex Steud. (1841) 459, nom. illegit., non G. Forst. (1786), nec Roxb. (1832).
— Voucher: *Chapelier s.n.* (P?, n.v.).
Ricinus lanceolatus Thouars ex Baill. (1861) 255, nom. nud. — Voucher: *Dupetit-Thouars s.n.* (P?, n.v.).

Shrubs to small trees up to 9 m high, dbh up to 25 cm, monoecious to dioecious. *Indumentum* composed of short and long simple hairs and sessile peltate-stellate hairs with a central cell. *Resin* yellowish. *Stipules* linear-triangular, 6.5–20 by 0.5–0.8 mm, persistent to caducous, margin entire, apex acute, sparsely hairy on both sides. *Leaves*: petiole 22–134 by 1–3 mm, not grooved, sparsely hairy; blade ovate, 7–24 by 4–12 cm, length/width ratio 2–2.5, coriaceous, base not peltate, rounded to obtuse to acute, margin entire to crenate, apex acute to acuminate, upper surface glabrous, lower surface sparsely hairy on midrib and nerves, glabrescent to subglabrous, nerves 7–13 per side, looping close to the margin, with hair-tuft domatia. *Inflorescences* single to 2 together, unisexual or bisexual; peduncle 8–30 mm long; bracts linear-triangular, margin entire, apex acute, upper surface sparsely hairy to scattered, lower surface subglabrous. *Flowers*: pedicels sparsely hairy; sepals: margin entire, apex acute, sparsely hairy outside, subglabrous inside. *Staminate inflorescences* racemes, sometimes panicles, 3–10 cm long, 1–3 flowers per node, nodes per branch 5–30; bracts 2.5–7 by 0.3–0.4 mm; bracteoles absent. *Staminate flowers* 5–6 mm diam.; pedicels 2.8–3.5 mm long; sepals 2 or 3, ovate to obovate, 3.5–4 by 4–4.5 mm, sparsely hairy outside, subglabrous inside; stamens 200–250, glabrous, filaments 0.5–0.8 mm long, thecae ovoid, 0.2–0.3 by 0.2–0.25 mm, connective not widened. *Pistillate inflorescences* racemes and/or developing one terminal flower, 8–10 cm long; bracts 5–10, 6–10 by 0.5–0.8 mm, nodes per branch (when racemes) 3–5, bracteoles 1–3 by 0.2–0.25 mm, early caducous. *Pistillate flowers* 2.8–3.5 mm diam.; pedicels 1–1.5 mm long; sepals 4 or 5, linear-triangular, 5–7 by 0.5–0.8 mm, valvate, ovary 2–2.5 by 2–2.5 mm, densely hairy, 3-locular; style 0.5–2 mm long; stigma 10–25 mm long; staminodes sometimes present. *Fruits* 10–14 by 12–20 mm, outer surface subglabrous, spines 6 or 8 (see note), slightly curved, 3–10 by 0.8–1.5 mm, sparsely hairy; wall 0.8–1 mm thick; column 5–6 by 5–6 mm. *Seeds* 7–7.5 by 5.5–6 by 5.5–6 mm, surface smooth, dull, brown.

Distribution — Mauritius and Réunion.

Habitat & Ecology — Degraded wet forest and marshy ground. Altitude 200–700 m. Flowering and fruiting: November to May.

Note — *Bernardi 14966* has bifurcating spines.

4. *Cordemoya spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen, *comb. nov.* — Fig. 5c, d; Map 1

- Mallotus spinulosus* McPherson, Bull. Mus. Natl. Hist. Nat., B, Adansonia IV, 17 (1995) 170. — Type: *Schatz & Lowry 1301* (holo MO; iso G, K, P, S, WAG, see note), Madagascar, Tamatave, Ambila-Lemaitso.

Shrubs up to 4 m high, monoecious to dioecious. *Indumentum* composed of short simple and sessile peltate-stellate hairs with a central cell. *Stipules* linear-triangular, 2–5 by 0.3–0.6 mm, early caducous, margin entire, apex acute, subglabrous on both sides. *Leaves*: petiole 13–55 by 0.8–1.2 mm, usually grooved, subglabrous; blade ovate to elliptic, 8–14 by 3–6 cm, length/width ratio 2.3–2.6, coriaceous, base not peltate, obtuse to acute, margin entire to crenate, apex acuminate, upper and lower surface (sub)glabrous, nerves 6–9 per side, looping close to the margin, with hair-tuft domatia. *Inflorescences* single, unisexual to bisexual; bracts: margin entire, apex acuminate, hairy or not, upper surface sparsely hairy, lower surface glabrous; bracteoles absent. *Flowers*: pedicels glabrous; sepals: margin entire, apex acute, subglabrous to glabrous outside, glabrous inside. *Staminate inflorescences* racemes, 2–5 cm long, peduncle 3–4 mm long, 1–3 flowers per node, nodes per branch 7–23; bracts triangular, 0.5–0.8 by 0.3–0.4 mm; bracteoles absent. *Staminate flowers* 4.5–5 mm diam.; pedicels 3–4 mm long; sepals 3, ovate to obovate, 1.8–2.2 by 1.8–2 mm, glabrous; stamens 70–90, glabrous, filaments 1–2 mm long, red, thecae ovoid, 0.2–0.3 by 0.2–0.25 mm, brownish red, connective not widened. *Pistillate inflorescences* racemes or developing one terminal flower, 1.5–3 cm long; bracts 4–8, narrowly triangular, 1.2–2 by 0.2–0.4 mm, nodes (when racemes) 4; bracteoles absent. *Pistillate flowers* 1.8–2 mm diam.; pedicels 0.8–1 mm long; sepals 5 or 6, 1.5–2.2 by 0.2–0.3 mm, valvate, sparsely hairy outside, subglabrous inside; staminodes absent; ovary 1.5–1.7 by 1.5–1.7 mm (covered with a resin), 2- or 3-locular; style 0.5–1 mm long; stigma 5–10 mm long. *Fruits* 5–6 by 8–9 mm, green, outer surface subglabrous, spines 4 or 6, slightly curved, 2–4 by 0.8–1 mm, subglabrous; wall 0.3–0.5 mm thick; column 3.5–4 by c. 3 mm. *Seeds* 4–4.2 by 4–4.1 by 4–4.1 mm, surface smooth, shiny, dark brown.

Distribution — Endemic to Madagascar.

Habitat & Ecology — Coastal dune forest, sclerophyllous mountain forest. Altitude: sea level up to 1240 m. Flowering and fruiting: August to May.

Vernacular names — Madagascar: Ampalay rano.

Note — McPherson (1995) lists the following additional isotypes: BR, C, DAV, DSM, EA, ERE, GH, IT, LE, NY, PRE, SRGH, TAN, US.

Subgenus *Diplochlamys*

Subgenus *Diplochlamys* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Diplochlamys Müll. Arg., Flora 47 (1864) 539; Müll. Arg. (1866) 1023. — *Mallotus* Lour. sect.

Diplochlamys (Müll. Arg.) Baill. ex T. Durand (1888) 370; Müll. Arg. ex Pax (1890) 55, isonym.

— Type: *Diplochlamys griffithianus* Müll. Arg. [= *Cordemoya griffithiana* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen].

Hancea Seem. (1857) 409. — *Mallotus* Lour. sect. *Hancea* (Seem.) Pax & K. Hoffm. (1914) 199.

— Type: *Hancea hookeriana* Seem. [= *Cordemoya hookeriana* (Seem.) S.E.C. Sierra, Kulju & Welzen].

Mallotus Lour. sect. *Oliganthae* Airy Shaw 21 (1968) 389. — Type: *Mallotus subpeltatus* Blume [= *Cordemoya subpeltata* (Blume) M. Aparicio].

Branches with slender or conspicuously swollen nodes. *Indumentum* composed of simple hairs and capitate glandular hairs with multicellular stalks. *Stipules* interpetiolar

or axillary, margin entire or serrate. *Leaves* opposite (strongly unequal) or alternate; blade peltate or not, coriaceous to chartaceous, margin entire (rarely serrate), extrafloral nectaries absent, venation pinnate or triplinerved (rarely palminerved), looping close to the margin (rarely ending in the margin). *Inflorescences* axillary or ramiflorous, with one flower per bract. *Staminate inflorescences* racemes or panicles. *Male flowers*: sepals (2 or) 3 or 4, free to basally connate; connective sometimes widened. *Pistillate inflorescences* racemes and/or developing one terminal flower. *Pistillate flowers*: 3- (or 4-)locular. *Fruits* opening loculicidally-septicidally or septicidally-loculicidally, inside glabrous to densely hairy.

Distribution — From Burma to South China throughout Southeast Asia and Malesia to New Guinea.

Section *Diplochlamys*

Section *Diplochlamys* (Müll.Arg.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Diplochlamys Müll.Arg., Flora 47 (1864) 539; Müll.Arg. (1866) 1023. — *Mallotus* Lour. sect.

Diplochlamys (Müll.Arg.) Baill. ex T. Durand (1888) 370; Müll.Arg. ex Pax (1890) 55, isonym.

— Type: *Diplochlamys griffithianus* Müll.Arg. [= *Cordemoya griffithiana* (Müll.Arg.) S.E.C. Sierra, Kulju & Welzen].

Hancea Seem. (1857) 409. — *Mallotus* Lour. sect. *Hancea* (Seem.) Pax & K. Hoffm. (1914) 199.

— Type: *Hancea hookeriana* Seem. [= *Cordemoya hookeriana* (Seem.) S.E.C. Sierra, Kulju & Welzen].

Branches with conspicuously swollen nodes. *Stipules* interpetiolar, margin entire. *Leaves* opposite, strongly unequal, one of each pair stipuliform; blade not peltate, margin entire (rarely serrate), venation pinnate, rarely palminerved, looping close to the margin, rarely ending in the margin. *Inflorescences* axillary. *Staminate inflorescences* racemes or panicles. *Staminate flowers*: sepals (2 or) 3 or 4, free to basally connate. *Pistillate inflorescences* racemes and/or developing one flower terminally. *Pistillate flowers*: sepals (3 or) 4–6; ovary 3- (or 4-)locular. *Fruits* opening septicidally-loculicidally, inside glabrous to hairy, spines with or without terminal glands.

Distribution — From South China throughout Southeast Asia and Malesia to New Guinea.

Descriptions, typification, synonymy, distribution maps, illustrations, and further details of the species of former *Mallotus* sect. *Hancea* can be found in Slik & Van Welzen (2001a). The type material mentioned on the list below was not studied during the present revision.

New combinations in *Cordemoya* sect. *Diplochlamys* (Müll.Arg.) S.E.C. Sierra, Kulju & Welzen:

5. *Cordemoya cordatifolia* (Slik) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus cordatifolius Slik, Blumea 43 (1998) 225. — Type: *PNH* (Gutierrez et al.) 117545 (holo L), Philippines, Samar Island, Mt Sohoon.

6. *Cordemoya eucausta* (Airy Shaw) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus eucaustus Airy Shaw, Kew Bull. 23 (1969) 80. — Type: *S (Sibat ak Luang) 23630* (holo K; iso L), Borneo, Sarawak, Third Division, Bukit Iju, Ulu Arip, Balingian.

7. *Cordemoya grandistipularis* (Slik) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus grandistipularis Slik, Blumea 43 (1998) 227. — Type: *Burley, Tukirin et al. 2021* (holo L; iso CANB, K, US), Indonesia, Sumatra, Riau Province, Tigapulu, 5 km W of Talanglakat.

8. *Cordemoya griffithiana* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Diplochlamys griffithianus Müll. Arg., Flora 47 (1864) 539. — Type: *Griffith KD 4961* (holo K).

9. *Cordemoya hirsuta* (Elmer) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus hirsutus Elmer, Leaflet Philipp. Bot. 7 (1915) 2648. — Type: *Elmer 13480* (holo PNH†; iso K, L, NY), Philippines, Mindanao, Agusan Province, Cabadbaran (Mt Urdaneta).

10. *Cordemoya hookeriana* (Seem.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Hancea hookeriana Seem., Bot. Voy. Herald (1857) 409. — Type: *Champion s.n.* (holo K), Hong Kong.

11. *Cordemoya kingii* (Hook. f.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus kingii Hook. f., Fl. Brit. India 5 (1887) 439. — Type: *King's collector 7414* (holo K; iso G, SING), Malaya, Peak.

12. *Cordemoya longistyla* (Merr.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus longistylus Merr., Philipp. J. Sci. 16 (1920) 560. — Type: *BS (Ramos & Pascasio) 35173* (holo PNH†; iso K), Philippines.

13. *Cordemoya papuana* (J.J. Sm.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus hookerianus (Seem.) Müll. Arg. var. *papuanus* J.J. Sm., Nova Guinea 8, 4 (1912) 787, t. 137. — Type: *Gjellerup 316* (holo L; iso A, BO, K, P, U), Irian Jaya, Bivak Hollandia.

14. *Cordemoya penangensis* (Müll. Arg.) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus penangensis Müll. Arg., Linnaea 34 (1865) 186. — Type: *Wallich 8576* (holo G; iso A, K, P), Malaysia, Pulau Penang.

15. *Cordemoya stipularis* (Meijer ex Airy Shaw) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus stipularis Meijer [Bot. News Bull. Forest Dept., Sabah 7 (1967) 53, anglice] ex Airy Shaw, Kew Bull. 21 (1968) 398. — Type: *Lörzing 14746* (holo K; iso L), Sumatra, N Sibajak, W of Bandarbaru.

16. *Cordemoya wenzeliana* (Slik) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus wenzelianus Slik, Blumea 43 (1998) 229. — Type: *Wenzel 2697* (holo G; iso A, UC), Philippines, Mindanao, Surigao Province, Jubud.

Section Oliganthae

Section Oliganthae (Airy Shaw) S.E.C. Sierra, Kulju & Welzen, *comb. nov.*

Mallotus Lour. sect. *Oliganthae* Airy Shaw, Kew Bull. 21 (1968) 389. — Type: *Mallotus subpeltatus* Blume [= *Cordemoya subpeltata* (Blume) M. Aparicio].

Branches with slender nodes. *Stipules* axillary, margin serrate. *Leaves* alternate; blade peltate, margin entire, venation triplinerved, looping close to the margin. *Inflorescences* ramiflorous to axillary. *Staminate inflorescences* racemes. *Staminate flowers*: sepals 3 (or 4), basally connate. *Pistillate inflorescences* developing one terminal flower. *Pistillate flowers*: sepals 5–7; ovary 3-locular. *Fruits* opening loculicidally-septicidally, inside densely hairy, spines without terminal glands.

Distribution — From Burma to Thailand, Peninsular Malaysia, Sumatra, Borneo and Java.

17. *Cordemoya subpeltata* (Blume) M. Aparicio, *comb. nov.* — Fig. 6; Map 2

Adisca subpeltata Blume, Bijdr. 11 (1826) 610. — *Rottlera subpeltata* (Blume) Baill. (1858) 423. — *Mallotus subpeltatus* (Blume) Müll.Arg. (1865) 189. — Lectotype (selected here): *Blume s.n. 1510* (holo L), Java, Krawong.

Mappa rhynchophylla Miq. (1859) 403. — *Rottlera rhynchophylla* (Miq.) Miq. (1861) 181, 454. — Lectotype (selected here): *Teijsmann HB 3645* (lecto U (see note)), Sumatra, Tubuan, Ogan Ulu.

Mappa acuminatissima Zipp. ex Span. (1841) 349, nom. nud. — Voucher: *Herb. Zippelius* (L?).

Shrubs to small trees up to 15 m high, dbh up to 15 cm, dioecious. *Outer bark* smooth, grey-brown. *Indumentum* composed of short (with a pointed tip), long simple and tufted hairs, and capitate glandular hairs with multicellular stalks¹. *Stipules* narrowly triangular, 5–7 by 1.8–2 mm, caducous to early caducous, margin serrate, hairy, apex acute, sparsely to densely hairy on both sides. *Leaves*: petiole 1–14 cm by 1–1.3 mm, not grooved, glabrescent; blade elliptic to narrowly ovate, 7.5–27 by 6–11 cm, length/width ratio 2.5–3, chartaceous, base subpeltate up to 2 mm, rounded to obtuse, margin entire, apex caudate, upper surface sparsely hairy, glabrescent, lower surface sparsely hairy on midrib and nerves, with few glandular hairs, nerves 5–7 per side, looping close to the margin, with hair-tuft domatia. *Inflorescences* ramiflorous or axillary, single or 2 together, unisexual; peduncle 0.5–1.2 by c. 1 mm; bracts triangular, 1.8–2.5 by 1–1.5 mm, persistent, margin entire, apex acute, upper surface hairy, lower surface densely hairy; bracteoles absent. *Flowers*: pedicels densely hairy; sepals margin entire, apex acute. *Staminate inflorescences* racemes, 0.5–0.8 cm long, nodes per branch 3–6; bracteoles absent. *Staminate flowers* 5–7 mm diam.; pedicels 5–7 mm long; sepals 3 (or 4), ovate, 4.5–5 by 2–2.5 mm, densely hairy outside, subglabrous to sparsely hairy inside; stamens 200–250, glabrous, filaments 2–7 mm long, thecae ellipsoid, 0.5–0.7 by 0.4–0.5 mm, connective widened. *Pistillate inflorescences* developing one terminal flower, 1.5–3 cm long; bracts 4 or 5; bracteoles absent. *Pistillate flowers* c. 5 mm diam.;

1) The presence of glandular hairs in *C. subpeltata* (formerly *M. subpeltatus*) has been ambiguous. Backer & Bakhuizen van den Brink f. (1964) observed their presence, while Airy Shaw (1968, 1974); Welzen, Slik & Bollendorff in Van Welzen et al. (2000), noted their absence. However, recent leaf anatomical studies by Ž. Fišer (in prep.) have confirmed their presence (Fig. 3c).

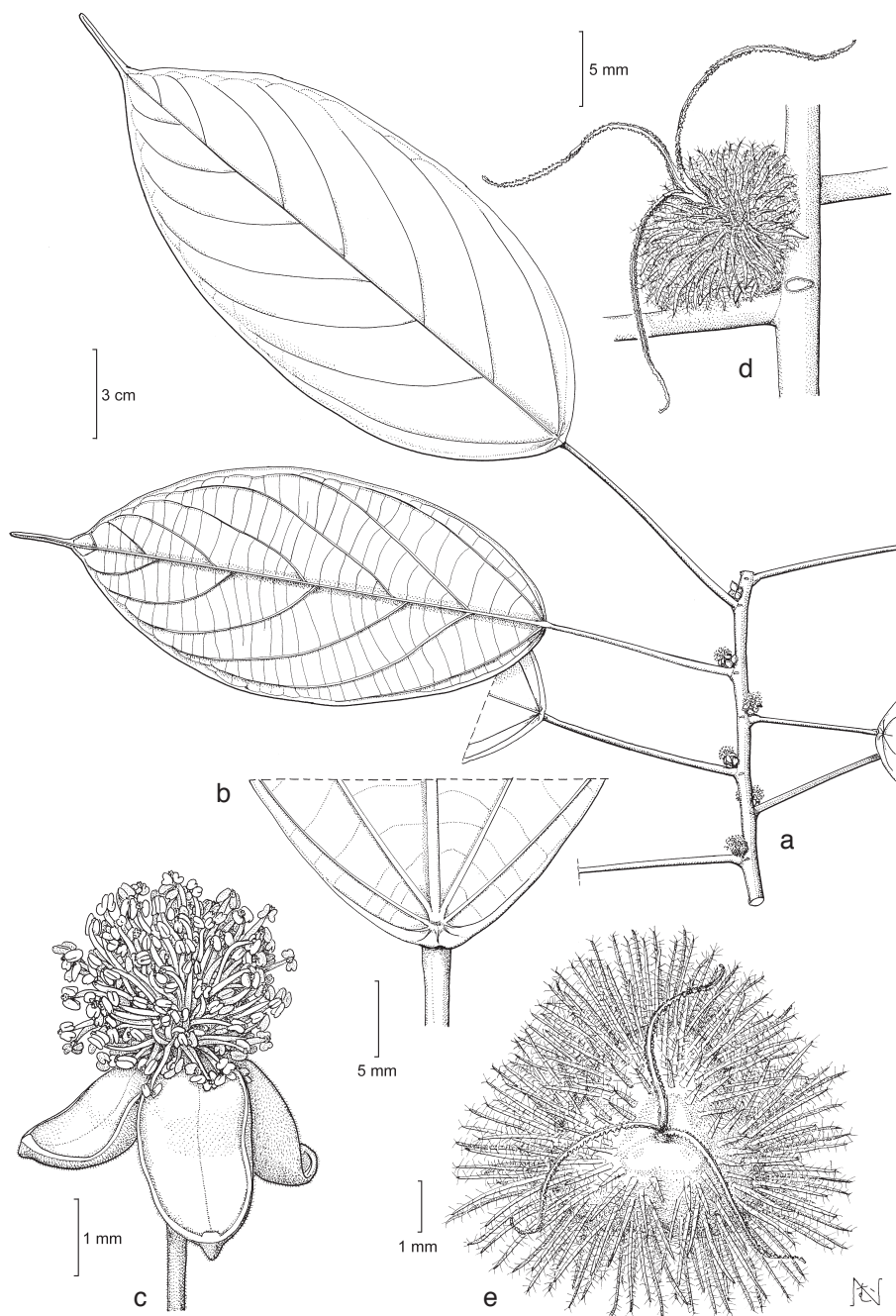
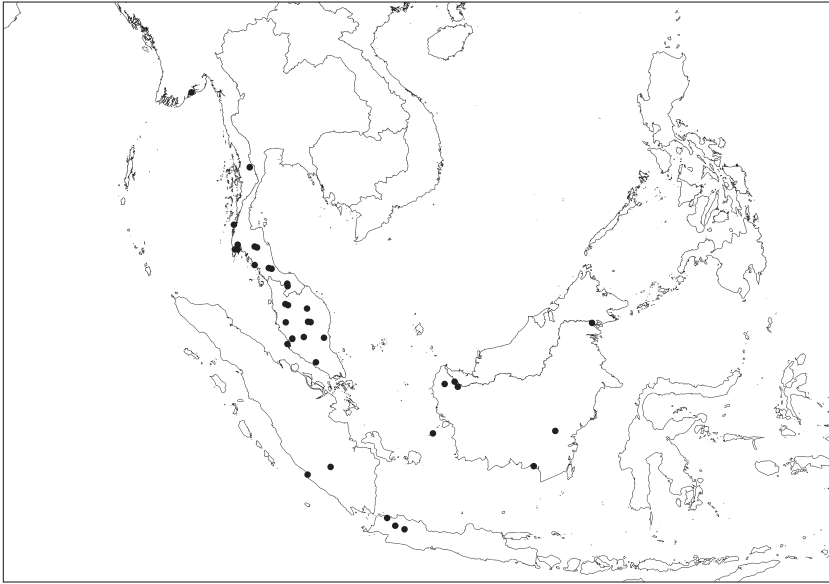


Fig. 6. *Cordemoya subpeltata* (Blume) M. Aparicio. a. Habit with male flowers; b. base of leaf upper surface; c. staminate flower; d. young fruit; e. mature fruit (a–c: Van Beusekom & Phengklai 533, L; d: Prawiroatmodjo 361, BO; e: Maxwell 86-514, A).



Map 2. Distribution of *C. subpeltata* (Blume) M. Aparicio.

pedicels 0.7–2 mm long; sepals 5 or 6, narrowly triangular, 4–6 by 1–1.5 mm, valvate and/or imbricate, hairy outside and inside; staminodes absent; ovary 1–2 by 2–3 mm, 3-locular, densely hairy; style 1–1.5 mm long; stigma 8–12 mm long. *Fruits* 8–15 by 15–20 mm, pale green, outer surface densely hairy, spines 140–170, straight, 6–10 by 1 mm, densely hairy; wall 1–2 mm thick, inside densely hairy; column 9.5–15 by 9–14 mm. *Seeds* 9–12 by 9–11 by 8–10 mm, surface smooth, shiny, dark brown.

Distribution — From Burma to Thailand, Peninsular Malaysia, Sumatra, Borneo and Java.

Habitat & Ecology — Locally in understory of evergreen forest. Altitude: sea level up to 1400 m. Flowering: February to May; fruiting: June to January.

Note — Miquel in 1861 mentions that the Zollinger collection cited in 1859 comes from Sumatra and not from Java. Additionally he mentions two collections by Teijsmann in Sumatra. We did not find any collections with the name *Mappa rhyncophylla* Miq. from Zollinger in Sumatra, therefore, we have appointed as lectotype one of the collections from Teijsmann in Sumatra.

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REFERENCES

- Airy Shaw, H.K. 1968. Malesian and other Asiatic Euphorbiaceae. *Kew Bull.* 21: 379–400.
- Airy Shaw, H.K. 1969. Malesian and other Asiatic Euphorbiaceae. *Kew Bull.* 23: 80, 81.
- Airy Shaw, H.K. 1974. Noteworthy Euphorbiaceae from tropical Asia. *Hooker's Icon. Pl.* 38, 1: 1–3, f. 1.
- Backer, C.A. & R.C. Bakhuizen van den Brink Jr. 1964. *Flora of Java 1*. Noordhoff, Groningen.
- Baillon, H.E. 1858. *Étude générale du groupe des Euphorbiacées*. Masson, Paris.
- Baillon, H.E. 1861. *Species Euphorbiacearum. Euphorbiacées africaines. Deuxième partie, Afrique orientale (Bourbon, Maurice, Madagascar, Zanguebar, etc.)*. *Adansonia* 1: 255.
- Baillon, H.E. 1891a. Liste des plantes de Madagascar. *Bull. Mens. Soc. Linn. Paris* 2: 977–978.
- Baillon, H.E. 1891b. In: A. Grandidier, *Histoire physique, naturelle et politique de Madagascar: Histoire naturelle des plantes* 34: t. 175. Grandidier, Paris.
- Benthams, G. 1880. Euphorbiaceae. In: G. Benthams & J.D. Hooker, *Genera Plantarum* 3: 319–320. Reeve & Co, London.
- Blume, C.L. 1826. *Bijdragen tot de Flora van Nederlandsch-Indië* 11: 610. Lands drukkerij, Batavia.
- Bojer, W. 1837. *Hortus Mauritianus*. Aime Mararot & Co., Mauritius.
- Bojer, W. 1846. In: L. Bouton, *Trav. Soc. Hist. Nat. Maurice 1842–1846*: 151–153.
- Coode, M.J.E. 1982. Euphorbiaceae. In: *Flora des Mascareignes* 160: 50–51. The Sugar Industries Research Institute, Mauritius. L'office de la Recherche Scientifique et Technique outre-mer, Paris; The Royal Botanical Gardens, Kew.
- De Candolle, A.P. 1838. *Revue sommaire de la famille des Bignoniacées*. *Biblioth. Universelle Genève* II, 17: 134, reprinted in *Ann. Sci. Nat., Bot.* II, 11 (1839): 296.
- Durand, T.A. 1888. *Index generum phanerogamorum*: 370. Durand, Brussel, etc.
- Elmer, A.D.E. 1915. Two hundred twenty six new species. *Leaf. Philipp. Bot.* 7: 2648.
- Forster, G. 1786. *Florulae insularum Australium prodromus*. Joann, Christian & Dieterich, Gottingae.
- Hooker, J.D. 1887. *Flora of British India* 5. Reeve & Co., Brook nr Ashford.
- Léandri, J. 1957 ('1956'). Euphorbiaceae malgaches nouvelles récoltées par M.R Capuron. *Bull. Soc. Bot. France* 103: 605–606.
- McPherson, G. 1995. On *Mallotus* and *Deuteromallotus* (Euphorbiaceae) in Madagascar. *Bull. Mus. Natl. Hist. Nat., B, Adansonia* IV, 17: 170.
- Meijer, W. 1967. Euphorbiaceae. Key to about 50 arboreous genera occurring in Sabah. *Bot. News Bull. Forest Dept., Sabah* 7: 53.
- Merrill, E.D. 1920. Notes on Philippine Euphorbiaceae, III. *Philipp. J. Sci.* 16: 559–561.
- Miquel, F.A.W. 1859. *Flora van Nederlandsch Indië*. Van der Post, Amsterdam.
- Miquel, F.A.W. 1861. *Flora van Nederlandsch Indië, Eerste Bijvoegsel*. Van der Post, Amsterdam.
- Müller Argoviensis, J. 1864. Neue Euphorbiaceen des Herbarium Hooker in Kew. *Flora* 47: 539.
- Müller Argoviensis, J. 1865. Euphorbiaceae. *Linnaea* 34: 184–197.
- Müller Argoviensis, J. 1866. Euphorbiaceae tribus Acalypheae. In: A. de Candolle, *Prodromus Systematis Naturalis Regni Vegetabilis* 15, 2: 956–983, 1023. Masson & Fili, Paris.
- Pax, F.A. 1890. Euphorbiaceae. In: A. Engler, *Die natürlichen Pflanzenfamilien* 3, 5: 53–55. Engelmann, Leipzig.
- Pax, F.A. & K. Hoffmann. 1914. Euphorbiaceae–Acalypheae–Mercurialinae. In: A. Engler, *Das Pflanzenreich* IV.147.vii: 145–212, 396–397. Engelmann, Leipzig.
- Roxburgh, W. 1832. *Flora Indica* 3. Thacker & Co., Calcutta.
- Seemann, B.C. 1857. *Flora of the Island of Hong Kong. The Botany of the Voyage of H.M.S. Herald*: 409–410. Reeve, London.
- Slik, J.W.F. 1998. Three new Malesian species of *Mallotus* section *Hancea* (Euphorbiaceae). *Blumea* 43: 225–232.
- Slik, J.W.F. & P.C. van Welzen. 2001a. A taxonomic revision of *Mallotus* sections *Hancea* and *Stylanthus* (Euphorbiaceae). *Blumea* 46: 3–66.
- Slik, J.W.F. & P.C. van Welzen. 2001b. A phylogeny of *Mallotus* (Euphorbiaceae) based on morphology: Indications for a pioneer origin of Macaranga. *Syst. Bot.* 26: 786–796.
- Smith, J.J. 1912. Euphorbiaceae. *Nova Guinea* 8, 4: 779–796, t. 130–142.

- Spanoghe, J.B. 1841. Prodrum Florae Timorensis. Linnaea 15: 349.
 Steudel, E.T. 1841. Nomenclatur Botanicus 2: 459. J.G. Cottae, Stuttgartiae & Tubingae.
 Van Welzen, P.C., R.M.A.P. Haegens, J.W.F. Slik, S.M. Bollendorff, S. Dressler & H.-J. Esser. 2000.
 Checklist of the genera of Thai Euphorbiaceae. Thai Forest Bull., Bot. 28: 93–111.
 Webster, G.L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.
 Willdenow, C.L. 1805. Species Plantarum, ed. 4, 1. Nauk, Berlin.

IDENTIFICATION LIST FOR SECTION CORDEMOYA AND OLIGANTHAE
 (for Sect. Diplochlamys see Slik, 2001a)

The numbers behind the collector numbers refer to the following taxa:

- 1 = *C. acuminata* (Baill.) Baill.
 2 = *C. capuronii* (Léandri) S.E.C. Sierra, Kulju & Welzen
 3 = *C. integrifolia* (Willd.) Baill.
 4 = *C. spinulosa* (McPherson) S.E.C. Sierra, Kulju & Welzen
 17 = *C. subpeltata* (Blume) M. Aparicio

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