BLUMEA 44 (1999) 149–215

# A PARTIAL REVISION OF THE HIPPOMANEAE (EUPHORBIACEAE) IN MALESIA

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## SUMMARY

The Hippomaneae (Euphorbiaceae) are revised for Malesia. Only *Excoecaria* and *Homalanthus* are excluded. A key to all Malesian genera is provided. The generic concepts applied differ markedly from previous treatments for the region with the following genera accepted: *Balakata*, *Falconeria*, *Gymnanthes*, *Microstachys*, *Sapium*, *Shirakiopsis*, *Stillingia* and *Triadica*. All of these genera show peculiarities in biogeography and ecology, which are discussed.

Among these genera only *Stillingia* is kept as traditionally used. *Balakata* (based on *Sapium* sect. *Pleurostachya*) and *Shirakiopsis* (based on *Sapium* sect. *Parasapium* but excluding its type) are described as new genera; *Falconeria*, *Microstachys* and *Triadica* are re-established as distinct genera having been treated as *Sapium* sect. *Falconeria*, *Sebastiania* sect. *Microstachys* and *Sapium* sect. *Triadica* for a long time. *Gymnanthes* is cited for the first time in Malesia based on two former species of *Sebastiania*, and the African genus *Duvigneaudia* is united with it. *Sapium* and *Sebastiania* are no longer considered as indigenous to Malesia, with *Sapium* (= *Sapium* sect. *Americana*) formerly being cultivated.

Altogether 13 species are accepted in the present revision. No new species are described, but only two of the well-known names are accepted as previously used (*Sapium glandulosum*, *Stillingia lineata* subsp. *pacifica*). Numerous new combinations are proposed in the present revision: *Balakata baccata*, *Balakata luzonica*, *Gymnanthes borneensis*, *Gymnanthes inopinata*, *Gymnanthes remota*, *Shirakiopsis indica*, *Shirakiopsis sanchezii*, *Shirakiopsis virgata*. Several other, previously available but uncommon names are re-introduced, namely *Falconeria insignis*, *Microstachys chamaelea*, *Triadica cochinchinensis* (the correct name for the former *Sapium discolor*), and *Triadica sebifera*. Finally, two new synonyms are proposed by uniting *Sebastiania lancifolia* with *Gymnanthes borneensis*, and *Sapium plumerioides* with *Stillingia lineata* subsp. *pacifica*. Lectotypes are selected for eight names.

***Key words***: Euphorbiaceae, Hippomaneae, Malesia.

## INTRODUCTION

The tribe Hippomaneae A. Juss. ex Bartl. of the Euphorbiaceae consists of c. 30 genera with c. 300 species (Esser, 1994). It is sufficiently well characterized by elongate, monoecious thyrses, large, biglandular floral bracts, inclinate floral buds, flowers without petals and discs and with comparatively small sepals. Its diversity is centered in the Neotropics, with fewer taxa in Malesia.

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For many parts of Malesia, the species have been quite recently revised by Airy Shaw (e.g., 1975), who followed predominantly the generic concepts of Pax & Hoffmann (1912). These were based mostly on floral characters. The highly reduced flowers of the Hippomaneae, however, are quite uniform, in contrast to the very diverse leaves and fruits. For this reason, the generic limits in the tribe were revised in a recent conspectus (Esser, 1994). This conspectus is applied now to the Malesian taxa, resulting in many changes of the generic concepts. These changes have been corroborated by a recent phylogenetic analysis of the Malesian Hippomaneae (Esser et al., 1998). Some of these had already been discussed by Webster (1994), although not effected.

The various revisions of Airy Shaw included the following genera of Malesian Hippomaneae: *Excoecaria* L., *Homalanthus* A. Juss., *Sapium* Jacq., *Sebastiania* Spreng., *Stillingia* Garden ex L. The genus *Hura* L. has often been allied to the Hippomaneae (e.g., by Pax & Hoffmann, 1912), but separated into the tribe Hureae Dumort. by Webster (1994).

From these genera, *Excoecaria* is currently being revised by Djarwaningsih (in prep.), *Homalanthus* (the largest genus) has been revised by the author and was published separately (Esser, 1997), and *Hura* will remain excluded from the tribe. [N.B. *Homalanthus* will probably be conserved against the older spelling *Omalanthus* that was still used by Esser, 1997 (Brummitt, pers. comm.)] One isolated species of uncertain affinity, *Excoecaria (?) myrioneura* Airy Shaw, does not fit into any genus of the Hippomaneae but can probably be excluded from the Hippomaneae because of its infructescence (Esser et al., 1998; flowers still unknown).

The remaining genera are treated in the present revision. Whereas *Stillingia* remains unchanged, *Sapium* and *Sebastiania* are split into several genera; the 'true' *Sapium* and *Sebastiania*, with Neotropical types, are separated from the indigenous Malesian taxa. A key to all Malesian genera will be provided.

## GENERAL DESCRIPTION OF MALESIAN HIPPOMANEAE

A general description of Malesian Hippomaneae can be summarized as follows:

Trees to herbs, often (always?) with sympodial branching. Monoecious (although pistillate flowers may be lacking sometimes and then dioecy may be assumed), very rarely dioecious (*Excoecaria agallocha*). *Latex* present, white. *Indumentum* absent or consisting of multicellular uniseriate hairs. *Bark* smooth to variously fissured, rarely with spines. *Stipules* quite small to large, caducous. *Leaves* simple, alternate, sometimes crowded, rarely opposite in *Excoecaria*; petiole distinct, canaliculate, glandless or apically glandular; blade symmetric, margin entire or serrate; venation pinnate, basal pair of side veins not or slightly different; glands nearly always present, on the adaxial or abaxial base of the blade, and/or abaxially on the blade close to or remote from the margin. *Inflorescences* terminal or axillary, elongated thyrses, simple or compound, many-flowered, 1–20 mm diam., uni- or bisexual. *Bracts* spirally arranged, squamaceous and elliptic to triangular to ovate, (0.4–)1.5 mm long, covering floral buds, usually few basal ones subtending single pistillate flowers and sometimes caducous, usually many distal ones subtending cymules of several staminate flowers, persistent and with one (rarely divided) pair of glands, rarely glandless. Staminate part caducous after flowering. *Staminate cymules* (1–)3–18-flowered. *Staminate flowers* inclinate in bud, nearly sessile to distinctly pedicellate, pedicel articulate; radially symmetric to bilateral to zygomorphic (*Homalanthus*); petals absent; sepals free or fused to a different degree, glandless; disc and pistillode absent; stamens 2–4(–20), free or slightly connate at base, filaments present, anthers basifixed, opening latrorsely to extrorsely with longitudinal slits, connective present. *Pistillate flowers* inclinate in bud, solitary in the axil of each bract, sometimes surrounded by staminate flowers; petals absent; sepals 2–6, triangular, entire; disc and staminodes absent; ovary 2–3-locular, smooth or with excrescences, with one descending epitropous ovule per locule; style 1, stigmata 2–3, undivided (sometimes bifurcate in *Homalanthus*), recurved. *Fruits* 3–31 mm long, indehiscent or dehiscent in various ways, outside smooth or with excrescences, with 1–3 seeds. *Seeds* pendant, anatropous.

## KEY TO THE MALESIAN GENERA OF HIPPOMANEAE

1a. Herbs to small shrubs up to 90 cm tall. Leaves minutely serrate, up to 12 mm wide. Fruits with 6 rows of spiny appendages ............ **4. Microstachys**

b. Shrubs to trees. Leaves entire or distinctly serrate, at least 15 mm wide. Fruits without rows of spiny appendages, smooth or rarely with 6 pairs of hooks ('muricate') ............................................ 2

2a. Leaves shallowly to distinctly serrate, not whitish beneath ............... 3

b. Leaves entire, beneath whitish or not ................................ 7

3a. Young leaves and inflorescences with yellowish hairs. Staminate flowers distinctly (1–3 mm) pedicellate. Fruits with pedicel of 8–30 mm, with massive pericarp at least 2 mm thick .................................. **6. Shirakiopsis**

b. Plants completely glabrous. Staminate flowers sessile to shortly (less than 1 mm) pedicellate. Fruits with pedicel of less than 5 mm, with thin (sometimes fleshy) pericarp less than 2 mm thick .................................. 4

4a. Pistillate and staminate flowers in separate, elongate thyrses, often flowering on leafless twigs. Pistillate flowers/fruits at least 20 per inflorescence/infructescence. Fruits irregularly dehiscent; seeds with pale fleshy surface ..... **2. Falconeria**

b. Pistillate and staminate flowers in one elongate thyrse (although sometimes only one sex present), flowering on leafy twigs. Pistillate flowers/fruits less than 20 per inflorescence/infructescence. Fruits regularly dehiscent; seeds with dry or reddish-fleshy surface ........................................ 5

5a. Leaves without glands on petiole apex or lamina base visible from above. Staminate flowers 1–3 per bract, with free sepals and 3 stamens. Seeds dry, carunculate; caruncle separating from seed, remaining at central columella and leaving a tiny scar on seed top ........................................ ***Excoecaria***

b. Leaves with glands on petiole apex or lamina base visible from above. Staminate flowers 4–18 per bract, with fused sepals and 2 stamens. Seeds with reddish-fleshy surface or dry and carunculate, caruncle not separating from seed .... 6

6a. Plants with succulent stems. Petiole with a quite inconspicuous pair of glands on the junction with the lamina base. Fruits with woody, indehiscent base that remains as a tricornute structure after dehiscence; seeds dry. Indigenous .. **7. Stillingia**

b. Plants not succulent. Lamina base adaxially glandless but petiole apex with a pair of glands usually separated from the lamina. Fruits without woody indehiscent base, leaving an alate columella without a tricornute base; seeds with reddish arilloid. Only in cultivation ............................... **5. Sapium**

7a. Leaves with gland(s) on petiole apex or lamina base visible from above ... 8

b. Leaves without gland(s) on petiole apex or lamina base visible from above 10

8a. Stipules up to 2 mm long. Leaf blades with tertiary venation reticulate. Staminate flowers radially symmetric with 2 or 3 stamens. Fruits 3-locular; seeds dry and brownish or whitish with sarcortesta ............................... 9

b. Stipules 5–200 mm long. Leaf blades with tertiary venation usually percurrent, only in narrow leaves rarely reticulate. Staminate flowers bilateral or zygomorphic with (4–)6–20 stamens. Fruits 2(–3)-locular; seeds with reddish arilloid .... ............................................ ***Homalanthus***

9a. Leaf blades with lowermost pair of veins originating at lamina base. Monoecious. Staminate flowers (3–)5–8 per bract. Seeds with whitish sarcotesta **8. Triadica**

b. Leaf blades with lowermost pair of veins originating above lamina base. Dioecious. Staminate flowers 1–3 per bract. Seeds dry and brownish ........... ........................................ ***Excoecaria agallocha***

10a. Stipules 5–200 mm long. Leaf blades with tertiary venation usually percurrent, only in narrow leaves rarely reticulate. Inflorescences and infructescences terminal, simple. Fruits tardily dehiscent; seeds with reddish arilloid ......... ............................................ ***Homalanthus***

b. Stipules up to 2 mm long. Leaf blades with tertiary venation reticulate to rarely percurrent. Inflorescences and infructescences terminal and compound or axillary and simple to compound. Fruits regularly dehiscent or indehiscent; if dehiscent, with dry seeds ............................................ 11

11a. Staminate flowers 5–9 per bract. Fruits 1- or 2-seeded, fleshy-indehiscent .. ............................................ **1. Balakata**

b. Staminate flowers 1–3 per bract. Fruits 3-seeded, dry, dehiscent ........... ............................................ **3. Gymnanthes**

## 1. BALAKATA

### INTRODUCTION

The history of the two relevant species is quite different, and up to now they were never classified as being closely related.

*Balakata luzonica*, with its 1-seeded globose berries very untypical for Euphorbiaceae, was described as a species of the Myricaceae (*Myrica luzonica*, Vidal, 1883) and of the Icacinaceae (*Urandra elliptica*, Merrill, 1910), but these errors were soon recognized by Rolfe (1886) and Merrill (1920), respectively. *Myrica luzonica*, the oldest available specific epithet, was supposed to be a *Sapium* by Rolfe (1886) and was formally transferred by Merrill (1920). A few years earlier, Merrill (1906), when studying the first available flowering specimens, described the same species as *S. lateriflorum*. The latter name, however, was illegitimate, being a later homonym of the

Neotropical *S. lateriflorum* Hemsl., and was replaced by Pax & Hoffmann (1912) with *S. merrillianum.*

Pax & Hoffmann (1912) were the first (and only) authors discussing the relationships of this species in more detail. They considered it to be quite isolated within *Sapium* and erected a separate, monotypic section (*Pleurostachya*) for it, most closely related to *Falconeria* Royle because of the globose, fleshy fruits.

*Balakata baccata* differs most obviously from *B. luzonica* by its bilobed 2-seeded fruits; therefore it has always been recognized as an Euphorbiacea. It was described by Roxburgh (1832) as *Sapium baccatum.* Wight (1853) contributed the first illustrations under the name *S. populifolium*, a name that had already been used by Wallich (1847; based on different collections) as distinct from *S. baccatum.* Wight recognized even on the text pages of the same book that both were identical, although he could not change the figure captions. One year later, Griffith's description of *Excoecaria affinis* was published (1854); it had been prepared many years earlier and was based on the same specimen as Wight's illustration. Finally, Miquel (1861) described *Stillingia paniculata* from another collection. The synonymy of all of these names was established by Hooker (1888).

*Sapium baccatum*, together with the whole genus *Sapium*, was transferred to *Stillingia* by Baillon (1858, but without publishing the combination under *Stillingia*) and to *Excoecaria* by Müller Argoviensis (1866). Kurz (1877) listed it under *Carumbium* Reinw. (= *Homalanthus*), as he also did with several other, not very closely related species. Since Hooker (1888), however, its position within *Sapium* was not questioned any more; only Kruijt (1996) moved it to *Excoecaria.* Pax & Hoffmann (1912) placed it in the section *Triadica* (Lour.) Müll.Arg. of *Sapium.* To fit their diagnosis of the section, they added the sentence "semina in columella centrali longe adhaerentia" to the species description, which is, however, hardly applicable for its indehiscent fruits. In this way, *Balakata baccata* was separated from *Balakata luzonica*, and remained so until now.

## CHARACTERS

### Vegetative characters

The genus is characterized by the quite remarkable leaf glands: adaxial ones are absent, but abaxially near the base a pair of quite large, more or less circular glands is visible without magnification (Fig. 1b). Additional marginal glands may be present or absent, but are always conspicuously smaller.

Otherwise, the leaves of both species show several differences, e.g., in petiole (much longer in *B. baccata*), shape (ovate in *B. baccata*, elliptic in *B. luzonica*), and abaxial surface (often whitish in *B. baccata*, always green and shining in *B. luzonica*). Additionally, the basal glands, although present and distinct in both species, are larger in *B. baccata.*

### Inflorescences and flowers

The regularly branched thyrses are unique in Malesian Hippomaneae and allow easy recognition of the genus in flowering and fruiting stage. Other notable characters of the inflorescences are the sterile region at the base of each thyrsal branch (peduncle, absent in related genera), the large and conspicuous, undivided bracteoles of the staminate cymules, and the bracteal glands, which are quite irregularly shaped and decurrent along the main axis. The individual flowers are hardly diagnostic and plesiomorphic in many characters. The bilocular ovaries and the constantly bistaminate male flowers, however, may be noted.

Again, the differences between the species are remarkable. Very characteristic for *B. luzonica* is the sterile peduncle of each thyrse branch, which is densely covered with distichously arranged sterile bracts (in contrast to the spirally disposited fertile bracts; Fig. 1d). *Balakata baccata* lacks this, but is characterized by the, at least superficially, fractioned and multiple bracteal glands.

### Fruits and seeds

Like in many other Hippomaneae, the fruits are most typical for the genus. In *Balakata*, they are indehiscent, fleshy, uni- or bilocular berries, and unique among the fruits of the c. 30 genera that constitute the Hippomaneae.

In *B. luzonica*, only one seed develops, so that globular 1-seeded berries with a nearly terminal style result (Fig. 1e, f). In *B. baccata*, usually both seeds develop, and the 2-seeded berries are flattened and sulcate. Not rarely, however, one seed aborts; in this case the resulting globular, 1-seeded berries have a distinctly lateral style.

## BIOGEOGRAPHY AND RELATIONSHIPS

*Balakata* is one of the few genera of Hippomaneae restricted to Asia, and the only one nearly endemic to Malesia (Map 1). Its relationships within the whole tribe cannot be elaborated sufficiently yet. Compound thyrses, present also in some African (*Anomostachys* Baill.) and Neotropical (*Mabea* Aubl., *Senefeldera* Mart.) genera, may have arisen independently as parallelisms. Its relationships within the Malesian Hippomaneae are elaborated in a separate paper (Esser et al., 1998). The bistaminate flowers agree with those of *Falconeria*, *Sapium*, and *Stillingia*, but leaves and fruits are quite different in these genera. In some vegetative characters, *Triadica* shows the closest similarities to *Balakata* (long petioles, similar stipules, entire leaves with few side veins and submarginal leaf glands).

The genus is clearly separated into two vicariant species (Map 1), one in W Malesia, hardly reaching India (*B. baccata*), and one in E Malesia, not reaching Australia (*B. luzonica*). Their diaspores are markedly zoochorous, and their distribution seems to be restricted by the ecological requirements of the inhabited forest types.

### **Balakata** Esser, *gen. nov.*

Genus novus glaber foliis distincte petiolatis integris adaxialiter eglandulosis sed abaxialiter glandulis submarginalibus instructis earundem basalibus insigniter auctis, thyrsis compositis, cymulis masculinis 5–9-floris bracteolis membranaceis indivisis ornatis, floribus masculinis pedicellatis, sepalis connatis, staminibus 2, ovariis 2-locularibus, fructibus distincte pedicellatis 1–2-spermis indehiscentibus bacciformibus pericarpio carnoso, aliter cum characteribus tribus Hippomanearum. — Type: *Balakata luzonica* (S. Vidal) Esser, based on *Myrica luzonica* S. Vidal.

*Sapium* sect. *Pleurostachya* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 243; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 202 ('*Pleurostachys*'). — Type: *Sapium merrillianum* Pax & K. Hoffm. [= *Balakata luzonica* (S. Vidal) Esser].

Trees. Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* absent. *Stipules* triangular, 1.5–2 mm long, entire, glandless. *Leaves* regularly alternate; petiole short to long (1–9.5 cm long), much shorter to nearly half as long as blade, glandless; blade ovate to oblong to elliptic, 3.5–11 cm wide, base attenuate to acute to slightly cordate, margin entire, apex acuminate to cuspidate, glandless above, below smooth or pale-papillate and with a row of several marginal to submarginal glands, basal ones conspicuously enlarged and usually visible without magnification, rarely absent, secondary veins distinct, arching but not to hardly joined towards the margin, basal ones not differing, intersecondary veins present, tertiary veins percurrent to reticulate, smaller veins reticulate. *Inflorescences* terminal and axillary, yellowish, once to twice branched, each branch with a distinct sterile basal region, staminate part 20–70 by 2–7 mm; pistillate and staminate flowers in same inflorescence. *Bracts of staminate cymules* triangular, apically acute, at base with a pair of irregularly pillow-shaped to slightly flattened, sometimes fragmented glands touching the axis of the inflorescence and slightly decurrent. *Staminate cymules* 5–9-flowered; bracteoles present, membranous, undivided, entire. *Staminate flowers* with pedicel elongating when flowering, but present also in bud; calyx basally fused with usually 2 irregular, acute tips; stamens 2, filaments slightly longer than anthers. *Pistillate flowers* (1–)3–13 at base of staminate thyrse or absent; pedicel quite short but distinct (0.5–5 mm long); calyx with 2 sepals, triangular to elliptic, slightly fused at base, entire, glandless; ovary 2-locular, smooth; style short, stigmata 2, undivided, glandless. *Fruits* with distinct pedicel (1.5–27 mm long); 1–2-seeded, smooth, fleshy berries, indehiscent. *Seeds* without caruncle, with a thin sarcotesta and a stony seed coat.

Distribution — Two vicariant species, distributed from NE India to Vietnam and throughout Malesia, but unknown from Java, the Lesser Sunda Islands, and parts of New Guinea.

Note — The name refers to the official Philippine name for one of the species, *balakat gubat*. This means 'shoulder tree'. Thanks are due to C. Ridsdale for providing this translation.

## KEY TO THE SPECIES

1a. Leaves ovate to elliptic, below often whitish, petiole (2.5–)3.5–9 cm long. Fruits 2-seeded and sulcate, rarely 1-seeded and globose but then with lateral style .. .......................................................... **1. B. baccata**

b. Leaves oblong to elliptic, below not whitish, petiole 1–2.2 cm long. Fruits 1-seeded, globose, with apical style .................................. **2. B. luzonica**

### 1. **Balakata baccata** (Roxb.) Esser, *comb. nov.* — Map 1

*Sapium baccatum* Roxb. [Hort. Bengal. (1814) 69, nomen] Fl. Indica ed. 1832, 3 (1832) 694; Wight, Icon. Pl. Ind. Orient. 5, 2 (1853) 6; Baill., Étude Euphorb. (1858) 513; Müll. Arg., Linnaea 32 (1863) 121; Hook.f., Fl. Brit. India 5 (1888) 470; G. Watt, Dict. Econ. Prod. India 6, 2 (1893) 471; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 295; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 240; Ridl., Fl. Malay Pen. 3 (1924) 315; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 395, 400; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1960; Corner, Ways. Trees Malaya 1 (1940) 276; K. Heyne, Nutt. Pl. Indon. ed. 3, 1 (1950) 960; Wyatt-Sm., Malay. For. Rec. 23, III-7 (1964) 14; Malay. For. Rec. 17 (1965) 51, 113, 345; Medway, Biol. J. Linn. Soc. 4 (1972)

131, 138, 142; Airy Shaw, Kew Bull. 26 (1972) 329; Whitmore, Tree Fl. Malaya 2 (1973) 128, 129; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 191; Kew Bull. 36 (1981) 341; Ng, Malay. For. Rec. 34 (1991) 83, f. 65A; Verheij & Coronel (eds.), Pl. Res. SE Asia (PROSEA) 2. Edible fruits and nuts (1991) 382; P.H. Hô, Câyco Viêtnam 2, 1 (1992) 355; I.M. Turner, Gard. Bull. 47 (1995) 231. — *Excoecaria baccata* (Roxb.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1211; Kruijt, Biblioth. Bot. 146 (1996) 83. — *Carumbium baccatum* (Roxb.) Kurz, Forest Fl. Burma 2 (1877) 412. — Type: *Roxburgh s.n.* (A, P; Icones Roxburghianae 2397), Bangladesh, Silhet.

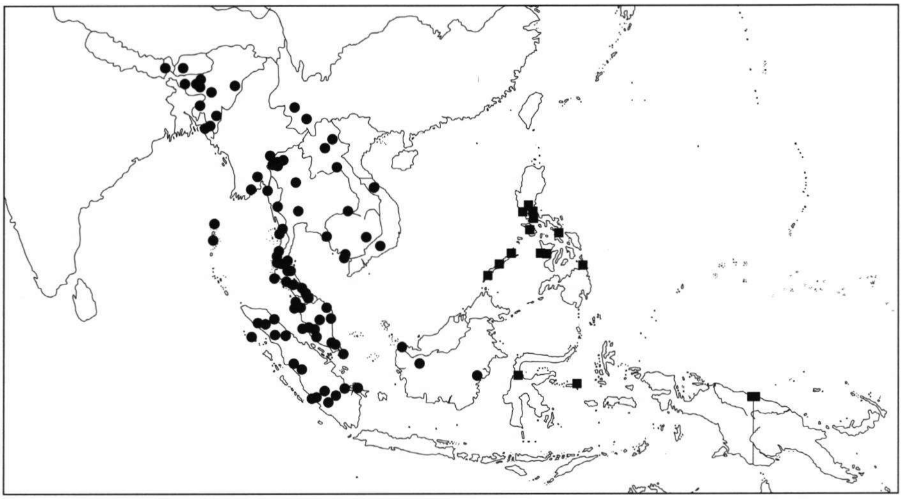
*Sapium populifolium* Wight, Icon. Pl. Ind. Orient. 5, 2 (1853) t. 1950, f. 2. — *Excoecaria affinis* Griff., Not. Pl. Asiat. 4 (1854) 486, nom. superfl. & illeg., non Endl. [Prodr. Fl. Norfolk. (1833) 83]; Müll.Arg. in DC., Prodr. 15, 2 (1866) 1223; Hook.f., Fl. Brit. India 5 (1888) 470. — Type: *Griffith 704* or *706* (GH, K, TCD), Burma, Mergue.

*Stillingia paniculata* Miq., Fl. Ind. Bat. Suppl. 1 (1861) 183, 461. — Lectotype (proposed here): *Teijsmann HB 3677* (holo U; iso K), Sumatra, Palembang, inter Kebus et Labat.

Tree, up to 26 m high, stem up to 60 cm diam., bole bending and twisting with many knobs, with irregular buttresses up to 4 m high, crown densely leaved. Evergreen. *Bark* dirty yellow when living, brown to dark grey when dead, with deep longitudinal cracks and fissures; inner bark fibrous. *Sapwood* cream to white, soft, with a sour to sweet smell. *Twigs* usually in whorls. *Stipules* c. 1.5 by 0.5 mm, early caducous and rarely seen. *Leaves* pinkish brown when young, withering yellow; petiole (2.5–)3.5–9.5 cm long; blade mostly ovate, rarely elliptic, (8–)10–22 by 4–11 cm, base acute to obtuse, rarely attenuate or cordate, not auriculate, margin not revolute, apex acuminate, upper surface hardly shining, lower surface pale-papillate, with (1–)3–12 glands per side, 0.4–0.8(–1.5) mm diam. and 0–1(–3) mm distant from margin, basal glands 1.5–2.25 mm diam., usually 4–10 mm above base of blade and sometimes touching midrib, secondary veins 10–16 pairs, angle with midrib initially 75–85°, but soon becoming 45–70°, tertiary veins conspicuous, percurrent. *Inflorescences* in terminal whorls and in the axils of few uppermost leaves, each branch with an initial covering of numerous elliptic, 2–3 mm long, caducous bracts, later with a sterile basal region 8–12 mm long with no to few bracts, staminate part 20–70 by 2–4 mm. *Bracts of staminate cymules* c. 0.6 mm long, their glands 1–1.75 by 0.5–1 mm, at least superficially disintegrating into numerous nearly circular fragments. *Staminate cymules* c. 5-flowered. *Staminate flowers:* pedicel 0.5–1.5 mm long; calyx c. 0.5–1 mm long; stamens with filaments 0.4–0.6 mm long when flowering, anthers 0.25–0.5 mm long. *Pistillate flowers* 10–13 per thyrse branch or sometimes absent; pedicel 0.6–1 mm long; calyx c. 1 mm long, connate at base; ovary c. 1.5 mm long; style 0.1–0.5 mm long, stigmata 0.75–2 mm long. *Fruits:* pedicel 1.5–4 mm long; (1–)2-seeded, nearly circular in shape, 8–9 by 9–11 mm, flattened with smallest diameter of 4–5 mm, if 2-seeded sulcate, if 1-seeded with lateral style. *Seeds* c. 5 by 4.5 mm, blackish.

Distribution — E Himalaya, India (Sikkim) and Bangladesh to Indochina and SW China (only known from Yunnan), Andamans, and in W Malesia: Peninsular Malaysia (excl. Singapore), Sumatra, Borneo (Kalimantan).

Habitat & Ecology — Found in primary and disturbed Dipterocarp forest, bamboo forest, secondary forest, mixed deciduous forest, also along streams and on hills and slopes; in Selangor (Malaya) it is very common and forms, together with *Endospermum malaccense* Müll.Arg., a distinctive forest community of the late succession, poor in Dipterocarps (Wyatt-Smith, 1964). Soil: brown and yellow clay and loam, sandy loam, over limestone, granitic and volcanic bedrock. Altitude 15–1800 m. Flowers collected



Map 1. Distribution of *Balakata baccata* (Roxb.) Esser (●), and *B. luzonica* (S. Vidal) Esser (■).

in Dec.–Sept.; fruits collected in Jan.–Oct. According to Medway (1972) the trees do not flower annually, and fruit set is rare in the Malayan population studied. The flowers exude a sweet smell (Griffith, 1854).

Vernacular names — Sumatra: bedi, damar kulihap, doelpak dollong, handoelpak, ludai, ludai kantijl. Simaloer Is.: banai delok, banai etem.

Uses — Used as a timber tree and as a wayside plant. The wood is not very durable. The fruits are mealy and sweet and in Sumatra sometimes used for flavouring (Burkill, 1935; Heyne, 1950).

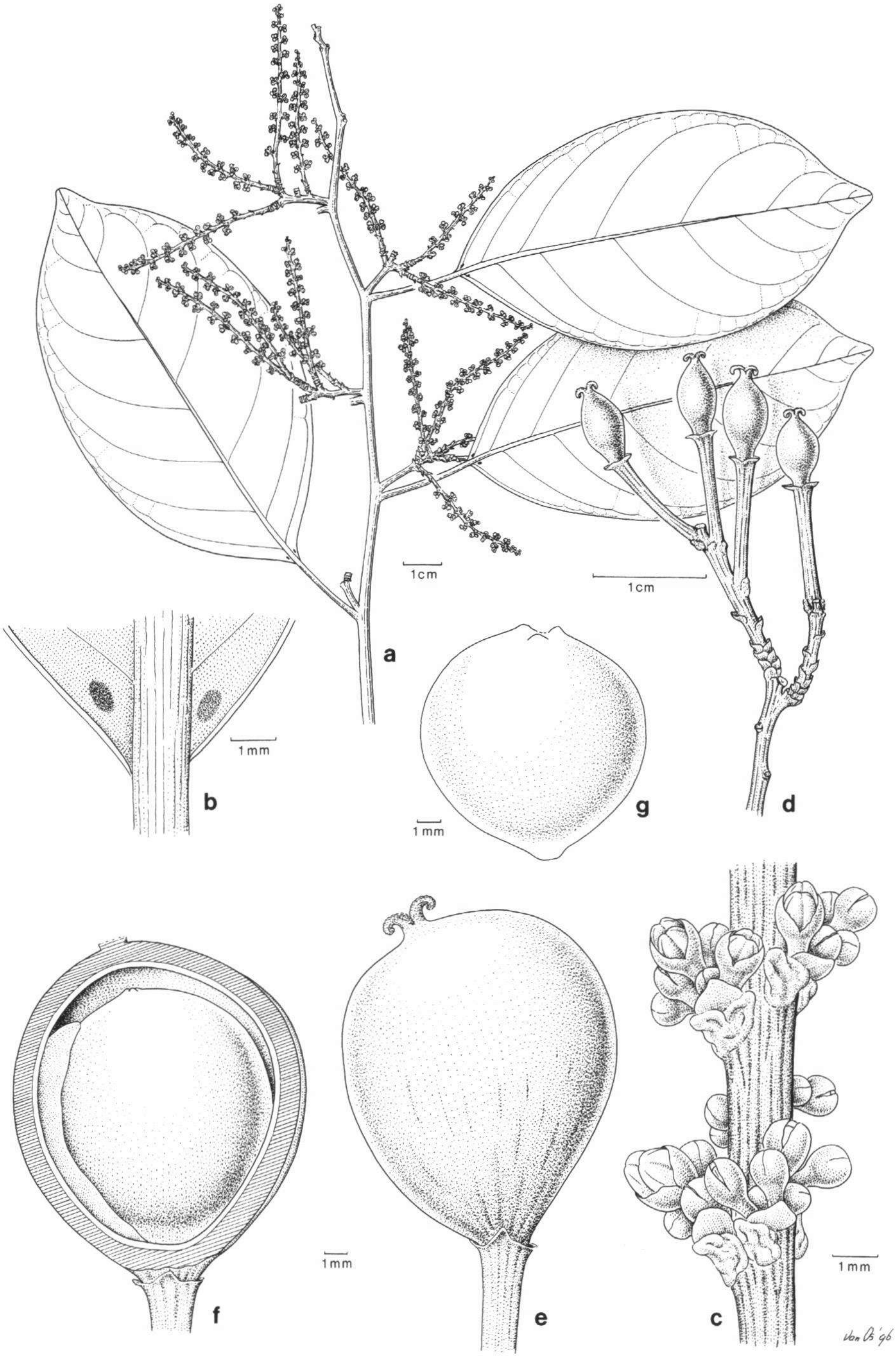
Note — Two types of inflorescences can be found: purely staminate ones, regularly branched with long branches (each usually 5–7 cm long), and bisexual ones, hardly branched and with shorter branches (each 2–3 cm long); in the last case, the basal pistillate part of the thyrse usually exceeds the staminate part in length.

### 2. Balakata luzonica (S. Vidal) Esser, *comb. nov.* — Fig. 1, Map 1

*Myrica luzonica* S. Vidal, Sin. Gen. Pl. Leños. Filip. Atlas (1883) 40, t. 90 B; Rolfe, J. Linn. Soc., Bot. 21 (1886) 294; Backer, Fl. Males. I, 4 (1951) 279. — *Sapium luzonicum* (S. Vidal) Merr., Philipp. J. Sci. 16 (1920) 577; Enum. Philipp. Flow. Pl. 2 (1923) 461; Salvosa, Lex. Philipp. Trees (1963) 123; Airy Shaw, Alph. Enum. Euph. Philipp. Is. (1983) 44. — Lectotype (proposed here): *Vidal 610* (K), Philippines, Luzon, San Mateo, Manila; see note.

*Sapium lateriflorum* Merr., Philipp. J. Sci. 1, Suppl. (1906) 83, nom. illeg., non Hemsl. [Hooker's Icon. Pl. (1901) t. 2680]; Elmer, Leafl. Philipp. Bot. 4 (1911) 1303; Merr., Philipp. J. Sci. 16 (1920) 577. — *Sapium merrillianum* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 243, nom. nov.; Kruijt, Biblioth. Bot. 146 (1996) 90. — Lectotype [proposed by Merr., Philipp. J. Sci. 16 (1920) 577]: *FB (Borden) 2565* (holo PNH†; iso K, P, US), Philippines, Luzon, Prov. Bataan, Lamao River, Mt Mariveles.

*Urandra elliptica* Merr., Philipp. J. Sci., Bot. 5 (1910) 195, non Schellenb. [Bot. Jahrb. 59 (1924) 17, nom. illeg. = *Stemonurus ammui* (Kaneh.) Sleumer]; Philipp. J. Sci. 16 (1920) 577; Sleumer, Blumea 17 (1969) 263. — Type: *FB (Topacio) 20003* (holo PNH†; iso US), Philippines, Luzon, Prov. Bataan.


1 cm
1 cm
a
1 mm
b
1 mm
g
d
1 mm
1 mm
f
e
c
Van Os '96

Tree, up to 36 m high, dbh up to 90 cm, bole up to 17 m high. *Bark* shallowly fissured, strongly peeling with small scales, mid to dark brown; inner bark light brown to white, 10 mm thick. *Slash* light yellow to red, moderately soft, odour- and tasteless; heartwood dark yellow; cambium white, turning brown. *Stipules* 1.5–2 by 1.5–2.5 mm. *Leaves:* petiole 1–2.2 cm long; blade oblong to elliptic, (7–)8–18 by (3.5–)4.5–10.5 cm, base attenuate to obtuse to slightly cordate, often conspicuously auriculate, margin usually revolute, apex acuminate to cuspidate, upper surface shining, lower surface not papillate but smooth and only slightly paler, with 1 or 2(–8) glands per side, 0.2–0.3 mm diam. and 0.2–0.5 mm distant from margin, basal glands circular to elliptic, 0.5–1.25 by 0.25–0.6 mm, usually 0.5–1 mm above base of blade and not touching midrib, secondary veins 7–9 pairs, angle with midrib 55–65°, tertiary veins inconspicuous and indistinctly percurrent to reticulate. *Inflorescences* in numerous leaf axils, each branch with basal region 5–10 mm long with tightly packed, distichously arranged, sterile bracts c. 1 mm long, staminate part c. 35–40 by 6–7 mm. *Bracts of staminate cymules* c. 1.5 mm long, their glands 1.5–2 by 0.6–0.7 mm, not fragmented. *Staminate cymules* 7–9-flowered. *Staminate flowers:* pedicel c. 1 mm long; calyx c. 1.25 mm long; stamens with filaments c. 0.75 mm long when flowering, anthers 0.6–0.7 mm long. *Pistillate flowers* 1–3 per thyrse branch or sometimes absent; pedicel 4–5 mm long; calyx c. 1.25–2 mm long, with nearly free sepals; ovary 3–4 mm long; style c. 0.25 mm long, stigmata c. 1.5 mm long. *Fruits:* pedicel 8–27 mm long; 1-seeded, nearly circular in shape, 12–17 by 11–15 mm, not flattened and not sulcate, yellowish to green, with fleshy outer layer c. 0.4 mm thick, woody part of pericarp 0.15–0.25 mm thick, style apical.

Distribution — Endemic to Malesia: Philippines (Luzon, Mindoro, Palawan, Ticao, Bucas Grande, Mindanao), Celebes, Moluccas (Mangoli), New Guinea.

Habitat & Ecology — Found in the canopy of primary or secondary, dry semi-deciduous forests, also on steep hillsides and slopes and on the foot of a limestone hill bordering mangrove swamp. Locally very common and dominant. Soil: clay, sand, volcanic rock. Altitude 10–120 m. Flowers collected in Oct.–Dec., Mar.; fruits collected in Feb.–June, Sept.

Vernacular names — Philippines: balákat-gúbat [official common name fide Philipp. J. For. 5 (1974) 75, 135], mogalmod (Tagbanua); several additional ones are listed by Merr., Enum. Philipp. Flow. Pl. 2 (1923) 461. New Guinea: seganamuung, sogonam, sogonamung (Kemtoek).

Uses — The wood is of potentially commercial value [Lomibao, Philipp. Lumberman 19 (1973) 22–29].

Note — The original type citation is "Montalvan? (Manila)". No specimen with this locality information could be traced. However, the collection *Vidal 610*, from San Mateo, Manila, seen and annotated by Rolfe, can be considered as authentic material, and is therefore proposed as a lectotype.

Fig. 1. *Balakata luzonica* (S. Vidal) Esser. a. Habit of flowering plant, only staminate flowers present; b. detail of base of leaf blade, lower surface, showing glands; c. detail of staminate thyrse, late bud; d. young infructescence, with closely packed distichous bracts at base; e. fruit; f. fruit in longitudinal section, showing fleshy pericarp and stony seed coat; g. seed [a–c: *Ramos 2013*, L; d–g: *FB (Curran) 17601*, L].

# 2. FALCONERIA

## INTRODUCTION

*Falconeria* Royle (1839) was named after H. Falconer, at that time superintendent of the Botanic Garden at Serampore, India. Royle described two species simultaneously, *F. insignis* and *F. wallichiana.* They were hardly distinct and therefore united by most later authors with *F. insignis* as the accepted name. Pfeiffer (1874) designated *F. insignis* as lectotype of the genus, confirmed by Wheeler (1975). Wight (1853) described a third species, *F. malabarica*, distinguished by pistillate flowers and fruits with 3 instead of 2 carpels. Since then, no new taxa were described any more, but the opinions about the distinctiveness of the described species changed repeatedly.

Pax (1890) considered *Falconeria* as containing two species, and Gagnepain (1926) noted that the plants from Indochina are distinct from those of India and might be separated taxonomically. Sometimes *F. malabarica* was considered as a mere variety of *F. insignis*, and Hooker (1888) made the respective combination of var. *malabarica*, accepted also by Pax & Hoffmann (1912). Other authors united all taxa of *Falconeria* under *F. insignis* without distinguishing any further taxa, e.g., Airy Shaw (1972a).

*Falconeria* had first been classified in the Antidesmeae, close to *Antidesma* Burm. ex L. (Royle, 1839). Tulasne (1851) and Wight (1853) placed *Falconeria* in the Euphorbiaceae s.str., close to *Sapium*, and this opinion is still generally agreed with.

*Falconeria* was accepted as a separate genus for several decades after its establishment up to Müller Argoviensis (1863), distinguished particularly by its irregularly, hardly dehiscent fruits and the strictly unisexual inflorescences. A few years later, Müller Argoviensis (1866) moved *Falconeria* and *Sapium* as separate sections to *Excoecaria.* Bentham (1878) argued that *Falconeria* and *Sapium* may either be kept separate or classified as sections of one genus, and he finally (1880) retained *Falconeria* with uncertain position within *Sapium.* The combination of *Sapium insigne*, however, was not contributed by him but by Trimen (1885). Hooker (1888) was the first to cite *Falconeria* as a formal section of *Sapium.* Within the most recent decades, *Falconeria* has often been sunk into *Sapium* without further distinction, for instance by Airy Shaw (1972a) and Webster (1994). Only Kruijt (1996) returned, with doubt, to the view of a distinct genus *Falconeria.* A quite strange byway is the opinion of Kurz (1877), who classified *Falconeria* as part of *Carumbium* (= *Homalanthus*).

## CHARACTERS

### Vegetative characters

*Falconeria* is remarkable by its slightly succulent stems and deciduous leaves. Contrary to *Stillingia* (the only other succulent genus of the tribe), the flower-bearing branches are always leafless (Fig. 2c).

The leaves are characterized by petioles and blades very variable in length, by a pair of disc-shaped glands on the petiole apex on the junction with the blade (Fig. 2b), and by serrate margins. This combination of features may also be found in *Sapium*, but not in any other genus within the Malesian Hippomaneae.

### Inflorescences and flowers

The inflorescences are simple and strictly terminal at the top of older, leafless branches very different in diameter; they do not simply terminate an annual shoot. This is unique in the Hippomaneae. Likewise unique is the separation of sexes in strictly unisexual and many-flowered thyrses of equal size, although still on the same plant.

The bract glands are disc-shaped, and the staminate cymules many-flowered with the individual flowers bistaminate and sessile before but shortly pedicellate when flowering (Fig. 2d). The staminate thyrse, therefore, is hardly distinguishable from the staminate part of thyrses of *Sapium* and *Stillingia.*

The pistillate flowers are sessile. The carpel number is 2 or 3, but may vary on the same plant. Therefore, a taxonomic separation (var. *malabarica*!) does not seem to be justifiable.

### Fruits and seeds

The fruits are subsessile like the pistillate flowers and of the same shape and size as in *Sapium* and *Stillingia.* In contrast to those taxa, they are found in very large numbers in elongated infructescences, and the pericarp is very thinly membranous and opens irregularly. The seeds are covered by an aril and are completely whitish (never red). Therefore, the fruits of *Falconeria* are unique in the tribe.

## BIOGEOGRAPHY AND RELATIONSHIPS

*Falconeria* is monotypic and most common in the Himalayan region; it reaches only the NW part of Malesia (Peninsular Malaysia) and is certainly not a typical Malesian element (Map 2).

The recent cladistic analysis of Malesian Hippomaneae (Esser et al., 1998) confirmed the view that *Falconeria* is very closely related to *Sapium* and *Stillingia.* Leaves and staminate flowers of the three genera are hardly distinguishable, and *Falconeria* shares arillate seeds with *Sapium,* succulence with *Stillingia.* But the spatial separation of sexes, the leaves lacking on flowering branches, the variable carpel number, and particularly the irregularly opening fruits without a woody base (characteristic for *Stillingia*) support separation of *Falconeria.*

*Stillingia* has most of its species in the New World, and *Sapium* as well as some other, closely related genera (like *Hippomane* L., *Senefelderopsis* Steyerm.) are restricted to the Neotropics (Esser, 1994). All of these genera are characterized by similar flowers, but their fruits are unique, showing several autapomorphic characters. More precise hypotheses about the relations within this clade are not yet achievable. *Falconeria,* however, is very different in its distribution, being restricted to Asia.

## **Falconeria** Royle

*Falconeria* Royle, Ill. Bot. Himal. Mts (1839) 354, t. 84; Endl., Gen. Pl. Suppl. 1 (1836–1840) 1376; Wight, Icon. Pl. Ind. Orient. 5, 2 (1853) 20, t. 1866; Baill., Étude Euphorb. (1858) 526; Müll.Arg., Linnaea 32 (1863) 83; Benth., J. Linn. Soc., Bot. 17 (1878) 242; L.C. Wheeler, Taxon 24 (1975) 535; Kruijt, Biblioth. Bot. 146 (1996) 90. — *Excoecaria* sect. *Falconeria* (Royle) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1211. — *Sapium* sect. *Falconeria* (Royle) Hook.f., Fl. Brit. India 5 (1888) 471; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 98; T. Post & Kuntze, Lex. Gen. Phan. (1903) 498; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 241; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 202. — Lectotype [proposed by Pfeiffer, Nomencl. Bot. 1, 2 (1874) 1334]: *Falconeria insignis* Royle.

*Gymnobothrys* Wall. in Baill., Étude Euphorb. (1858) 526, nomen in synon.

Trees, with whorled distal branches, slightly succulent and shrinking when dry. Monoecious. Deciduous, fruiting when leafless. *Indumentum* absent. *Stipules* divided into 2 or 3 ciliae, glandless. *Leaves* alternate but apically crowded; petiole 0.6–6 cm long, much shorter than blade, apically above with a symmetrical or asymmetrical pair of disc- to cup-shaped glands on the junction with the blade; blade elliptic, 2–11 cm wide, base attenuate to acute, margin serrate with mostly persistent glandular teeth (1–)2–3.5 mm apart, apex acuminate, glandless above, lower surface neither whitish-farinose nor papillate and with a row of few marginal glands, basal glands not differing, secondary veins distinct, arching but not joined towards the margin, basal ones not to slightly different in angle with midrib, intersecondary veins present but indistinct, smaller veins densely distinct, reticulate. *Inflorescences* terminal, yellowish, not compound, basally with no or inconspicuous (less than 10 mm long) sterile basal region, unisexual with staminate and pistillate flowers in separate thyrses of equal size, 90–170 mm long, staminate thyrses 5–7 mm diam. *Bracts of staminate cymules* transversely ovate, apically rounded, at base with a pair of oblong-flattened to disc-shaped glands touching the axis of the inflorescence. *Staminate cymules* 9–15-flowered; bracteoles present, completely divided into 2 or 3 ciliae. *Staminate flowers* nearly sessile in bud, with short pedicel (less than 1 mm) during flowering, pedicel apically articulate; calyx with 2 largely fused sepals; stamens 2, filaments slightly longer than anthers. *Pistillate flowers* in separate thyrse, c. 30–60 per thyrse; pedicel very short; calyx with 3 sepals, basally fused, glandless; ovary 2- or 3-locular, smooth; style short, sometimes hardly visible, stigmata 2 or 3, undivided, glandless. *Fruits* with a short pedicel (0.5–2 mm long); 2- or 3-seeded, smooth, pericarp partly fleshy in young fruits, later on dry, very thin (c. 0.1 mm) and fragile, tardily and irregularly dehiscing; columella alate with marginal vascular bundle, central part membranous and caducous. *Seeds* pale, with a thin fleshy arillus, not carunculate.

Distribution — One species, distributed from India and Sri Lanka to Vietnam and China, in Malesia only known from Peninsular Malaysia (excl. Singapore).

Note — The characters used to distinguish taxa within this genus are not reliable. Obviously, a further division of this apparently monotypic genus is not justified.

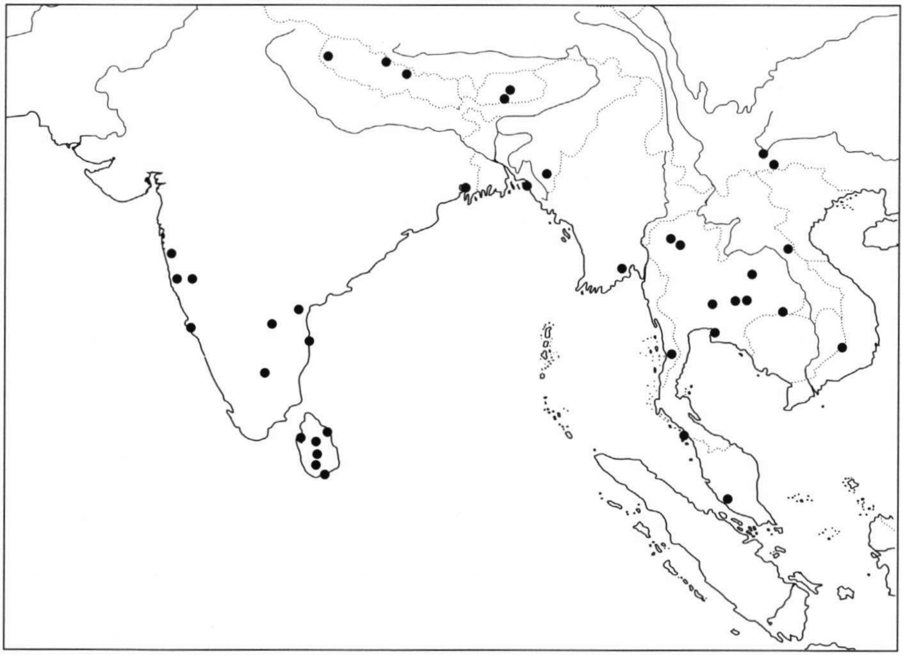
### 1. **Falconeria insignis** Royle — Fig. 2, Map 2

*Falconeria insignis* Royle, Ill. Bot. Himal. Mts (1839) 354, t. 84a or 98, f. 2; Kruijt, Biblioth. Bot. 146 (1996) 90. — *Excoecaria insignis* (Royle) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1212. — *Carumbium insigne* (Royle) Kurz, Forest Fl. Burma 2 (1877) 412. — *Sapium insigne* (Royle) Trimen, Syst. Cat. Fl. Pl. Ceylon (1885) 83; Hook.f., Fl. Brit. India 5 (1888) 471; G. Watt, Dict. Econ. Prod. India 6, 2 (1893) 471; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 241; Burkill, J. & Proc. Asiat. Soc. Bengal 12 (1916) 263; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 394, 395; Airy Shaw, Kew Bull. 26 (1972) 330; Whitmore, Tree Fl. Malaya 2 (1973) 128, 129; P.H. Hô, Câyco Viêtnam 2, 1 (1992) 355; I.M. Turner, Gard. Bull. 47 (1995) 231. — *Sapium insigne* (Royle) Trimen var. *genuinum* Pax in Engl., Pflanzenr. IV.147.v (1912) 242, nom. inval. — Lectotype (proposed here): *Royle s.n.* (LIV 7022 i), India, 'Deyra Doon and above Rajpore'; see note 1.

*Falconeria wallichiana* Royle, Ill. Bot. Himal. Mts (1839) 354. — *Falconeria wallichii* Royle, Ill. Bot. Himal. Mts (1839) t. 84a or 98, f. 3. — Lectotype (proposed here): *Royle s. n.* (LIV 7022 iii pro parte), 'Burupa in Nepal'; see note 1.
*Gymnobothrys lucida* Wall. in Baill., Étude Euphorb. (1858) 527, nomen in synon.

Tree, up to 40 m high, dbh up to 50 cm, bole unbuttressed, crown spreading. *Bark* extremely thick and very rough, light brown; inner bark pale yellow. *Branchlets* light brown, with conspicuous leaf scars. *Slash* pale yellow. *Stipules* c. 0.75 by 1 mm. *Leaves:* petiole 0.6–6 cm long, with distal petiolar glands 0.75–1.5 mm diam.; blade elliptic, (4.5–)8–33 by (2–)4–11 cm, base attenuate to acute, margin hardly revolute, upper surface hardly shining, lower surface somewhat brighter and glandless or with 1–7 glands per side, 0.25–0.5 mm diam. and strictly marginal, often even in lateral auricles of the blade, secondary veins (13–)16–23 pairs, angle with midrib 65–75°, basal veins not differing or diverging with smaller angle. *Inflorescences* on conspicuously thicker branches, fertile part 90–170 mm long in both sexes, axis 1.5–2.5 mm diam. *Bracts* c. 0.75 mm long, their glands 1.75–3.5 by 1 mm and mostly completely along the axis, therefore often separate from the bract. *Staminate flowers:* pedicel up to 0.25–0.5 mm long; calyx 0.75–1 mm long; stamens with filaments 0.75–1 mm long, anthers 0.4–0.6 mm long. *Pistillate flowers:* pedicel 0–1 mm long; calyx 1.5–2 mm long; style c. 0.5 mm long, stigmata 0.5–1 mm long. *Fruits:* pedicel 0.5–2 mm long; schizocarp 7 by 4.5–6 mm. *Seeds* 5 by 4.5 mm.

Distribution — Sri Lanka and S India to Nepal, Bhutan, Laos, Vietnam, and SW China (Yunnan, Szechuan: Lee, 1956), reaching its southern limit in Malesia: Peninsular Malaysia (excl. Singapore).



Map 2. Distribution of *Falconeria insignis* Royle.

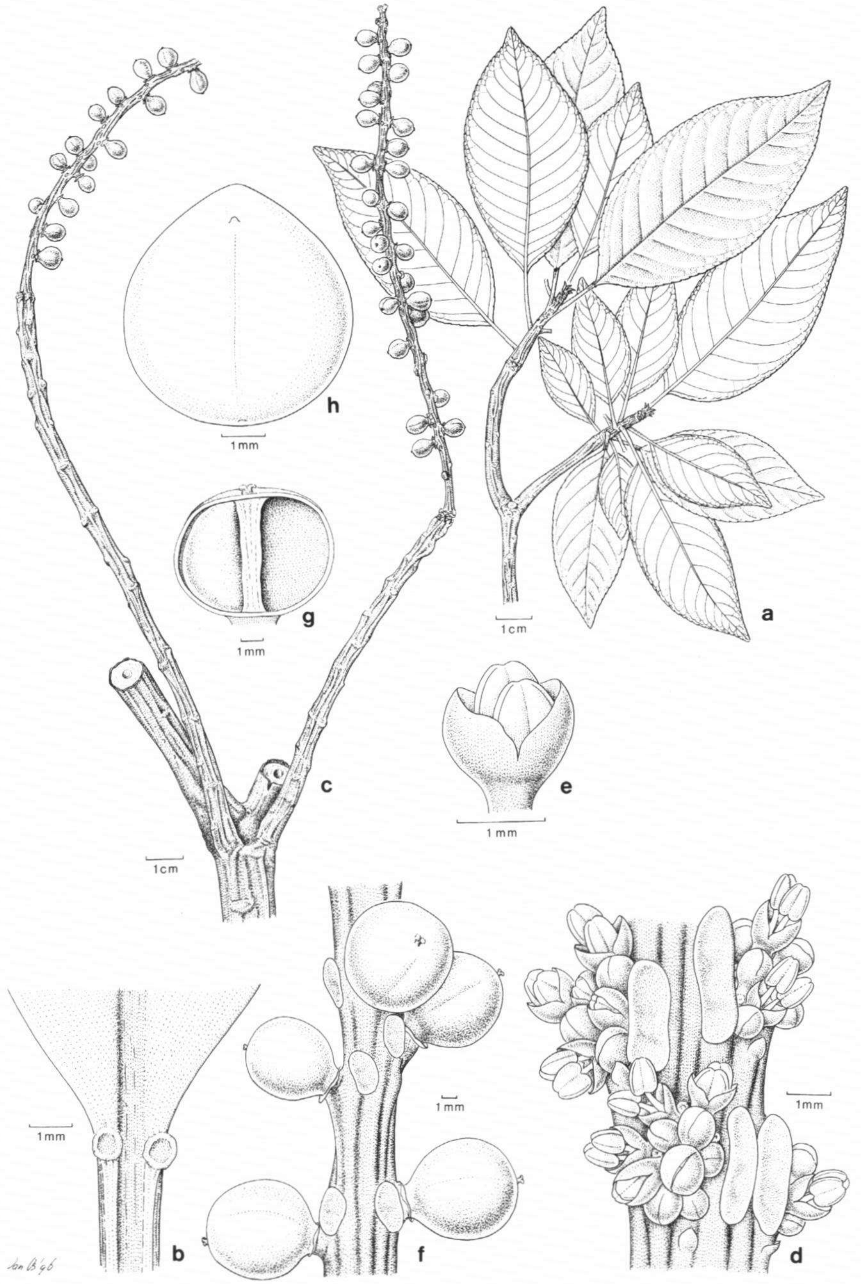


Fig. 2. *Falconeria insignis* Royle. a. Habit of sterile plant with crowded leaves; b. detail of base of leaf blade, upper surface, showing glands; c. habit of flowering plant with pistillate thyrses, leafless; d. detail of staminate thyrses, flowering; e. staminate flower with short pedicel and fused sepals; f. part of infructescence with sessile bicarpellate fruits; g. bicarpellate fruit in longitudinal section, showing thin pericarp; h. seed [a, b: *KEP FRI (Ng) 1626*, L; c, f–h: *Maxwell 90-201*, L; d, e: *Maxwell 92-6*, L].

Habitat & Ecology — Found in deciduous forest, on slopes, in rocky places, in full sun. Soil: limestone, granitic bedrock. Occasional to locally common. Altitude 100–900 m. Flowers collected in Mar.–Apr.; fruits collected in Feb., Apr., Oct. The flowers are visited by *Melipona* bees [Burkill, J. & Proc. Asiat. Soc. Bengal 12 (1916) 263].

Vernacular name — Thailand: tang ta bawl.

Uses — The species was recently recorded as a fish-stupefying plant [Kulkarni et al., Indian Forester 116 (1990) 333]. The latex is toxic to skin and eyes.

Notes — 1. The Royle types, preserved at LIV, were not cited in the publication of Harrison (1978). Through the efforts of A. Gunn, however, they could be traced at LIV. There are three sheets at LIV (7022 i–iii). Only the first one (7022 i) has a label, citing the locality "Doon" and the native names "Chhiria", "Chirun", and "Khira"; it contains only female flowers. The sheet 7022 ii has no label and only female flowers. The third one, 7022 iii, has two envelopes with fragments of female and male flowers; one of the envelopes contains immature male flowers (with short filaments), the other one immature and mature male flowers (the latter with long filaments). The sepals are nearly entire and similar in all cases. The sheet 7022 i is selected as lectotype for *Falconeria insignis* because it has the label with all details given by Royle, although the specimen does not show Royle's characters for the species, which was based on male flowers ("sepalis denticulatis, filamentis longioribus"). No label data for *Falconeria wallichiana* are present except the native name "Kheera" (= ?"Khira"). The first envelope of sheet 7022 iii is selected as lectotype for *F. wallichiana* ("sepalis integerrimis, filamentis brevioribus").

Müller Argoviensis (1866) cited an isotype at K, which could not be found during a visit to K.

2. The carpel number of *Falconeria* is a much discussed matter. In fact, usually the carpel number is constant in a single plant, and 2-locular ovaries are most common. However, at least two collections studied showed 2- and 3-locular ovaries or fruits together in the same thyrse (*Beddome 7443, Maxwell 90-201*). Therefore, a separation on species level is certainly not justified. The recognition of varieties may be reasonable, but will not be applied here. The only available Malesian specimens, *Congdon 747* and *KEP FRI (Ng) 1626*, contain only staminate flowers and leaves, thus the carpel number is unknown.

## 3. GYMNANTHES

### INTRODUCTION

*Gymnanthes* was described by Swartz in 1788. In its traditionally accepted circumscription (following Pax & Hoffmann, 1912) it is characterized only by its greatly reduced sepals of the staminate flowers. Although it has recently been revised superficially by Oe (1988), it is actually still full of nomenclatural and taxonomic difficulties, including its distinction from *Ateramnus* P. Browne (compare, e.g., Webster, 1983 against Kruijt & Zijlstra, 1989). The reduced sepals are not sufficient and probably not necessary for delimitation, as homoplasies are to be expected (compare, e.g., South American *Adenopeltis* Bertero ex A. Juss., also with naked flowers but otherwise very distinct). Other defining characters are not yet available. But considering the whole range of species currently assigned to *Gymnanthes* (compare Pax & Hoffmann, 1912, whose circumscription is still upheld or even extended by Webster, 1994, who included another Neotropical genus, *Actinostemon* Mart. ex Klotzsch), inclusion of other taxa like *Sarothrostachys* is plausible. A critical revision of *Gymnanthes* in a broad circumscription is badly needed.

*Sarothrostachys* was described by Klotzsch in 1841. It was considered as identical with *Gymnanthes* by Müller Argoviensis (1863), but assigned as a distinct section or subsection to other genera by different authors, including Müller Argoviensis himself in later publications. In 1866, e.g., he moved it to *Sebastiania*, a position doubted but not changed by Bentham (1878) and upheld until today. Only Léonard (1959) removed a single, African species to a new genus, *Duvigneaudia* J. Léonard.

The first Malesian species, *Sebastiania borneensis* Pax & K. Hoffm., was correctly assigned to *Sebastiania* sect. *Sarothrostachys*. Van Steenis (1948), who described the next two related species (*S. lancifolia* and *S. remota*), was not sure about their sectional classification. Yet, all three species fit well into *Sarothrostachys*. In the present revision, *S. lancifolia* is united with *S. borneensis*, as was already suspected by Airy Shaw (1975), and *S. remota* is retained as a distinct species.

*Sarothrostachys* is distinguished by its filiform, axillary, basally branching thyrses, resulting in axillary bunches of inflorescences, but is otherwise very similar to some other taxa of the Hippomaneae. It is, however, now considered to be identical with *Gymnanthes*, not with *Sebastiania*. The main difference between *Gymnanthes* and *Sarothrostachys* is the inflorescence being branched in *Sarothrostachys*, and unbranched in *Gymnanthes*.

*Sarothrostachys* shares several characters with *Gymnanthes* s.str. but not with *Sebastiania:* leaves abaxially often whitish, with marginal to submarginal glands; staminate flowers, when flowering, shortly but distinctly pedicellate; fruits often (in Malesia always) remarkably long pedicellate; pericarp comparatively thick (fruit length/pericarp thickness c. 10/1); septa with separate basal triangle, with only 1(–2) vascular strands; seeds with smooth surface.

The characters shared with *Sebastiania* are also found in several other genera of the tribe: staminate flowers with well-developed sepals, and 3 stamens.

## CHARACTERS OF MALESIAN TAXA

### Indumentum

The Malesian species are, in contrast to some of the Neotropical ones, totally glabrous.

### Leaves

Compared to other genera of the tribe, the leaves have only few distinguishing characters. *Gymnanthes borneensis* is distinguished by its mostly whitish lower surface and the submarginal row of abaxial glands, the lowermost ones usually conspicuously enlarged. *Gymnanthes remota* shows leaves not whitish below and with characteristic, longitudinally linear glands strictly on the abaxial margin (Fig. 3c). Furthermore, *G. remota* exhibits lateral veins with a larger angle and with more conspicuous loops.

### Inflorescences

The thyrses of *G. borneensis* mostly branch several times, whereas those of *G. remota* rarely do so (but are often simple: Fig. 3a), although this is only a statistical difference. It is remarkable, however, that most inflorescences of *G. remota* studied were bisexual, but in *G. borneensis* pistillate flowers are rare and thyrses usually staminate. Intermixed flowers of both sexes within one inflorescence, as described for African *Duvigneaudia*, were not detected. Individual flowers are quite uniform, but the floral bracts give distinctive features. They are biglandular and touch the thyrsal axis in *G. remota*, glandless and elevated from the axis by a 'peduncle' in *G. borneensis*. Perhaps correlated with this, the pedicels of staminate flowers are much shorter in *G. borneensis*, resulting in a comparable width of each thyrsal branch in both species.

### Fruits

There are no significant differences between the fruits of the Malesian species. The elongated pedicels (Fig. 3a) are very distinctive within the Hippomaneae, but they are absent in some Neotropical species of *Gymnanthes*, at the same time also known from other Neotropical genera of the Hippomaneae like *Actinostemon*. Mericarps and seeds agree with those of many genera in the Hippomaneae.

## BIOGEOGRAPHY AND RELATIONSHIPS

The Malesian taxa of *Gymnanthes* have a quite restricted distribution (Map 3). This may be related with their habitat (primary rain forests). Moreover, except for the very long fruiting pedicels, no adaptations to zoochory are obvious, so that their dispersal capabilities may be restricted.

*Gymnanthes borneensis* is restricted to W Malesia, but more widely distributed than *G. remota*. It occurs in rain forests from quite different elevations, but always in lower altitudes than *G. remota*. Therefore, it is possible that *G. borneensis* is a paraphyletic species and *G. remota* a peripheral offspring.

More inclusive phylogenetic hypotheses are difficult to assess. In contrast to, e.g., *Microstachys* A. Juss., the generic limits, in particular to some Neotropical taxa, are still in need of further study. Regarding *Sarothrostachys* s.str. as next inclusive taxon (i.e., all species with compound thyrses), this shows a remarkable geography. If we consider the large indehiscent fruits of '*Duvigneaudia inopinata* (Prain) J. Léonard' as sufficient only for species delimitation but not for separation into an own genus, and if we exclude species of dubious affinity (like *Sebastiania hexaptera* Urb.), then 2 species are Malesian, 2 occur in Central Africa (Kruijt & Roebers, 1996), and 2 or 3 are known from E and S Brazil. *Sarothrostachys* certainly has a pantropical distribution without any conspicuous centre of diversity. This is the only case among the c. 30 genera of the Hippomaneae. As all species are obviously rain forest trees with limited dispersal abilities (except the drupes of '*D. inopinata*'), this may point to *Sarothrostachys* being a considerably old taxon. Within *Sarothrostachys*, the relationships are uncertain: The African species are delimited by their own autapomorphies [drupes in *D. inopinata*, red flower colours in *D. leonardii-crispi* (J. Léonard) Kruijt & Roebers], the Neotropical ones are still poorly known but obviously are very similar to the Malesian species.

If *Gymnanthes* proves to be congeneric with *Sarothrostachys*, as proposed here, the picture may change somewhat, as *Gymnanthes* sensu Pax & Hoffmann (1912), without *Sarothrostachys*, is restricted to the Neotropics. *Gymnanthes* s.l. therefore has a centre of diversity in the New World.

## Gymnanthes Sw.

*Gymnanthes* Sw., Prodr. (1788) 95; Baill., Etude Euphorb. (1858) 530; Benth. in Benth. & Hook.f., Gen. Pl. 3 (1880) 255, 337; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 100; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 81; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 191; G.L. Webster, J. Arnold Arbor. 48 (1967) 387; Taxon 32 (1983) 304; Ann. Missouri Bot. Gard. 81 (1994) 122. — *Excoecaria* sect. *Gymnanthes* (Sw.) Griseb., Fl. Brit. W. Ind. (1859) 50. — *Sapium* sect. *Gymnanthes* (Sw.) T. Post & Kuntze, Lex. Gen. Phan. (1903) 498. — Lectotype [proposed by Britton & Shafer, N. Amer. Trees (1908) 600]: *Gymnanthes elliptica* Sw.

?*Ateramnus* P. Browne, Hist. Jam. (1756) 339; Hallier, Meded. Rijksherb. Leiden 36 (1918) 4; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xvii, add. VII (1924) 204; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 207; Rothm., Feddes Repert. Spec. Nov. Regni Veg. 53 (1944) 5; G.L. Webster, Taxon 32 (1983) 304; Oe, Een revisie van Ateramnus (1988) 2; Kruijt & Zijlstra, Taxon 38 (1989) 322; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 122. — Lectotype [proposed by Rothm., Feddes Repert. Spec. Nov. Regni Veg. 53 (1944) 5]: *Ateramnus lucidus* (Sw.) Rothm., based on *Gymnanthes lucida* Sw; see note 2.

*Sarothrostachys* Klotzsch, Arch. Naturgesch. 7 (1841) 185; Baill., Étude Euphorb. Atlas (1858) 13; L.C. Wheeler, Taxon 24 (1975) 537. — *Stillingia* sect. *Sarothrostachys* (Klotzsch) Baill., Étude Euphorb. (1858) 524; Adansonia 1 (1861) 351; Adansonia 6 (1867) 325. — *Sebastiania* sect. *Gussonia* (Spreng.) Müll.Arg. subsect. *Sarothrostachys* (Klotzsch) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1175. — *Sebastiania* sect. *Sarothrostachys* (Klotzsch) Benth. in Benth. & Hook.f., Gen. Pl. 3 (1880) 336; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 94; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 118; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 193. — Lectotype [proposed by L.C. Wheeler, Taxon 24 (1975) 537]: *Sarothrostachys multiramea* Klotzsch ex Wawra [= *Gymnanthes multiramea* (Klotzsch ex Wawra) Müll.Arg.].

*Duvigneaudia* J. Léonard, Bull. Jard. Bot. Etat 29 (1959) 15; Kruijt & Roebers in Kruijt, Biblioth. Bot. 146 (1996) 12; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 123. — Type: *Duvigneaudia inopinata* (Prain) J. Léonard, based on *Sebastiania inopinata* Prain [= *Gymnanthes inopinata* (Prain) Esser, comb. nov.].

Shrubs to trees. Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* absent (rarely present in Neotropical species). *Stipules* broadly ovate-triangular, 0.5–2 mm long, undivided, glandless. *Leaves* regularly alternate; petiole short (up to 2 cm long), much shorter than blade, glandless; blade ovate to elliptic, 3–13 cm wide, base acute to subcordate, sometimes slightly attenuate, margin entire (serrate in some Neotropical species), apex acute to acuminate (rarely retuse in Neotropical species), glandless above, lower surface whitish-farinose or smooth and with a row of strictly marginal or submarginal glands, basal ones sometimes enlarged, secondary veins 10–16 pairs, arching and joined or not joined towards the margin, tertiary venation reticulate. *Inflorescences* terminal and axillary, yellowish, simple or compound, in the latter case several times branched only near base and giving the resemblance of crowded axillary thyrses, with short or no sterile basal region, pistillate and staminate flowers in same thyrse but pistillate flowers often lacking, staminate thyrse 6–60 by 2–5 mm. *Bracts* *of staminate cymules* broadly triangular to elliptic, sometimes removed by a peduncle, glandless or with a pair of globose-cylindrical glands touching the axis of the thyrse or removed by a peduncle. *Staminate cymules* 1–3(–5)-flowered; bracteoles present. *Staminate flowers* with short to distinct (up to 2 mm long) pedicel, hardly elongating when flowering; calyx with usually 3 sepals, quite small and fused only at very base (larger and mostly fused in some Neotropical species); stamens 3 (up to 12 in some Neotropical species), filaments slightly longer than anthers. *Pistillate flowers* 1–3 at base of thyrse; pedicel distinct and often considerably elongating after fertilization to up to c. 20 cm length; calyx with 3 sepals, triangular, free to basally united, glandless; ovary 3-locular, sometimes with 3 pairs of appendages but never with rows of multiple appendages; style present, stigmata undivided, glandless. *Fruit* with distinct, often very long (up to 20 cm) pedicel; 3-seeded, smooth or with 3 pairs of appendages, dry and regularly opening along the septa (indehiscent and drupaceous in an African species); pericarp moderately thick (fruit length/pericarp thickness = c. 10/1), septa with a separate basal triangle and one, sometimes divided, vascular strand each, remaining columella alate except at base. *Seeds* elliptic, dry, smooth, without caruncle (in some Neotropical species with a broadly conical caruncle).

Distribution — Including *Sarothrostachys* and *Duvigneaudia*, *Gymnanthes* comprises c. twenty-five species. Twenty-one of them occur in the New World from the USA (Florida) to the Antilles and Paraguay, two in Africa (Congo Basin from Cameroun to Zaire), and two in Asia (endemic to Malesia).

Notes — 1. Circumscriptions of *Sarothrostachys* (with compound thyrses) as well of *Gymnanthes* (with simple thyrses) in the sense of Pax & Hoffmann (1912), the latest available monograph, are still problematical and in need of revision. There is no doubt that the two Malesian species are closely related, but their generic affinity may have to be examined again when the Neotropical taxa are being revised.

2. *Ateramnus*, a poorly understood, Neotropical genus with very insufficient description and no known extant type, would have priority over *Gymnanthes*, if accepted as identical. However, the arguments given by Kruijt & Zijlstra (1989) are not convincing. In agreement with Webster (1994) I prefer a still doubtful position of *Ateramnus* instead of accepting a definite synonymy with *Gymnanthes* and changing the name of the latter. The neo-lectotype of *Ateramnus* proposed by Kruijt & Zijlstra, *A. glandulosus* (Sw.) C.D. Adams, is refused here; it is probably a species of *Sebastiania*, and the proposed choice was unnecessary.

## KEY TO THE MALESIAN SPECIES

1a. Glands of lower leaf surface slightly distant from margin, basal ones often conspicuously enlarged; leaves often whitish beneath, with secondary veins indistinctly joined towards the margin; floral bracts elevated from the axis, glandless .... ............................................ **1. G. borneensis**

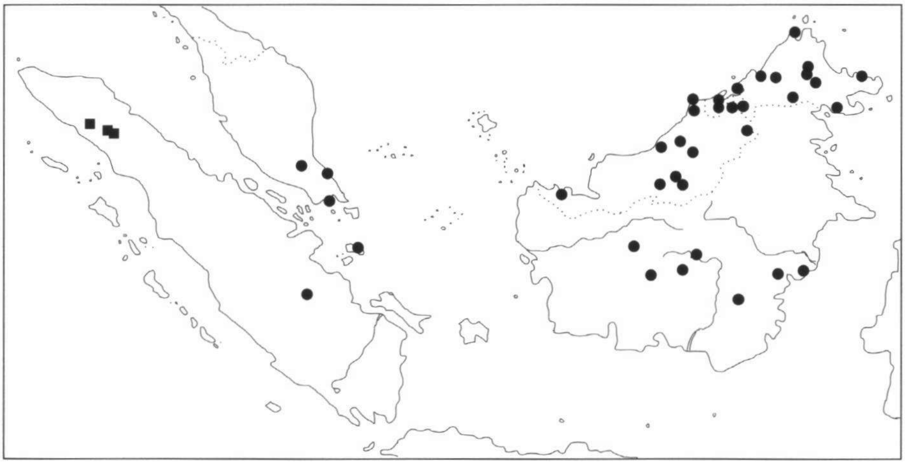
b. Glands of lower leaf surface strictly marginal, basal ones not enlarged; leaves not whitish beneath, with secondary veins distinctly joined towards the margin; floral bracts touching the axis, biglandular ........................ **2. G. remota**

### 1. Gymnanthes borneensis (Pax & K. Hoffm.) Esser, *comb. nov.* — Map 3

*Sebastiania borneensis* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 122; Merr., Bibl. Enum. Bornean Pl. (1921) 347; Steenis, Bull. Bot. Gard. Buitenzorg III, 17 (1948) 410; Airy Shaw, Kew Bull. 14 (1960) 396; Whitmore, Tree Fl. Malaya 2 (1973) 131; Airy Shaw, Hooker's Icon. Pl. 38 (1974) t. 3723; Kew Bull. Add. Ser. 4 (1975) 195; Keßler & Sidiyasa, Tropenbos Ser. 7 (1994) 135, f. 103; I.M. Turner, Gard. Bull. 47 (1995) 232. — Lectotype (proposed here): *Beccari PB 3127* (holo G; iso FI, n.v., K).

*Sebastiania lancifolia* Steenis, Bull. Bot. Gard. Buitenzorg III, 17 (1948) 410; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 195; Kew Bull. 36 (1981) 345. — Type: *Bünnemeijer 6925* (holo BO, n.v.; iso K, L), Sumatra, Lingga Archipelago, P. Lingga, Sg. Tanda. Syn. nov.

Shrub to small tree, up to 15 m high, girth up to 32 cm, with irregularly shaped stilt roots c. 50 cm long. Outer *bark* smooth, hooped, soft, pale yellowish to greyish-brown to dark green; inner bark hard, pale brown to creamish to orange-yellowish, 2.5 mm thick. *Sapwood* medium hard, whitish to yellowish to cream. *Stipules* not seen, scars c. 0.4 mm wide. *Leaves:* petiole (0.8–)1.2–2 cm long; blade ovate to elliptic, (10–)14–23 by (3–)5–13 cm, base acute to obtuse to rounded, often slightly attenuate, apex acute to acuminate, lower surface usually whitish-glaucous, rarely green and shiny, with 2–8 glands per side, 0.2–0.4 mm diam. and 0.5–3 mm distant from margin, basal glands enlarged and 0.75–3 mm diam. or rarely absent, secondary veins 10–16 pairs, angle with midrib 55–65(–75)°, arching and not or indistinctly joined. *Inflorescences* usually axillary and compound, entirely yellowish except for reddish bracts, with a sterile basal region up to 5 mm long, staminate part (6–)15–30 by 2–3 mm. *Bracts of staminate cymules* 0.4–1.2 by 0.4–0.8 mm, apex rounded to subacute, removed from the axis of the inflorescence by a peduncle 0.4–1 mm long, glandless. *Staminate cymules* 1-flowered. *Staminate flowers:* pedicel only up to 0.2 mm long; calyx 0.4–0.6 mm long; stamens with filaments 0.3–0.5 mm long when flowering, hardly present in bud, anthers c. 0.25 mm long. *Pistillate flowers:* pedicel nearly absent in bud, elongating to c. 10 mm length when flowering; calyx c. 0.8–1 mm long with free sepals; ovary smooth and without appendages; style 1–2 mm long,



Map 3. Distribution of *Gymnanthes borneensis* (Pax & K. Hoffm.) Esser (●) and *G. remota* (Steenis) Esser (■).

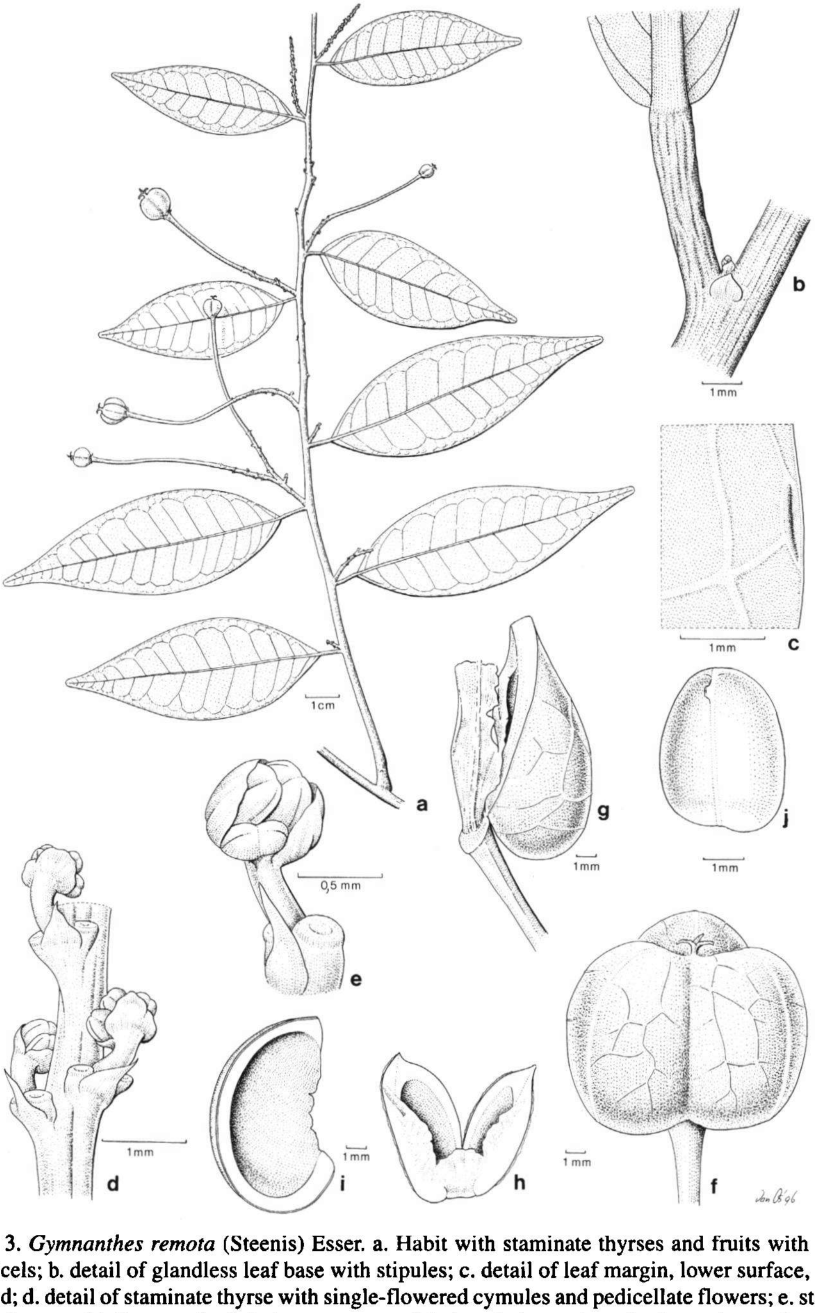


Fig. 3. *Gymnanthes remota* (Steenis) Esser. a. Habit with staminate thyrses and fruits with long pedicels; b. detail of glandless leaf base with stipules; c. detail of leaf margin, lower surface, with gland; d. detail of staminate thyrse with single-flowered cymules and pedicellate flowers; e. staminate flower with free sepals; f. fruit; g. remnant of fruit and alate columella; h. mericarp after septicidal dehiscence with the two septa, showing apical vascular strand and basal separate split ('triangle'); i. half of mericarp after loculicidal dehiscence with pericarp of medium thickness; j. ecarunculate seed [a–f: *De Wilde & De Wilde-Duyfjes 15911*, L; g–j: *De Wilde & De Wilde-Duyfjes 18260*, L].

stigmata c. 3–4 mm long. *Fruits* pendant on pedicel (5–)8–17 cm long; schizocarp nearly circular to transversely elliptic in outline, 9–11(–13) by 13–19 mm, deeply sulcate, without appendages, reddish-pinkish; pericarp c. 1 mm thick. *Seeds* c. 6–6.5 by 5–6.5 mm, without caruncle, brown, sometimes spotted.

Distribution — Peninsular Malaysia (incl. Singapore), C Sumatra, Lingga Archipelago, Borneo (Sabah, Sarawak, Brunei, C Kalimantan).

Habitat & Ecology — Found in the understorey of primary mixed Dipterocarp forest or old secondary forest, also on ridges or hillsides or in semi-riverine, swampy, periodically flooded, and submontane heath forest. Soil: yellow and red clay, sand, serpentine. Altitude 15–1000 m. Flowers collected in Feb., Mar., June–Nov.; fruits collected in Mar.–June, Aug.–Nov.

Vernacular name — W Kalimantan: kelampah.

Note — The lower leaf surface rarely lacks the whitish covering of waxes, but is shiny instead. At least in one case (*Vermeulen 883*) a specimen was found on ultrabasic (serpentine) soil; in this case, the petioles are remarkably short (8 mm).

### 2. Gymnanthes remota (Steenis) Esser, *comb. nov.* — Fig. 3, Map 3

*Sebastiania remota* Steenis, Bull. Bot. Gard. Buitenzorg III, 17 (1948) 410; Airy Shaw, Kew Bull. 36 (1981) 344. — Type: *Van Steenis 8273* (holo BO, n.v.; iso L), Sumatra, Atjeh, Gajolanden, Poetjoek Angasan, see note.

Shrub to small tree, up to 6.5 m high. *Stipules* c. 0.5–1 by 0.75 mm. *Leaves:* petiole 0.4–0.9 cm long; blade elliptic, 8–12 by 3.5–4 cm, base obtuse, apex subacuminate, lower surface smooth and brighter but never whitish-glaucous and with (0–)4 glands per side, longitudinally elliptic, c. 0.7 by 0.2–0.3 mm and strictly marginal, basal glands not enlarged, secondary veins 10–15 pairs, angle with midrib 75–80°, arching and distinctly looped. *Inflorescences* usually axillary and rarely compound, without a sterile basal region, staminate part (10–)40–65 by 2–5 mm. *Bracts of staminate cymules* 0.6–1 by 0.5 mm, not removed from the axis, apex subacuminate, their glands 0.4–0.6 mm diam. *Staminate cymules* 1-flowered. *Staminate flowers:* pedicel 1–1.7 mm long when flowering; calyx 0.5–0.75 mm long; stamens with filaments 0.5 mm long when flowering, hardly visible in bud, anthers 0.3–0.4 mm long. *Pistillate flowers:* pedicel elongating to 10–90 mm length; calyx with free sepals c. 0.5–0.7 mm long; ovary with 3 pairs of small appendages ('muricate'); style c. 0.5–1 mm long, stigmata 1–1.5 mm long. *Fruits* pendant on pedicel up to 9 cm long; schizocarp circular to transversely elliptic in outline, sulcate, mericarps 10–11 mm long; pericarp 1.2–1.5 mm thick. *Seeds* 0.7–0.75 by 0.55–0.65 mm, without caruncle, brown, spotted.

Distribution — Endemic to N Sumatra.

Habitat & Ecology — Found in montane rain forest, also on limestone; locally common. Altitude 1600–2000 m. Flowers collected in Jan., Mar., Aug.; fruits collected in June, July.

Note — The type cited by Van Steenis is *Van Steenis 8237*. According to his collection list at L, this specimen indeed is *Aneilema herbacea* Wall. ex Kunth [currently accepted name: *Murdannia japonica* (Thunb.) Faden], a Commelinacea. Obviously, the digits have been confused, and the two sheets of *Van Steenis 8273* present at L, typical specimens of *Gymnanthes remota*, therefore are supposed to be isotypes of this species.

# 4. MICROSTACHYS

## INTRODUCTION

*Microstachys* was published by De Jussieu in 1824, only a few months before Von Martius & Zuccarini (1824a) described the same genus as *Cnemidostachys*. De Jussieu based his genus on three species formerly included in *Tragia* L., two Neotropical ones and one (*Tragia chamaelea* L.) with an Indian type. The first (and only) species based on a Malesian type was *Cnemidostachys linearifolia* Miq.

*Microstachys* was accepted by subsequent authors up to Grisebach (1859) and Müller Argoviensis (1863). But Müller Argoviensis (1866) changed his mind and united it as a distinct section with *Sebastiania*, as he did with other genera. This was followed by all later authors up to Webster (1994), although it has often been noted that section *Microstachys* is very different from other species of *Sebastiania* (e.g., by Airy Shaw, 1975). Webster (1994) even admitted that it probably should be separated from *Sebastiania*. This was corroborated by Esser (1998b) and Esser et al. (1998).

*Elachocroton* was described by Mueller in 1857. It differs from *Microstachys* only in one minor character: its floral bracts are arranged spirally and not more or less distichously as in *Microstachys*. Both genera were united by Müller Argoviensis (1866) and most subsequent authors, but not by Pax & Hoffmann (1912); they classified *Elachocroton* and *Microstachys* as different sections of *Sebastiania*. The symmetry of the thyrses is the only difference, whereas several unique characters of leaves, flowers and fruits are shared, as discussed below. This distinction does not seem to be well founded and is therefore ignored here.

It is well established that in all of Australasia there is only one widespread species, *M. chamaelea*. It is quite variable, as are most species of *Microstachys*, but it poses no taxonomic difficulties and it should not be subdivided in any way.

*Microstachys* is easily recognizable by some characters unique in the Hippomaneae, particularly the inflorescences mostly opposite to leaves, the pistillate flowers often separated from the staminate part of the thyrse, i.e., situated at different parts of the stem, the multiple appendages of the always sessile pistillate flowers and fruits, the peculiar morphology of the central columella of the fruit with regularly parallel margins, and the cylindrical seeds with a large stipitate caruncle.

## CHARACTERS OF MALESIAN PLANTS

### Indumentum

The often dense, colourless and quite stiff hairs are widespread in *Microstachys*. However, in *M. chamaelea* they are shorter than in most other species, and the organs bearing them are very characteristic: stipules and all sepals are always at least ciliate if not totally hairy (glabrous in most other species); the ovaries instead are never hairy, and the leaves initially pilose but early glabrescent.

### Leaves

Extraordinary plasticity in leaf shape and size is typical for the genus (compare the name of the Neotropical *M. polymorpha* Müll.Arg.!). Especially the peculiar serrulation

(Fig. 4b), i.e., the densely packed, enlarged, glandular teeth usually touching each other, is useful for distinguishing *Microstachys* from other genera. The never ovate leaves with short but distinct petioles, the appressed (not erect) marginal teeth and the strictly marginal glands are, together with the indumentum, sufficient for recognition of *M. chamaelea* within the genus.

### Inflorescences

The inflorescences do not provide useful characters for species delimitation in *Microstachys*, not even quantitative ones. Noteworthy for the whole genus is, however, the insertion of the thyrses very often opposite the leaves. It originates by sympodial elongation of the axillary bud of the uppermost leaf. Typical is also the spatial separation of the sexes along the stem.

### Flowers

Most floral characters are remarkably constant within *Microstachys*. The stigmata of *M. chamaelea* are filiform, not thick and fleshy as in some other species. Within the Hippomaneae the very narrow thyrses, the stipitate to falcate bract glands, the free sepals of the staminate flowers and the sessile pistillate flowers with the typical excrescences make *Microstachys* easily recognizable.

### Fruits

The fruits of *Microstachys* are unique within the tribe. Notable are in particular the oblong-cylindrical mericarps and seeds, the multiple excrescences of the fruit surface (Fig. 4f; absent in few extra-Malesian species), the large disc-shaped and (when dry) stipitate caruncle, and the central columella remaining after fruit dehiscence which is alate along its whole length with nearly parallel margins (in most other genera the wings are completely absent or distinctly narrower at base, the columella shape then obovate). Otherwise, there are no differences between species of *Microstachys*.

## BIOGEOGRAPHY AND RELATIONSHIPS

*Microstachys* is a somewhat isolated genus without any very close relative. In Malesia, it is closer to *Excoecaria* than to the other species formerly included in the collective genus *Sebastiania* (Esser et al., 1998).

*Microstachys* is badly in need of revision. Only the South American taxa of *Elachocroton* were treated recently by De Oliveira (1983), but the separation of *Elachocroton* from *Microstachys* has probably always been quite artificial. Therefore, the relationships of the Malesian species cannot be discussed now.

In S and E Brazil, many species of *Microstachys* occur, some of them as local endemics, and often hardly variable in their characters. In Africa there are probably four species, three of them local endemics and one, *M. chamaelea*, more widespread (Esser, 1998b). In the New World north of the Amazon [*M. corniculata* (Vahl) Griseb.] as well as in Australasia (*M. chamaelea*) there is only a single species, each widespread and variable to a high degree. Therefore, *Microstachys* may have reached Malesia only by dispersal. *Microstachys chamaelea* is a shore plant with often gregarious occurrence and quite small seeds, and therefore probably easily dispersed. This is supported by the fact that it is widespread from Africa to Australia and has crossed the border of floristic regions. On the other hand, its absence from parts of Malesia is remarkable (Map 4). The lack of any collection from New Guinea may eventually be a collecting artifact, because seashore plants are usually underrepresented. The absence from the Philippines, however, seems to be sufficiently established and was stressed recently by Airy Shaw (1980).

## Microstachys A. Juss.

*Microstachys* A. Juss., Euph. Gen. (Feb. 1824) 48, t. 15, f. 50; Müll. Arg., Linnaea 32 (1863) 90; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 122; Esser, Kew Bull. 53 (1998) 955. — *Sebastiania* sect. *Microstachys* (A. Juss.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 1166; Benth. in Benth. & Hook. f., Gen. Pl. 3 (1880) 336; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 94; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 91; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 192. — *Sapium* sect. *Sebastiania* (Spreng.) T. Post & Kuntze subsect. *Microstachys* (A. Juss.) T. Post & Kuntze, Lex. Gen. Phan. (1903) 498. — Lectotype [proposed by G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 121]: *Microstachys bicornis* A. Juss. [= *Microstachys corniculata* (Vahl) Griseb.].

*Cnemidostachys* Mart. & Zucc., Flora 7.1 Beil. 4 (Apr.–June 1824) 136; Nov. Gen. Sp. Pl. 1 (Oct. 1824) 66, t. 40. — *Stillingia* sect. *Cnemidostachys* (Mart. & Zucc.) Baill., Etude Euphorb. (1858) 515; Adansonia 1 (1861) 350. — *Excoecaria* sect. *Cnemidostachys* (Mart. & Zucc.) Baill., Adansonia 6 (1867) 323. — *Sebastiania* sect. *Cnemidostachys* (Mart. & Zucc.) G.L. Webster, J. Arnold Arbor. 48 (1967) 386. — Lectotype [proposed by Esser, Kew Bull. 53 (1998) 957]: *Cnemidostachys myrtilloides* Mart. & Zucc. [= *Microstachys daphnoides* (Mart. & Zucc.) Müll. Arg.]; see note 2.

*Elachocroton* F. Muell., Hook. J. Bot. Kew Gard. Misc. 9 (1857) 17. — *Stillingia* sect. *Elachocroton* (F. Muell.) Baill., Étude Euphorb. (1858) 517. — *Sebastiania* sect. *Elachocroton* (F. Muell.) Pax in Engl., Pflanzenr. IV.147.v (1912) 114; Pax & K. Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 192; A.S. de Oliveira, Arq. Jard. Bot. Rio de Janeiro 27 (1983) 3. — Type: *Elachocroton asperococcus* F. Muell. [= *Microstachys chamaelea* (L.) Müll. Arg.].

Herbs to subshrubs, less than 2 m high. Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* consisting of multicellular, uniseriate, colourless hairs, mostly on vegetative parts, rarely absent. *Stipules* triangular, 0.5–2 mm long, undivided or apically divided into several ciliae, glandless. *Leaves* regularly alternate; petiole short (less than 1 cm long; absent to long in some Neotropical species), glandless; blade elliptic, ovate or linear, 0.3–2 cm wide, base acute to subcordate, margin with very dense, minute and persistent glandular teeth, 0.3–0.6 mm apart and often nearly touching each other (rarely fused into an entire, glandulous margin in some Neotropical taxa), apex rounded, acute or mucronate, above glandless and glabrous, lower surface paler and smooth to papillate but never white, glabrous to pilose, at base often with few marginal to submarginal glands, basal ones slightly larger, secondary veins arching and usually looped but often hardly visible, tertiary veins not visible but presumably reticulate. *Inflorescences* terminal and axillary, often opposite to leaves, yellowish, simple, without sterile basal region, pistillate and staminate flowers in same thyrse or pistillate flowers separated, staminate thyrse 5–60 by 1–2 mm, glabrous to pilose. *Bracts of staminate cymules* triangular, acute, with a pair of flattened-orbicular to falcate glands touching the axis of the thyrse. *Staminate cymules* 1–3-flowered; bracteoles absent. *Staminate flowers* with very short (less than 0.5 mm long) pedicel, hardly elongating when flowering; calyx with 3 spathulate, quite large, free sepals; stamens 3, filaments longer than anthers. *Pistillate flowers* 1 (very rarely 2) at base of staminate thyrse or often separated from staminate part and on different height, sessile; calyx with 3 sepals, triangular, free, glandless or with a pair of minute basal glands; ovary 3-locular, usually with 2 longitudinal rows of spine-like excrescences on each carpel, glabrous to hirsute; style usually absent, stigmata 3, undivided, glandless. *Fruits* with short (0–2 mm long) pedicel; 3-seeded, oblong with very regular shape, usually with 6 rows of spine-like excrescences, dry, dehiscing regularly along the septa, glabrous to hirsute; mericarps with a thin exocarp (fruit length/pericarp thickness > 10/1), septa very regular, with a small separate basal triangle and 1 furcate vascular strand; remaining central columella very regular, slightly alate with parallel margins over its whole length. *Seeds* elliptic-oblong with truncate ends, dry, with a large persistent caruncle stipitate and lenticular when dry.

Distribution — Fourteen species currently accepted, ten in tropical S America south of the Amazon, one in northern S America and C America up to Mexico, and one in the Old World from Africa through Asia to N Australia, throughout Malesia in the W part, but absent from the Philippines, and not yet known from New Guinea. Three additional African species have recently been attributed to *Microstachys* (Esser, 1998b).

Notes — 1. In the New World, the distinction between the species has notoriously posed problems, based primarily on characters of indumentum and leaf shape. The distinctiveness of the only Asian species, however, has never been questioned.

2. Von Martius & Zuccarini (1824a) described 17 species of *Cnemidostachys* simultaneously, and several previous authors avoided to select a lectotype (e.g., Webster, 1994). However, the plate illustrating *C. myrtilloides* was also cited as the one accompanying the diagnosis of the genus by Von Martius & Zuccarini (1824a), and it was also the only one of the several plates that included separate drawings of diagnostic characters (Von Martius & Zuccarini, 1824b) and therefore it was obviously meant as illustration representative for the genus. For this reason *C. myrtilloides* was proposed as lectotype by Esser (1998b).

### 1. **Microstachys chamaelea** (L.) Müll. Arg. — Fig. 4, Map 4

*Microstachys chamaelea* (L.) Müll. Arg., Linnaea 32 (1863) 95; see note 1. — *Tragia chamaelea* L., Sp. Pl. (1753) 981. — *Cnemidostachys chamaelea* (L.) Spreng., Syst. Veg. 3 (1826) 835. — *Excoecaria chamaelea* (L.) Baill., Adansonia 6 (1867) 323. — *Sebastiania chamaelea* (L.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 1175; Benth., Fl. Austral. 6 (1873) 151; Hook.f., Fl. Brit. India 5 (1888) 475; Kuntze, Revis. Gen. Pl. 2 (1891) 619; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 268, 296; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 116; Merr., Philipp. J. Sci., Bot. 10 (1915) 190; Ridl., Fl. Malay Penins. 3 (1924) 317; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 454, f. 55.5–14; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1988; M.R. Hend., Malay. Wild Fl. (1959) 464, f. 418; N.C. Nair & Maitreyi, Bot. Gaz. 124 (1962) 58; Backer & Bakh. f., Fl. Java 1 (1964) 498; Airy Shaw, Kew Bull. 26 (1972) 339; Whitmore, Tree Fl. Malaya 2 (1973) 131; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 195; Kew Bull. 35 (1980) 686; Muelleria 4 (1980) 244; H. Keng, Conc. Fl. Sing. (1990) 113; P.H. Hô, Câyco Viêtnam 2, 1 (1992) 352; I.M. Turner, Gard. Bull. 45 (1993) 87; Gard. Bull. 47 (1995) 232. — Lectotype (proposed here): Herb. Hermann vol. 4: 43, no. 335 (BM), Ceylon.

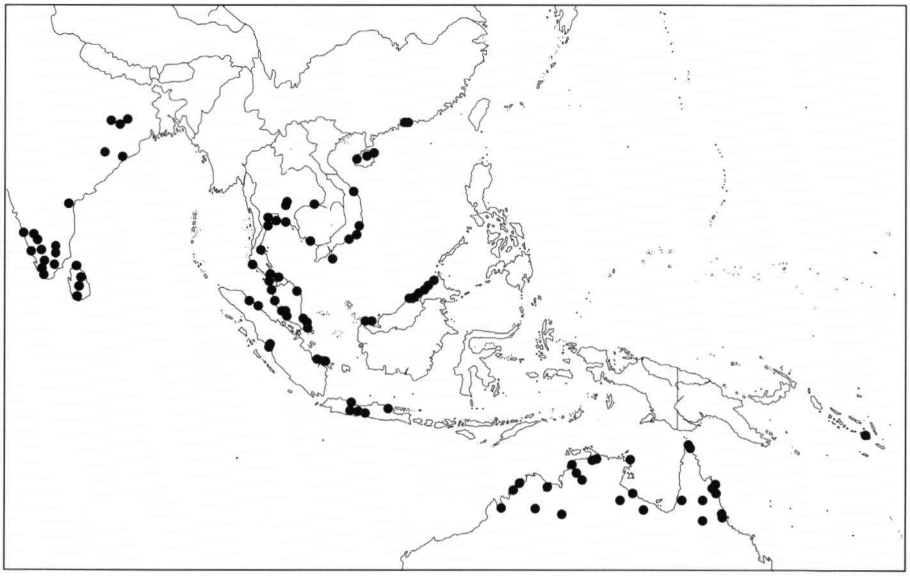
*Elachocroton asperococcus* F. Muell., Hook. J. Bot. Kew Gard. Misc. 9 (1857) 17. — *Sebastiania chamaelea* (L.) Müll. Arg. var. *asperococca* (F. Muell.) Pax in Engl., Pflanzenr. IV.147.v (1912)

117; Merr., Philipp. J. Sci., Bot. 11 (1916) 76; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xiv, add. VI (1919) 58; Merr., Bibl. Enum. Bornean Pl. (1921) 347. — Type: *F. Müller s.n.* (holo MEL, n.v.; iso K), Australia, 'in locis sterilioribus ad flumen Victoriae'.

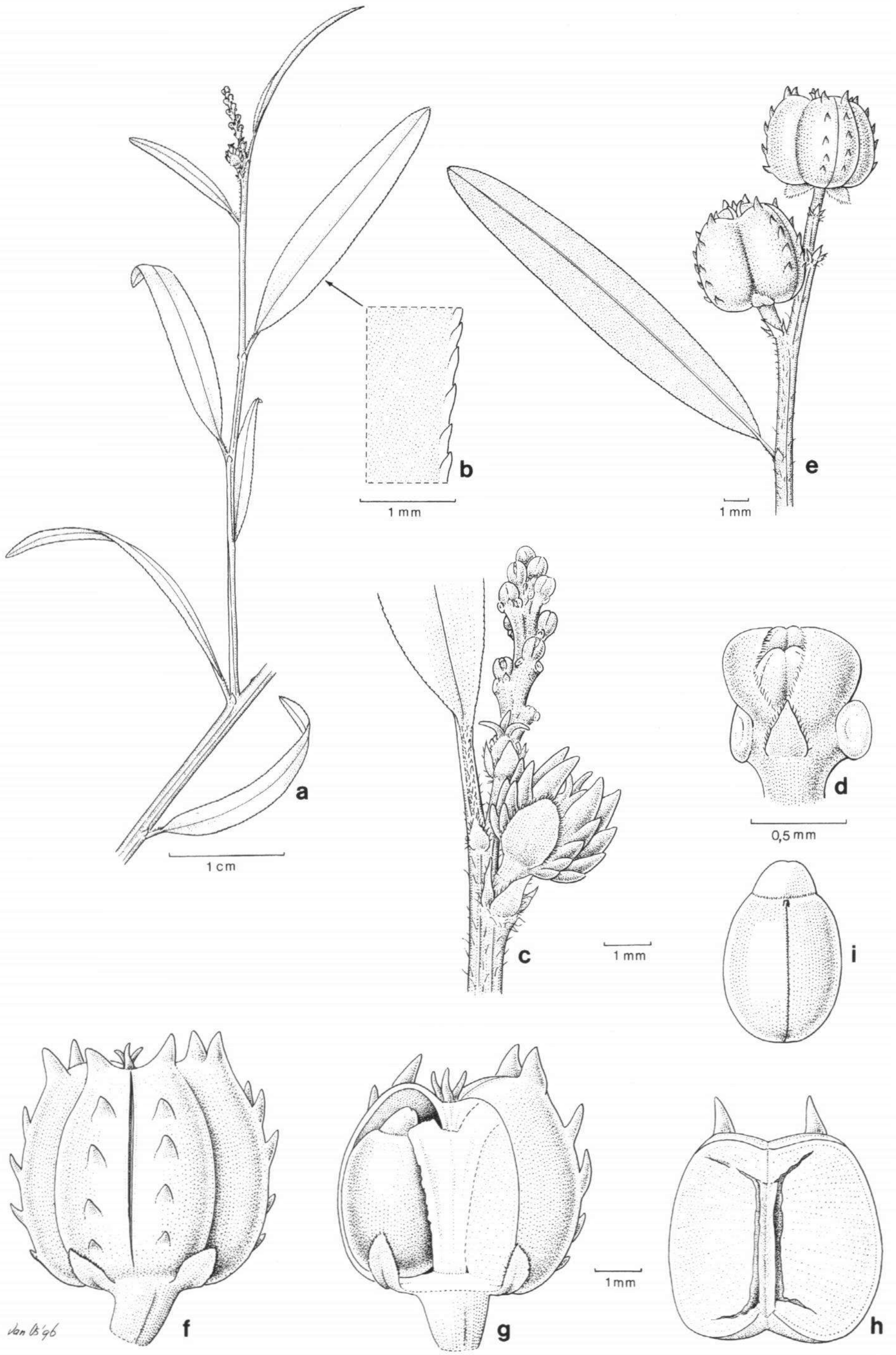
*Cnemidostachys linearifolia* Miq., Fl. Ind. Bat. Suppl. 1 (1861) 460. — Type: *Kurz* (as *'Amann'*) *9* (holo U; iso K), Java, Banka, 'in pratis aridis ad rivulam Muntok'.

Perennial herb to many-stemmed subshrub, up to 90 cm tall and 30 cm in total diameter; originating from a yellowish-brown tap root c. 15 cm long. *Indumentum* 0.25–0.4 mm long. *Stipules* 0.6–2 by 0.2–0.5 mm, densely pilose to ciliate. *Leaves:* petiole 0.1–0.25 cm long, pilose, glabrescent; blade elliptic to lanceolate, 1.6–6 by 0.3–0.8 (–1.2) cm, base acute to obtuse, margin with ± appressed teeth, apex rounded to mucronate, lower surface bright but smooth, pilose and glabrescent, with 0–6 strictly marginal glands per side, 0.2–0.25 mm diam., secondary veins 13–35 pairs, angle with midrib 45–75°, often hardly visible. *Inflorescences:* staminate part 5–15 by 1–1.5 mm, axis usually glabrous. *Bracts of staminate cymules* c. 0.4 mm long, nearly completely covered by the bract glands. *Staminate cymules* 1-flowered. *Staminate flowers* nearly sessile (pedicel 0.2–0.4 mm long); calyx 0.5 mm long, with distinctly ciliate sepals. *Pistillate flowers:* calyx 0.6–1.2 mm long, with distinctly ciliate sepals; ovary glabrous; stigmata filiform, c. 0.5–1 by 0.1 mm. *Fruits* 3.5–4.5 mm long, green, turning pinkish to olive brown to orange, with 0.6–1 mm long excrescences in 6 rows of 5–6 each; pericarp c. 0.15 mm thick. *Seeds* 2.5–2.75 by 2–2.25 mm, brown, sometimes brown-yellowish-whitish mottled.

Distribution — Widespread in Africa (e.g., Cameroun, Togo) and in Asia from India and Sri Lanka to Vietnam and S China, the Solomon Islands and N Australia; Malesia: Peninsular Malaysia (Thailand, Malaya, Singapore), Sumatra, Java, Borneo (Brunei, Sabah, Sarawak).



Map 4. Distribution of *Microstachys chamaelea* (L.) Müll. Arg.


a
1 cm
b
1 mm
e
1 mm
c
1 mm
d
0,5 mm
i
f
g
1 mm
h
Van Os '96

Habitat & Ecology — Found on beaches, sandy sites, roadsides and waste places, also on lateritic outcrops, grassfields and open woodland, often gregarious. Soil: sand, alluvial and lateritic ground. Altitude: sea level up to 300 m. Flowers and fruits collected the whole year through, but particularly in the rainy season.

Vernacular names — Peninsular Malaysia: ambin-ambin (Burkill, 1935). Borneo: daun merayat (Lundu Malay).

Uses — When cooked together with meat and vegetables, whole young plants are used for speedy recovery for women after giving birth [*S (Mamit) 35141*]. Dragendorff (1898; repeated by Burkill, 1935) mentions the use of the plant as astringent, tonic, against diarrhoea and syphilis in India.

Notes — 1. De Jussieu (1824), when describing *Microstachys*, mentioned *Tragia chamaelea* as belonging to his new genus. But because he did not definitely combine genus and species, the combination *Microstachys chamaelea* cannot be attributed to him (Art. 33.1 ICBN). Baillon (1858) cited this combination only as a synonym, which also does not constitute a valid publication (Art. 34.1 ICBN). Müller Argoviensis (1863), therefore, was the first to use and accept this name.

2. There has been confusion in the labels and the literature between *Cuming 2324* and *Cuming 2329*. Müller Argoviensis (1866) and Pax & Hoffmann (1912) cited both specimens under *Sebastiania (Microstachys) chamaelea*. Nevertheless, *Cuming 2324* (K) is the type collection of *Sarcotheca monophylla* (Planch. ex Hook.f.) Hallier f., based on *Connaropsis monophylla* Planch. ex Hook.f., an Oxalidacea. At K (including the herbaria of Bentham and Hooker), only *Cuming 2329* can be referred to *M. chamaelea*; the same is true for FR. At L, however, only *Cuming 2324* is an originally labelled *M. chamaelea*, and *Cuming 2329* was not found at all. Thanks are due to J.F. Veldkamp who recognized this confusion. Both specimens, labelled as collected in the Philippines, really are from Malaya.

3. Contrary to data in the literature, leaves with entire margins were never found, although the appressed teeth are very small and may be overlooked. In Malesia, the appendages of the fruits are a very regular feature. Those of Australian plants, however, are weaker to totally absent. Specimens from Australia may also be distinguished by their often wider leaves.

4. *Microstachys chamaelea* is sometimes confused with *Sauropus bacciformis* (L.) Airy Shaw in the herbaria, a herb with similar habit but entire leaves and smooth fruits with petals and carinate, reddish seeds. Thanks are due to C. Barker for providing the determination of the latter species.

Fig. 4. *Microstachys chamaelea* (L.) Müll. Arg. a. Habit with pistillate flower and staminate thyrses; b. detail of leaf margin with densely packed glandular teeth; c. detail of habit with stipules, inflorescence, and young fruit; d. staminate flower, nearly sessile, with large bract glands and free sepals; e. infructescence; f. fruit with typical excrescences; g. partly opened fruit with the characteristic alate columella; h. mericarp with the large septa, the apical vascular strand (left upper part) and the basal split, often as a typical triangle; i. seed with large caruncle [a–d: *Haviland & Hose 3709*, L; e–h: *Forman & Blewett 861*, L].

## 5. SAPIUM

### INTRODUCTION

*Sapium* in Malesia has long been known for its difficult circumscription. The name is an old Greek word of Plinius, used for *Pinus* but referring to its sap. *Sapium* was first described by Browne (1756), but has recently been conserved in the sense of Jacquin (1760), the former probably being a *Gymnanthes* (Kruijt & Zijlstra, 1989; Brummitt, 1994).

The first Malesian species described under *Sapium* was *S. indicum* (Willdenow, 1805). In the following decades, several species were assigned to *Sapium*, newly described or newly combined; but also several species were removed from *Sapium*. *Sapium* was even united with other genera, i.a., with *Stillingia* (Baillon, 1858), resulting in a quite complicated taxonomic history. Pax & Hoffmann (1912) applied a broad concept of *Sapium*, including several sections separated by earlier authors; it is still upheld by most authors up to Webster (1994). This circumscription, however, blurred the delimitation against other related genera. As a result, some species, e.g., *S. indicum*, were sometimes assigned to *Sapium* (Gagnepain, 1926), sometimes to other genera, e.g., to *Excoecaria* (Smith, 1910).

Indeed, *Sapium* is characterized by the red aril of the seeds, accompanied by constant features of the staminate flowers (two fused sepals, two stamens) and pollen ('equatorial ring'), as elaborated by Kruijt (1996). It is therefore identical with '*Sapium* subg. *Eusapium* Pax & K. Hoffm. sect. *Americana* Pax & K. Hoffm.' of Pax & Hoffmann (1912). This taxon is indigenous to the Neotropics and comprises c. 20 species, mostly distinguished by characters of their leaves.

All indigenous Malesian species described under *Sapium* lack the aril and, therefore, must be excluded from *Sapium* (the pollen has not been studied). Sometimes S American plants of *Sapium* have been introduced in Malesia as a source of rubber and are the only records of the genus for Malesia. At least six species of *Sapium* have been cited in this regard. This, however, is a consequence of the difficult determination of the species, *Sapium* being one of the most difficult genera in the Euphorbiaceae regarding the delimitation of species (Webster, 1967). Fortunately, the recent monograph of Kruijt (1996) allowed a clarification, although Kruijt did not explicitly consider the Malesian cultivars.

### **Sapium** Jacq.

*Sapium* Jacq., Enum. Syst. Pl. (1760) 9; nom. cons. [Taxon 43 (1994) 114], non *Sapium* P. Browne [Civ. Nat. Hist. Jamaica 2 (1756) 338]; A. Juss., Euphorb. Gen. (1824) 49; G.L. Webster, J. Arnold Arbor. 48 (1967) 391; Kruijt, Biblioth. Bot. 146 (1996) 27; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 123. — *Stillingia* subg. *Sapium* (Jacq.) Klotzsch, Arch. Naturgesch. 7 (1841) 187. — *Stillingia* sect. *Sapium* (Jacq.) Baill., Étude Euphorb. (1858) 513; Adansonia 1 (1861) 351. — *Sapium* sect. *Eusapium* Müll. Arg., Linnaea 32 (1863) 115, nom. inval.; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 98; T. Post & Kuntze, Lex. Gen. Phan. (1903) 498. — *Excoecaria* sect. *Sapium* (Jacq.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 1202. — *Sapium* subg. *Eusapium* Pax & K. Hoffm. sect. *Americana* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 200, nom. inval.; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 198. — Type: *Sapium aucuparium* Jacq., nom. illeg. [= *S. glandulosum* (L.) Morong]; compare Kruijt & Zijlstra (1989).

Trees. Monoecious. Leaves present on flowering and fruiting twigs. *Indumentum* absent. *Stipules* broadly ovate to triangular, 1.5–2.5 mm long, undivided, glandless. *Leaves* regularly spaced; petiole distinct, always less than half as long as the blade, usually apically glandular; blade quite variable, 2.5–9 cm wide, margin entire or indistinctly serrate with teeth 3–5 mm apart, glandless above, below usually neither papillate nor whitish-farinose and with marginal glands that often are found in small cilia-like marginal lobes, basal glands hardly different, secondary veins distinct, basal ones not different, intersecondary veins present, tertiary veins usually distinct, indistinctly percurrent to reticulate, smaller veins reticulate. *Inflorescences* terminal and axillary, yellowish, not compound, pistillate and staminate flowers in same inflorescence. *Bracts of staminate cymules* with a pair of disc-shaped glands touching the axis of the thyrse. *Staminate cymules* (3–)7–18-flowered; bracteoles present, mostly small. *Staminate flowers* with a pedicel c. 0.5 mm long only present when flowering; calyx with 2 largely fused sepals; stamens 2, filaments longer than anthers. *Pollen* with equatorial ring (fide Kruijt, 1996). *Pistillate flowers* up to 10 at base of staminate thyrse; pedicel absent to short; ovary 3-locular (1- or 2-locular in some species; not in Malesia), smooth; style short, stigmata undivided, glandless. *Fruits* sessile to shortly pedicellate; 3-seeded (1- or 2-seeded in some species; not in Malesia), smooth, dry, opening regularly along the septa, pericarp thin (fruit length/pericarp thickness > 10/1), septa with one vascular strand, remaining columella slightly alate. *Seeds* completely covered by a red aril.

Distribution — Approximately twenty-five species, indigenous and restricted to the Neotropics from Mexico and the Antilles to Argentina and Bolivia. Introduced into the USA, sometimes cultivated in other tropical regions.

### 1. Sapium glandulosum (L.) Morong

*Sapium glandulosum* (L.) Morong, Ann. New York Acad. Sci. 7 (1893) 227; Kruijt, Biblioth. Bot. 146 (1996) 44. — *Hippomane glandulosa* L., Sp. Pl. (1753) 1191. — *Sapium aucuparium* Jacq., Enum. Syst. Pl. (1760) 31, nom. superfl.; Hassk., Retzia 1 (1855) 162. — *Sapium biglandulosum* (L.) Müll. Arg. var. *aubletianum* Müll. Arg., Linnaea 32 (1863) 117, nom. superfl. — *Sapium aubletianum* (Müll. Arg.) Huber, Bull. Herb. Boiss. 2, VI (1906) 362, nom. superfl.; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1960. — Lectotype [proposed by Croizat, J. Arnold Arbor. 24 (1943) 176]: Plukenet, Phytographia Almagestum (1694) t. 229 f. 8.

Tree, measurements not known in Malesia but up to 20 m tall and dbh up to 40 cm in the Neotropics, slightly buttressed. *Bark* grey, smooth with irregular longitudinal fissures. *Stipules* 1.5–2.2 by 1.2–2 mm, often persistent. *Leaves:* petiole 0.8–2.4 cm long, apically with a pair of distinctly stipitate glands 0.5–1 mm diam. usually separate from the blade; blade elliptic to obovate, (5–)10–17 by 2.5–6.5 cm, base acute to obtuse, margin serrate when young, later nearly entire, apex acuminate, below with 0–3 glands per side strictly marginal and in small lateral auricles of the blade 0.4–1 by 0.5–1 mm, secondary veins (12–)14–23 pairs, angle with midrib 65–70°, arching but not joined towards the margin, basal ones not differing. *Inflorescences:* staminate part 60–140 by c. 6 mm. *Bracts of staminate cymules* c. 0.6 mm long, their glands 2–2.25 mm long and completely on the axis below the bract. *Staminate cymules* c. 7–8-flowered. *Staminate flowers:* pedicel up to 0.5 mm long; calyx 1.25 mm long; stamens with filaments 1.25 mm long when flowering, anthers 0.5–0.75 mm long.

*Pistillate flowers* c. 5–10 per thyrse; sessile; calyx 1 mm long, with 3 glandless sepals; ovary 3-locular; style c. 0.5 mm long, stigmata c. 1.5 mm long. *Fruits* sessile; 3-seeded, nearly circular, 9 mm long, green-brownish; pericarp c. 0.25 mm thick. *Seeds* c. 5 by 4.5 mm.

Distribution — Indigenous to the Neotropics from the Caribbean Islands and Mexico to the Guianas and Argentina. In the first half of this century planted in Malesia, e.g., in the Botanical Gardens of Singapore and Buitenzorg.

Habitat & Ecology — In the Neotropics found especially in secondary forests and in coastal regions, in the lowland up to 400 m altitude. It is the most common species of the genus.

Uses — Planted as a source of rubber. The rubber is of high quality, comparable and in some properties even superior to *Hevea* rubber, but is difficult to harvest; therefore it never became commercially important. Burkill (1935) mentions use of the poisonous latex against warts. It is also used by Indians to catch birds.

Notes — 1. This species is the most variable and taxonomically the most problematical one of this difficult genus. Kruijt (1996) suggests to unite 57 names (!) in this species.

2. Burkill (1935) cites two other American species whose cultivation had been tried in Singapore at the beginning of this century, namely *S. jenmanii* Hemsl. and *S. jamaicense* Sw. [an illegitimate name for *S. laurifolium* (A. Rich.) Griseb.: Kruijt (1996: 59)]. Both are distinct from *S. glandulosum*; they may be distinguished, e.g., by their elliptic, hardly obovate leaves with indistinct petiolar glands, *S. jenmanii* also by its 1-seeded fruits. Because no Malesian specimens of these species were seen, the names cannot be confirmed.

## 6. SHIRAKIOPSIS

### INTRODUCTION

Hurusawa (1954) described the genus *Shirakia*. The name is based on the earliest name applied by Von Siebold & Zuccarini (*Croton shiraki*, 1843, a nomen nudum) to the type species, *Shirakia japonica* (Siebold & Zucc.) Hurus. *Shirakia* was based on the section *Parasapium*, which was moved between different genera but finally allied to *Sapium* as *Sapium* sect. *Parasapium* (Müll.Arg.) Hook.f. The name, however, is illegitimate because a later homonym of a fossil fern genus, *Shirakia* S. Kawas., and was replaced with *Neoshirakia* by Esser (1998a).

Hurusawa included three species in *Shirakia* Hurus., namely *S. cochinchinensis* (Lour.) Hurus., *S. indica* (Willd.) Hurus., and *S. japonica*, the latter being the type. Kruijt (1996), in a preliminary synopsis of *Shirakia*, added two additional Malesian species and several African ones and provided the necessary combinations.

These species share similar inflorescences. Two of them, however, are quite different in their leaves and fruits: *S. cochinchinensis*, which is now transferred to *Triadica* (see there), and *S. japonica*. The latter differs by, e.g., being totally glabrous and by often entire leaves, different, laminar leaf glands, much larger stipules, and a thin fruit wall. A cladistic study of Malesian Hippomaneae, in which *S. japonica* was included (Esser et al., 1998) showed that Kruijt's concepts cannot be maintained.

Either a broad concept of *Shirakia* must include additional species of *Gymnanthes* (in this case *Gymnanthes* would have priority), or *S. japonica* has to be separated from the remainder of the genus. In the latter case, applied here, a new genus has to be established, congruent with most of the section *Parasapium*. This new genus, *Shirakiopsis*, includes three Malesian species.

*Shirakiopsis indica* was described by Willdenow (1805) as *Sapium indicum*. It had already been known under different names to several pre-Linnean authors, as was discussed by Hamilton (1837) and Merrill (1917). Wallich (1847) cited some additional nomina nuda (*Sapium bingyricum*, *S. hurmais*) for *S. indica*, which were taken up by some later authors. Wight (1853) contributed the first illustrations of this species. Later on, it was moved around between several genera, including *Excoecaria*, *Sapium*, *Shirakia*, and *Stillingia*.

Miquel (1861) described *Stillingia* [*Sapium*] *diversifolia*. This species, poorly known for a long time and even treated under *Triadica* by Müller Argoviensis (1866, as *Excoecaria* sect. *Triadica*), was considered as identical with *S. indica* by Airy Shaw (1981, as *Excoecaria indica*).

Another species of Miquel (1859), *Excoecaria virgata* Zoll. & Moritzi ex Miq., was recognized by all later authors and is accepted here too.

The third Malesian species was described by Merrill (1913) as *Sapium sanchezii*. It remained poorly known for several decades, and only Kruijt (1996) gave additional information.

## CHARACTERS

### Vegetative characters

The indumentum of coloured hairs is uncommon and remarkable. Also the leaves of the three species are characteristic. The short glandless petioles, the quite constant size and proportion of the blades, the serration, and the marginal glands with the basal ones usually enlarged (Fig. 5a–c), are unique in Malesian Hippomaneae.

*Shirakiopsis indica*, *S. sanchezii* and *S. virgata* are definitely indistinguishable by their leaves. This is very uncommon for Hippomaneae, where usually leaf characters are most useful for differentiation.

### Inflorescences and flowers

The inflorescences of *Shirakiopsis* are similar to those of most other Hippomaneae. The mentioned pubescence is, however, remarkable, as is the regularly elliptical shape of the bract glands and the higher number of long-pedicellate staminate flowers. The latter two characters agree with *Triadica*. Contrary to *Triadica*, the pistillate flowers are few and shortly pedicellate.

Like in characters of the leaves, *S. indica*, *S. sanchezii* and *S. virgata* have hardly distinguishable inflorescences and flowers. Contrary to the leaves, this is common in most genera of the tribe.

### Fruits and seeds

The fruits of each species of *Shirakiopsis* are very characteristic and, therefore, support their delimitation. The species have trimerous and comparatively large fruits with a thick pericarp and always one vascular strand per septum. They may dehisce immediately and regularly (*S. sanchezii*: Fig. 5h), or retardedly to irregularly (*S. indica* with woody, hard capsules, *S. virgata* with drupe-like fleshy ones). The caruncles are very indistinct to absent in all species.

## BIOGEOGRAPHY AND RELATIONSHIPS

The Malesian species of *Shirakiopsis* resemble each other very closely and have a vicariant distribution (Map 5): *S. indica* is widespread but absent from Java, the Philippines and the Lesser Sunda Islands, *S. virgata* is restricted to Java, and *S. sanchezii* is known from a few localities of the Philippines and the Lesser Sunda Islands. Although all species are shore plants, the difference between widespread and endemic species is remarkable. This is probably correlated with the different dispersal syndromes, the very thick-walled and hardly dehiscent capsules of *S. indica* being obviously well-adapted to floating in water for a long time; the seeds of *S. indica* germinate only after about one year (Ng, 1991).

Within Malesian Hippomaneae, *Shirakiopsis* may be easily recognized by its indumentum, especially of the inflorescences, by its serrate leaves without petiolar glands, and by its fruits with a remarkably thick fruit wall and dry seeds. The inflorescence characters, except for the pubescence, resemble *Triadica*, but this is based on some symplesiomorphies. Within Malesian Hippomaneae, the genus is however most closely related to *Gymnanthes*, as a recent cladistic study (Esser et al., 1998) corroborated. *Excoecaria* differs in several characters, e.g., the sessile staminate flowers with 3 free sepals and constantly 3 stamens, the fruits with a very thin wall and septa with several (mostly 3) vascular strands; it is not very closely related.

The three African species are very similar to the Malesian ones, differing mainly in reddish (not yellowish) hairs and two-carpellate, often very small fruits (Esser, 1994). *Shirakiopsis*, therefore, occurs in Africa and Asia, on both continents with a comparable diversity.

### **Shirakiopsis** Esser, *gen. nov.*

Genus novus tribu Hippomanearum pilis coloratis obtectis, petiolis eglandulosis, foliorum laminis serratis subtus nec papillatis nec albidis glandulas marginales ferentibus, inflorescentiis non ramosis, cymulis masculinis plurifloris, floribus masculinis distincte pedicellatis, sepalis connatis, fructibus septicidaliter dehiscentibus, seminibus siccis minutissime carunculatis vel ecarunculatis. — Type: *Shirakiopsis indica* (Willd.) Esser, based on *Sapium indicum* Willd.

*Shirakia* Hurus., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6 (1954) 317, pro parte excl. type; Kruijt, Biblioth. Bot. 146 (1996) 7, 91, pro parte excl. type. — *Excoecaria* sect. *Parasapium* Müll. Arg., Linnaea 32 (1863) 123. — *Excoecaria* sect. *Sclerocroton* (Hochst.) Müll. Arg. subsect. *Parasapium* (Müll. Arg.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 1216. — *Sapium* sect. *Parasapium* (Müll. Arg.) Hook. f., Fl. Brit. India 5 (1888) 471; Pax & K. Hoffm. in Engl., Pflanzenr. IV. 147.v (1912) 249; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 202.

Trees. Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* consisting of pale to yellowish (reddish in some African taxa), multicellular, uniseriate hairs. *Stipules* ovate to triangular, 1–2 mm long, undivided, glandless. *Leaves* regularly alternate; petiole 0.6–2 cm long, much shorter than blade, glandless; blade oblong to elliptic to ovate, base obtuse to slightly attenuate, margin serrate with teeth 3–5 mm apart, apex acute to acuminate, glandless above, lower surface paler than upper one but not whitish and not papillate, with 0–10 strictly marginal glands on each side, basal ones slightly larger but very similar, secondary veins quite numerous (15–26 pairs) and arching but not joined towards the margin, basal pair similar. *Inflorescences* terminal, yellowish, simple, without sterile basal region, pistillate and staminate flowers in same thyrse, each thyrse 40–120 by 4–6 mm, pilose. *Bracts of staminate cymules* triangular, pilose to ciliate, at base with a pair of elongate-spheroidal to elliptical glands touching the axis of the thyrse and sometimes decurrent. *Staminate cymules* (3–)5–7-flowered. *Staminate flowers* with distinct (1–3 mm long) pedicel in bud and when flowering; calyx with 3 sepals, fused at base; stamens 3, filament and anther of similar length. *Pistillate flowers* 1–3 at base of staminate thyrse, sometimes absent; pedicel distinct; calyx with 3 (2 in African species) sepals, irregularly triangular, fused at base, glandless; ovary 3-locular (2-locular in African species), smooth, usually glabrous; style present, stigmata 3 (2 in African species), undivided, glandless. *Fruits* distinctly (at least 8 mm) pedicellate; 3-seeded (2-seeded in African species) mericarps, smooth, dry and woody (partly fleshy in *S. virgata*), regularly dehiscent along the septa (sometimes tardily so); mericarps with very thick pericarp in Malesian taxa (fruit length/pericarp thickness < 10/1; but much thinner in African taxa), septa with a separate basal triangle and 1 vascular strand, central columella alate. *Seeds* elliptic, dry, caruncle very inconspicuous to absent.

Distribution — Six species, from these three in tropical Africa and three in tropical Asia from India to Cambodia and throughout Malesia up to the Caroline and the Solomon Islands in the Pacific.

Note — Except for the unusually thick pericarp of the fruits and the indumentum, the genus is characterized mostly by the absence of characters. Its circumscription is still insufficient, but an elaboration would require comparative studies of African and Neotropical taxa, too. The species are very similar to each other, but at least the fruits allow clear distinctions.

## KEY TO THE MALESIAN SPECIES

1a. Fruits acute at both ends, longer than wide, always with a fleshy outer layer. — Java ........................................ **3. S. virgata**

b. Fruits basally rounded to slightly attenuate, at least as wide as long, dry when ripe. — Not in Java ........................................ 2

2a. Fruits very hard, hardly and slowly but regularly opening, hardly sulcate. — Widespread in Malesia, but absent from the Lesser Sunda Islands and the Philippines ........................................ **1. S. indica**

b. Fruits regularly and easily opening, deeply sulcate. — Lesser Sunda Islands, Philippines ........................................ **2. S. sanchezii**

### **1. Shirakiopsis indica** (Willd). Esser, *comb. nov.* — Map 5

*Sapium indicum* Willd., Sp. Pl. ed. 4, 4 (1805) 572; Roxb., Hort. Bengal. (1814) 69; Fl. Indica ed. 1832, 3 (1832) 692; Buch.-Ham., Trans. Linn. Soc. 17 (1837) 229; Hassk., Retzia 1 (1855) 158; Wight, Icon. Pl. Ind. Orient. 6 (1853) t. 1950; Baill., Étude Euphorb. (1858) 513; Benth.,

J. Linn. Soc., Bot. 17 (1878) 242; in Benth. & Hook.f., Gen. Pl. 3 (1880) 335; Hook.f., Fl. Brit. India 5 (1888) 471; G. Watt, Dict. Econ. Prod. India 6, 2 (1893) 471; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 251; Merr., Interpr. Rumph. Herb. Amboin. (1917) 328; J.J. Sm. in Herderschee, Nova Guinea 12 (1917) 548; Merr., Bibl. Enum. Bornean Pl. (1921) 348; Ridl., Fl. Malay Pen. 3 (1924) 317; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 394–396; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1961; Corner, Ways. Trees Malaya 1 (1940) 277; K. Heyne, Nutt. Pl. Indon. ed. 3, 1 (1950) 961; Airy Shaw, Kew Bull. 26 (1972) 330; Whitmore, Tree Fl. Malaya 2 (1973) 128, 129; Ng, Malay. For. Rec. 34 (1991) 83, f. 65B; I.M. Turner, Gard. Bull. 47 (1995) 231. — *Excoecaria indica* (Willd.) Müll.Arg., Linnaea 32 (1863) 123; in DC., Prodr. 15, 2 (1866) 1216; Kurz, Forest Fl. Burma (1877) 413; J.J. Sm. in Koord. & Valeton, Bijdr. Boomsoort. Java 12 (1910) 615; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 114; Kew Bull. Add. Ser. 8 (1980) 89; Kew Bull. 36 (1981) 297; Kew Bull. 37 (1982) 20; Goel & Chakrab., J. Econ. Tax. Bot. 14 (1990) 738; Verheij & Coronel (eds.), Pl. Res. SE Asia (PROSEA handb.) 2, Edible fruits and nuts (1991) 376; Purwaningsih in Lemmens & Wulijarni-Soetjipto (eds.), Pl. Res. SE Asia (PROSEA handb.) 3, Dye and tannin-producing plants (1991) 73, 74; P.H. Hô, Câyco Viêtnam 2, 1 (1992) 353. — *Shirakia indica* (Willd.) Hurus., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6 (1954) 317; Kruijt, Biblioth. Bot. 146 (1996) 93. — Type: *Herb. Willdenow fol. 17946* = *Buchanan Hamilton s.n.* (holo B-WILLD, n.v., IDC microfiche 1297/7), India, Tripura; see note 1.

*Sapium bingiricum* Roxb. ex Baill., Etude Euphorb. (1858) 513, Atlas (1858) pl. 6, f. 10–11. — Type: *Herb. Roxburgh s.n.* (holo G; ?iso BM, BR; Icones Roxburghianae 1296); see note 1.

*Stillingia diversifolia* Miq., Fl. Ind. Bat. Suppl. 1 (1861) 461. — *Excoecaria diversifolia* (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1211; Kruijt, Biblioth. Bot. 146 (1996) 88. — *Sapium diversifolium* (Miq.) Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 296. — Type: *Teijsmann HB 4215* (holo U; drawing of U sheet in A; iso G-DC, n.v., IDC microfiche 2619/9), Sumatra, Lampong, a fluv. Toelang bawang.

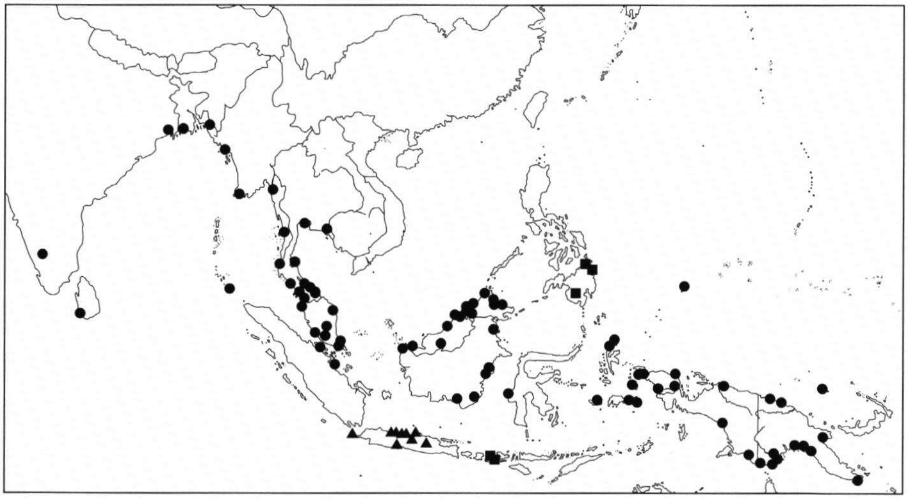
Tree, up to 30 m high, stem diameter up to 40 cm, bole twisting, with spines at base and buttresses up to 2 m high, branching from base. Young *twigs* pilose, especially in axils. *Indumentum* pale to yellowish. *Bark* brown greyish to olive, 2–4 mm thick, vertically furrowed and fissured, peeling in small rectangles; outer bark thin; inner bark yellow to light brown, darkening rapidly, fibrous. *Slash* with strong, sweet smell. *Sapwood* and heartwood homogeneous, dirty white to pale yellow to straw-coloured, of moderate weight and hardness, with numerous pores. *Leaves:* petiole 1.1–1.4 cm, sparsely pilose to glabrous; blade oblong to elliptic to slightly ovate, 7–14 by 3–4 cm, base obtuse, apex subacuminate to acuminate, lower surface with 2–4 glands per side, 0.25–0.4 mm diam., basal glands 0.5–0.9 mm diam. and often touching the midrib, secondary veins 18–24 pairs, angle with midrib 60–66°, smaller veins distinct. *Inflorescences* 30–55 by 6–8 mm, axis pilose. *Bracts of staminate cymules* 1.25–2 mm long, pilose to ciliate, their glands 1–1.75 by 0.5–0.9 mm. *Staminate flowers* sparsely pilose; pedicel 1–2 mm long; calyx 0.6–0.8 mm long, ciliate; stamens with filaments 0.5–0.6 mm long when flowering, nearly absent in bud, anthers 0.4–0.5 mm long. *Pistillate flowers:* 1 (rarely 2) per thyrse or absent; pedicel c. 5 mm long; calyx 1.25–1.75 mm long, pilose; ovary 2.5 mm long; style c. 1.5 mm long, stigmata 4–6 mm long. *Fruits:* pedicel 8–22 mm long; schizocarp nearly globose in outline, 18–30 by 20–32 mm, rounded at both ends or slightly attenuate at base, not or very slightly sulcate, green and becoming black when ripe, dry and without fleshy outer layer; hardly and tardily dehiscent and often shed unopened, sometimes irregularly broken or opened partly septicidally or loculicidally; often with less than three seeds, but always regularly trimerous; mericarp with pericarp wall (2–)3–4 mm thick, septum remaining completely at mericarp, therefore without any septal gap or basal triangle; remaining columella only c. 4 mm long to nearly absent, not alate. *Seeds* 11–13 by 7–8.5 mm, keeled on the back, medium to pale brown, not spotted, without caruncle.

Distribution — Widely distributed from Sri Lanka and India (Malabar coast, Ganges) to Thailand, the Caroline Islands and Solomon Islands; in Malesia known from Peninsular Malaysia (incl. Singapore), E Sumatra, Borneo, Celebes, Moluccas, and New Guinea including the Bismarck Archipelago.

Habitat & Ecology — Found along rivers and seashores, in gallery, tidal and mangrove forests, in primary and advanced secondary forests of swampy and seasonally inundated places. Soil: clay, sand, mud. Very common to scattered. Altitude: sea level up to 75 m. Flowers in Malesia collected in Dec.–Jan., June–July, outside Malesia however, the whole year through; fruits collected the whole year through. The seeds germinate only after 318–413 days (Ng, 1991).

Uses — The timber is used for canoes and is supposed suitable for indoor work. Leaves have been applied to cure fever and gonorrhoea (Burkill, 1935). Fruits and leaves are boiled together with clothes as black dye, but also yellow-green colours can be obtained from it (e.g., in lower Siam: Burkill, 1935). The green fruits are used as a fish poison, e.g., by the Dusun (Borneo). The 'juice of the fruits' is applied by Kinomeri to cure toothache [*NGF (Floyd) 8039*]. The seeds contain a drying oil (Burkill, 1935) and can be eaten, whereas the fruit wall as well as other parts of the plant contain toxic latex, also known as fish poison (Dragendorff, 1898). In view of the variety of uses, the species is considered as an interesting crop species for places too wet for other crops (Purwaningsih, 1991).

Vernacular names — Thailand: kula. Peninsular Malaysia: gurah. Borneo: apid apid, gurah (Bisaya and Malay), keboean. New Guinea: Irian Jaya: fa (Asmat), farid, sakottoebo; Papua New Guinea: dordi (Kinomeri).



Map 5. Distribution of *Shirakiopsis indica* (Willd.) Esser (●), *S. sanchezii* (Merr.) Esser (■), and *S. virgata* (Merr.) Esser (▲).

Notes — 1. Hamilton (1837) explained that Roxburgh, to whom he sent his collection, transmitted it to Willdenow under the name *Sapium bingirium*. It may be, therefore, that the collections *Roxburgh s.n.* (BM, BR, G) and *Wallich Cat. 7963 A = Herb. Roxburgh s.n.* (K, K-WALL, P), both labelled as *Sapium bingirium*, are in fact isotypes of *S. indica*, and *Sapium bingiricum* of Baillon (1858) a homotypic synonym.

2. Merrill (1917) certainly was right that *Ichthyoctonos litorea* Rumph. must be referred to *S. indica*, not to *S. virgata* as had been done by earlier authors.

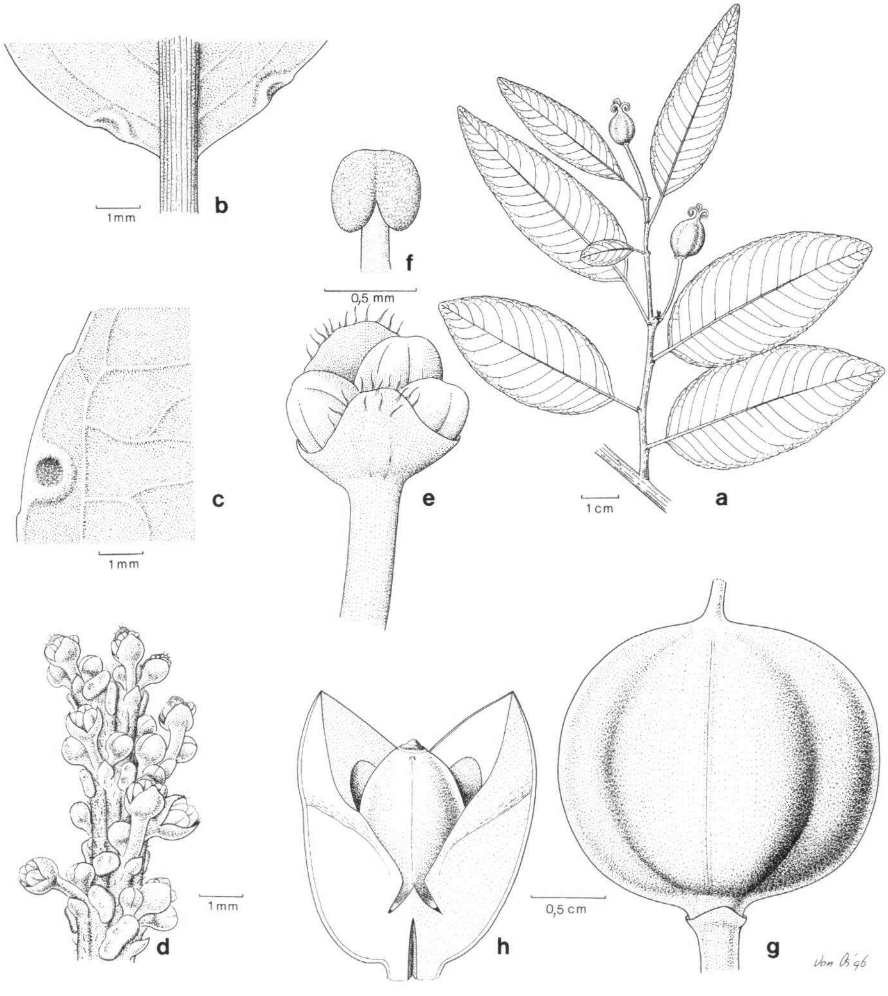


Fig. 5. *Shirakiopsis* Esser. a–c: Vegetative characters of *S. sanchezii* (Merr.) Esser; a. habit of fruiting plant; b. detail of leaf base, lower surface, with glands; c. detail of leaf margin, lower surface, with gland; d–f: flower characters of *S. virgata* (Zoll. & Moritzi ex Miq.) Esser; d. staminate thyrse with indumentum and pedicellate flowers; e. staminate flower with partly fused sepals, late bud; f. basifixed stamen; g & h: fruit characters of *S. sanchezii*; g. sulcate fruit; h. mericarp after septicidal dehiscence with thick pericarp and septa with single vascular strand and basal split ('triangle') [a–c: *PNH (Mendoza & Convocar) 10342*, L; d–f: *Zondag s.n.*, L; g, h: *Kartawinata 233*, L].

### 2. Shirakiopsis sanchezii (Merr.) Esser, *comb. nov.* — Fig. 5a–c, g–h, Map 5

*Sapium sanchezii* Merr., Philipp. J. Sci., Bot. 7 (1913) 406; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 423; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 461; Salvosa, Lex. Philipp. Trees (1963) 123; Airy Shaw, Alph. Enum. Euph. Philipp. Is. (1983) 44. — *Shirakia sanchezii* (Merr.) Kruijt, Biblioth. Bot. 146 (1996) 93. — Lectotype (proposed here): *Bolster 373* (UC), Philippines, Mindanao, Prov. Surigao, Surigao.

Tree, up to 15 m high. Young *twigs* pilose. *Indumentum* pale to yellowish. *Bark* c. 4 mm thick, somewhat rough, deeply fissured; inner bark brown, paler inside. *Stipules* 1.5–2 by 1.5–2 mm, entire to ciliate. *Leaves:* petiole 0.6–1.3 cm long, sparsely pilose to glabrous; blade ovate to elliptic, 5–10 by 2–3.5 cm, base obtuse, often slightly attenuate, apex acute to acuminate, upper surface pilose on midrib, lower surface almost glabrous and with 0–3 glands per side, 0.3–0.4 mm diam., basal glands 0.5–0.7 mm diam. and c. 1–2 mm above base of blade, secondary veins 17–25 pairs, angle with midrib 60–75°, smaller veins distinct. *Inflorescences* only studied in bud, these c. 20 by 4 mm, axis pilose. *Bracts of staminate cymules* c. 0.75 by 0.5 mm, pilose, further details not visible in bud. *Staminate flowers* sparsely pilose; pedicel c. 1 mm long in bud; calyx 0.6–0.7 mm long in bud. *Pistillate flowers* not studied, but according to fruits: distinctly pedicellate; calyx 1–1.5 mm long. *Fruits:* pedicel 15–30 mm long; schizocarp nearly circular in outline, 15–19 by 17–20 mm, deeply sulcate, fleshy only when young, dry when mature; style c. 2.5 mm long, stigmata 3–6 mm long; mericarps separating easily, glabrous; pericarp 2.5–3 mm thick; remaining columella 7–8 mm long. *Seeds* c. 8 by 5.5–6 mm, rounded on the back, brown, caruncle absent to very inconspicuous.

Distribution — Endemic to Malesia: Philippines (Mindanao), Lesser Sunda Islands (Sumbawa).

Habitat & Ecology — In thickets and forests along or near the seashore, in monsoon forest on ridges. Flowers and fruits collected in May, June.

Vernacular names — Lesser Sunda Islands, Sumbawa: k. tanduk; Philippines: bantiáno [fide Merrill, Enum. Philipp. Flow. Pl. 2 (1923) 461; Salvosa, Lex. Philipp. Trees (1963) 123].

Note — The collections studied from Sumbawa differ from the Philippine plants only in their fruits, being 18–19 mm long (instead of 15–17 mm). Obviously no taxonomic separation can be corroborated.

### 3. Shirakiopsis virgata (Zoll. & Moritzi ex Miq.) Esser, *comb. nov.* — Fig. 5d–f, Map 5

*Excoecaria virgata* Zoll. & Moritzi ex Miq., Fl. Ind. Bat. 1, 2 (1859) 416; Müll.Arg., Linnaea 32 (1863) 123; in DC., Prodr. 15, 2 (1866) 1216; J.J. Sm. in Koord. & Valeton, Bijdr. Boomsoort. Java 12 (1910) 613; Koord., Exkurs.-Fl. Java 2 (1912) 506; Backer & Bakh.f., Fl. Java 1 (1964) 499; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 114. — *Sapium virgatum* (Zoll. & Moritzi ex Miq.) Hook.f., Fl. Brit. India 5 (1888) 471; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 295; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 249. — *Shirakia virgata* (Zoll. & Moritzi ex Miq.) Kruijt, Biblioth. Bot. 146 (1996) 93. — Type: *Zollinger 3035* (holo U; iso A, BM, G, K, L, P; G-DC, n.v., IDC microfiche 2620/1), Java, Bantam.

Tree up to 40 m high, dbh up to 60 cm, branching 5 m above base. Not deciduous. Young *twigs* pilose, especially in the axils. *Indumentum* yellowish to pale. *Bark* brown, vertically fissured; inner bark pale yellow. *Stipules* c. 2 by 1–1.5 mm, ciliate. *Leaves:* petiole 0.8–2 cm long, pilose to glabrous; blade oblong to elliptic, (5–)7–13 by 2.5–4 cm, base obtuse, often slightly attenuate, apex acuminate, upper surface nearly glabrous, lower surface sparsely pilose to glabrous and with 2–10 glands per side, 0.25–0.4 mm diam., basal glands 0.4–0.7 mm diam., secondary veins (15–)19–26 pairs, angle with midrib 60–65°, basal pair with smaller angle, therefore parallel to leaf margin, intersecondaries distinct, smaller veins distinct. *Inflorescences* 40–70 by 5.5–6 mm, axis pilose. *Bracts of staminate cymules* 1.25–1.5 mm long, entire, pilose on whole surface or only on margin (ciliate), their glands 1.25–1.75 by 0.6–0.7 mm. *Staminate flowers* sparsely pilose; pedicel up to 1.5 mm long; calyx 0.5–0.7 mm long, ciliate; stamens with filaments 0.3–0.5 mm long when flowering, nearly absent in bud, anthers 0.25–0.4 mm long. *Pistillate flowers* 1 (or 2) per thyrse or absent; pedicel 4 mm long; calyx c. 1.5–1.75 mm long, entire; style not studied. *Fruits:* pedicel 8–15 mm long; schizocarp elliptic in outline, 23–31 by 16–18 mm when dry, acute at both ends, slightly sulcate, with leathery-fleshy outer layer, green but becoming blackish and wrinkled; style 4 mm long; hardly and tardily dehiscent; mericarp with fleshy outer layer 2–4 mm thick when dry, woody part of pericarp 18–21 mm long, wall 2–2.25 mm thick. *Seeds* 9–10 by 5–5.5 mm, pale brown to cream, without caruncle.

Distribution — Endemic to Malesia: Java.

Habitat & Ecology — Grows in primary and disturbed coastal forests on alluvial plains, periodically inundated. Soil: loam. Altitude: sea level up to 550 m. Flowers collected in July, fide Backer & Bakhuizen van den Brink Jr. (1964) flowering the whole year through; fruits collected in Apr., July–Sept.

Vernacular name — Java: kisereh; see also Smith (1910) and Pax & Hoffmann (1912).

Uses — The wood is durable and can be used for tools and houses (*McDonald & Afriastini 3421*). The uses listed by Dragendorff (1898) for India probably refer to *S. indica* and are erroneous.

Notes — 1. Smith (1910) and Airy Shaw (1975) regarded *S. virgata* to be only a variety of *S. indica*, although they never formally transferred it. However, the fruits of the two taxa are sufficiently distinct to recognize them as distinct species.

2. The first citation of the species by Baillon (1858, as *Excoecaria virgata* Zoll.) was not accompanied by any additional information and does not constitute a valid publication.

3. Müller Argoviensis (1866) cited *S. virgata* from Moulmein, Burma, which probably was erroneous (Hooker, 1888). The species has never been collected outside Java, and the specimen seen by Müller Argoviensis (G-DC, IDC microfiche 2620/3) is a flowering one. Because the fruits are typical for this species, the mentioned specimen cannot be identified as *S. virgata*.

## 7. STILLINGIA

### INTRODUCTION

The genus *Stillingia* was established by Linnaeus (1767), based on the authority of Garden and named after Benjamin Stillingfleet, an English botanist of the 18th century. Because the generic limits within the Hippomaneae have always been a matter of dispute, for some decades many, very different species of all parts of the tropics were assigned to *Stillingia*. Especially Baillon (1858 and later) united a considerable part of the whole tribe under this name.

Bentham (1878, 1880) defined *Stillingia* by the peculiar fruits, the upper part dehiscing regularly and being caducous, the lower part instead remaining on the plant and forming a (2–)3-horned, wooden structure, the carpophor. The South American genus *Adenopeltis* Bertero ex A. Juss., however, has very similar fruits but naked staminate flowers, and therefore the large, fused sepals of *Stillingia* are diagnostically important for *Stillingia* too.

The latest complete monograph was presented by Pax & Hoffmann (1912). Most of the species of *Stillingia* are restricted to the New World. They have been revised by Rogers (1951). Of the three species from Madagascar and the Mascarenes, one, *S. thouarsiana* Baill., should probably be separated from the genus, the other two may be conspecific (Coode, 1982). In Asia, there is only one rare species, *S. pacifica*, reported from Malesia for the first time by Airy Shaw (1963). Croizat (1942) had already described it under the name *Sapium plumerioides*, but their conspecificity was never recognized and is established in the present revision for the first time. Because of its rareness and remarkable geography, as noted below, *S. pacifica* has been discussed several times (Airy Shaw, 1963, 1972b; Smith, 1978, 1981; Van Steenis, 1966). The only matter of opinion was its distinction from the very similar *S. lineata* from Mauritius, and therefore its taxonomic status. A distinction of only one species with two subspecies, as proposed by Van Steenis (1966) and supported by Coode (1982), seems preferable; it should be noted, however, that Smith (1978, 1981) objected to this view, accepting two distinct species.

The position of *Stillingia* in the Hippomaneae is without doubt. It is very similar to *Sapium*, distinguished particularly by the fruits, as noted above.

Within the genus, the only Malesian species fits in subg. *Stillingia*, as it has well-developed sepals of the pistillate flowers, at least 3-flowered staminate cymules and carunculate seeds, and within the subgenus in its series *Dichotomae* D.J. Rogers (= sect. *Pachycladae* Pax) because of its succulence (the palynological characters of *S. lineata* have not been studied).

## CHARACTERS OF MALESIAN STILLINGIA

### Vegetative characters

The stems of *S. lineata* are succulent (a rare character in the Hippomaneae!) with apically crowded, non-succulent leaves and very conspicuous leaf scars (Fig. 6a).

The plasticity of leaf shape and index, noted by Van Steenis (1966) and Coode (1982), is remarkable but not unique when compared with other members of the Hippomaneae, e.g., *Microstachys*.

The leaves of Malesian plants are membranous and serrate with mostly persistent glandular setae. The blades bear marginal glands abaxially. The adaxial glands on the junction of blade and petiole (Fig. 6c) are often not very obvious or absent, and may vary on the same plant; they are usually not separated from the blade, unlike the otherwise comparable glands of *Sapium*. The texture and distinct serrulation of the leaves, together with the never lacking marginal glands and the easily visible venation, are the only characters distinguishing the Asian from the African specimens of *S. lineata*.

### Floral characters

The inflorescences are unbranched, which is common in the Hippomaneae. The bracts bear a pair of quite large, at least when dried disc-shaped to semi-cylindrical, but never cyathiform glands. The variation in length and shape of these glands observed in *S. lineata* does not seem to be taxonomically significant.

The flowers of both sexes are typical for *Stillingia* subg. *Stillingia* and are quite uniform, as is to be expected in Hippomaneae. The staminate cymules usually are 5–7-flowered. Their flowers are sessile when young, but have short pedicels at anthesis, each with a large, 2-lobed calyx and two stamens with short but distinct filaments; the latter are only visible at anthesis. The pistillate flowers are 3-carpellate and sessile.

### Fruiting characters

The dry, sessile fruits are typical for the genus. The distal part dehisces regularly into three mericarps, but the thickened, woody base remains on the plant, forming the remarkable structure resembling a three-horned cupule (Fig. 6g) and named gynobase, carpophor, carpidiophor or coccophore by various authors.

## BIOGEOGRAPHY AND RELATIONSHIPS

*Stillingia* is very closely related to *Sapium* and *Falconeria*, as was shown in a recent cladistic study (Esser et al., 1998). In particular the staminate thyrses and leaves are very similar in these three taxa, and the genera are best separated by their fruits. In addition, there are some comparably close Neotropical genera, like *Senefelderopsis* (Esser, 1994).

Hypotheses about the exact relationships of *S. lineata* within the genus are hindered by the fact that Rogers' revision (1951) lacks any phylogenetic hypotheses. The *Dichotomae* consist of 6 or 7 species and may be monophyletic. Rogers cited two putatively unique (autapomorphic) characters for them, namely succulence and peculiar pollen with only one lateral pore. The succulence, however, may be restricted to the leaves (*S. uleana* Pax & K. Hoffm.), to the stems (*S. lineata* subsp. *pacifica*), or to both (*S. trapezoidea* Ule) and is a variable character. The pollen has not been studied in all species by Rogers (1951). Therefore, his diagnosis of the *Dichotomae* is not sufficient; because his revision concentrated on the North American taxa, Rogers treated the tropical *Dichotomae* only superficially, and a phylogeny cannot be established without re-evaluating his work. Within this series, the species most similar to *S. lineata* in the New World is *S. uleana*. It differs from *S. lineata* only in the non-succulent stems and the succulent leaves with distinct marginal serration and basal glands purely marginal, never adaxial-petiolar.

Remarkably, there is a clear distinction in the distribution between series *Dichotomae* and the remainder of the genus, as recognized by Rogers (1951) for the New World. The other four series of the genus are all strictly American, confined to temperate or subtropical regions and the margin of the tropics or higher elevations in the Andes, but they are completely absent from the core tropics. All species of the *Dichotomae*, however, are truly tropical, only known from the dry areas of NE Brazil (a region rich in succulents), the Mascarenes (Mauritius, La Réunion), some scattered islands in Malesia, and from Fiji.

*Stillingia lineata* has a scattered distribution in the Mascarenes, Malesia and Fiji (Map 6), which is quite remarkable but not unique. Van Steenis (1966) mentioned several other taxa with a disjunction between Mauritius and Fiji. Fiji as the eastern limit for Australasian taxa is not rare, and this could point to a geological explanation for the present-day distribution correlated with the old Australian landmass. But because Malesian *Stillingia* is predominantly growing at shores, one could postulate dispersal causing the remarkably wide distribution, especially because all closely related genera are much more restricted in their distribution.

## **Stillingia** Garden ex L.

*Stillingia* Garden ex L., Mant. (1767) 19; Syst. Nat. ed. 12, 2 (1767) 637; A. Juss., Euphorb. Gen. (1824) 49; Benth. in Benth. & Hook.f., Gen. Pl. 3 (1880) 334; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 96, f. 61, 62; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 180; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 198; D.J. Rogers, Ann. Missouri Bot. Gard. 3 (1951) 207; G.L. Webster, J. Arnold Arbor. 48 (1967) 388, f. 5; Ann. Missouri Bot. Gard. 81 (1994) 122. — *Stillingia* sect. *Eustillingia* Klotzsch ex Baill., Etude Euphorb. (1858) 510, nom. inval.; Müll.Arg. in DC., Prodr. 15, 2 (1866) 1155. — *Sapium* sect. *Stillingia* (Garden ex L.) T. Post & Kuntze, Lex. Gen. Phan. (1903) 498. — Type: *Stillingia sylvatica* Garden ex L.

Shrubs to trees (succulent in series *Dichotomae*, some New World species perennial herbs). Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* absent. *Stipules* ovate-triangular with a long acumen, less than 2 mm long, often divided into several ciliae, basally glandulous. *Leaves* alternate, sometimes apically crowded (opposite in some New World species); petiole short (less than 2 cm long), much shorter than blade, glandless or apically with a pair of conspicuous to inconspicuous (even stipitate in some New World species) glands on the junction with the blade that is usually not separate from the blade; blade elliptic in various proportions, sometimes succulent (series *Dichotomae*), margin serrate with teeth 0.5–3(–5) mm apart, often indistinct but never truly entire, above glandless or with a pair of glands on the junction with the petiole (see there), below smooth and neither whitish nor papillate, with or without a row of strictly marginal glands, basal glands not different, secondary veins distinct, arching but mostly not joined towards the margin, smaller veins reticulate but often hardly visible. *Inflorescences* terminal or axillary, yellowish, simple, pistillate and staminate flowers in same thyrse, very variable in size. *Bracts of staminate cymules* triangular to ovate to transversely ovate, with a pair of cup- to disc-shaped glands touching the axis of the thyrse. *Staminate cymules* 5–13-flowered (1–3-flowered in some New World species); bracteoles present, filiform. *Staminate flowers* with short (up to 1 mm long) pedicel only present when flowering; calyx with 2 largely fused sepals; stamens 2, filaments slightly longer than anthers. *Pollen* (fide Rogers, 1951) spheroidal to prolate, tricolporate or with 1 lateral pore (series *Dichotomae*). *Pistillate flowers* several (less than 15) at base of staminate thyrse, nearly sessile; calyx with 3 sepals; sepals triangular, free, glandless (absent in some New World species); ovary

3-locular (2-locular in a few New World species), smooth; style usually short but distinct, stigmata 3 (2 in a few New World species), undivided, glandless. *Fruits* nearly sessile; 3-seeded (2-seeded in few New World species), smooth, dry, dehiscing regularly along the septa in the upper part, but with a thickened, woody lower part remaining at the plant to form a (2- or) 3-lobed, woody coccophor; mericarps with persistent septae and 1 or 2 vascular strands visible on each septum. *Seeds* elliptic, dry, with or without caruncle.

Distribution — Thirty species currently accepted, twenty-seven of which (as well as four of the five series) strictly American, ranging from Argentina to Kansas, USA. Series *Dichotomae,* instead, includes four species in S America (dry regions of NE Brazil) and three in Mauritius, La Réunion, Fiji and a few islands in Malesia: Lesser Sunda Islands, Moluccas, Philippines.

Habitat & Ecology — Preferably growing under xerophytic conditions, rocky hills, open woods, scrubland, roadsides, semideserts, at least the Paleotropical species often on seashores.

Note — The species boundaries in some of the New World series of *Stillingia* are quite vague, hybridization occurs frequently, as shown by Rogers (1951) for N America. The *Dichotomae,* however, are still poorly known and rarely collected.

### 1. **Stillingia lineata** (Lam.) Müll.Arg.

*Stillingia lineata* (Lam.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1157; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 183; Coode, Fl. Masc. 160 (1982) 86, pl. 17. — *Sapium lineatum* Lam., Encycl. 2 (1790) 734; Müll.Arg., Linnaea 32 (1863) 115. — Type: *Commerson s.n.* (holo P-LA, microfiche 597/1; ?iso G, L, P, P-JU), Mauritius.

Shrub to small tree, up to 12 m high. *Twigs* succulent, apical diameter c. 6 mm. *Bark* smooth, covered with leaf-scars 2.5–3 mm diam. *Stipules* 0.8–1.5 by 0.3–0.75 mm, divided. *Leaves* alternate but apically crowded; petiole 0.3–1.7 cm long, glandless or with a pair of glands above on the junction with the blade; blade membranous and hardly to slightly succulent, orbiculate to elliptic to slightly obovate, (4–)7–24 by (3–)5–8 cm, base cuneate to obtuse, margin serrate with teeth 2–3(–4) mm apart, apex acute to rounded to retuse, above with a pair of cup-shaped glands on the junction with the petiole that sometimes are very indistinct to absent and varying even on the same twig, below with 0–17 strictly marginal glands per side, 0.5–0.75 mm long, secondary veins 16–26 pairs, distinct to indistinct, indistinctly joined towards the margin, smaller veins distinct to indistinct. *Inflorescences* 4–6 cm by c. 5 mm, greenish-yellow. *Bracts of staminate cymules* 1–2 mm long, their glands disc-shaped to flattened-cylindrical, 1.5–3 by 1.25–2.5 mm, mostly along the axis and partly below the bract. *Staminate cymules* 5–9(–15)-flowered. *Staminate flowers:* pedicel 0.2–0.5 mm long; calyx c. 0.75 mm long; stamens with filaments 1 mm long when flowering, anthers c. 0.4 mm long. *Pistillate flowers* 5–9 per thyrse; calyx 1.5 mm long; ovary c. 4 mm long; style up to 1 mm long, stigmata 1.5 mm long. *Fruits* 5–6 mm long, deeply sulcate, apically retuse; pericarp c. 0.5 mm thick; remaining carpophor up to 11 mm in diameter. *Seeds* 5 by 4–5 mm, carunculate, brown, dotted.

Distribution — Mauritius, La Réunion, Fiji and in Malesia a few localities from the Lesser Sunda Islands, the Moluccas and the Philippines.

Habitat & Ecology — Often found on beaches, but also in forests up to 300 m elevation.

Note — The morphological distinction between the subspecies seems sufficiently well established (Smith, 1978; Coode, 1982). The typical subspecies from Mauritius and La Réunion has firm to slightly succulent, entire leaves with hardly visible venation and no marginal glands, whereas the Malesian plants are distinguishable by thin leaves with obvious serration, venation and glands; they do not differ in generative characters. Airy Shaw (1972b) and Smith (1978) doubt the ecological distinction between the subspecies (beach vs. inland plants) proposed by Van Steenis (1966).

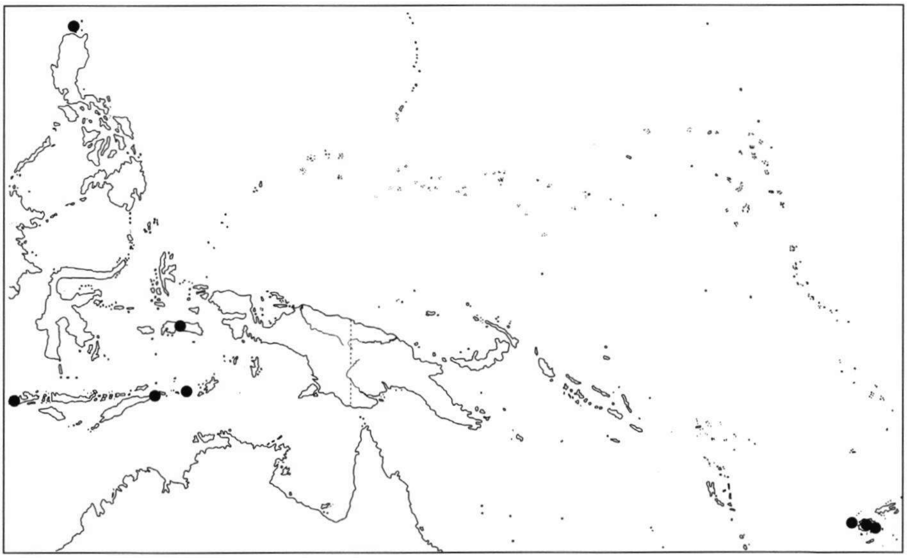
### **a.** subsp. **pacifica** (Müll.Arg.) Steenis — Fig. 6, Map 6

*Stillingia lineata* (Lam.) Müll.Arg. subsp. *pacifica* (Müll.Arg.) Steenis, Blumea Suppl. 5 (1966) 302, map 169; Airy Shaw, Kew Bull. 27 (1972) 93; Kew Bull. 37 (1982) 35. — *Stillingia pacifica* Müll.Arg. in DC., Prodr. 15, 2 (1866) 1156; Seem., Fl. Vitiens. (1867) 232; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 183; Croizat, Occ. Papers Bishop Mus. 18 (1944) 71; Airy Shaw, Kew Bull. 16 (1963) 372; A.C. Sm., Allertonia 1 (1978) 397, f. 20; Fl. Vitiens. Nov. 2 (1981) 567, f. 151. — Type: *U.S. Expl. Exped. Capt. Wilkes* (holo presumably G or G-DC, n.v.; iso GH, US), Fiji, Ovalau.

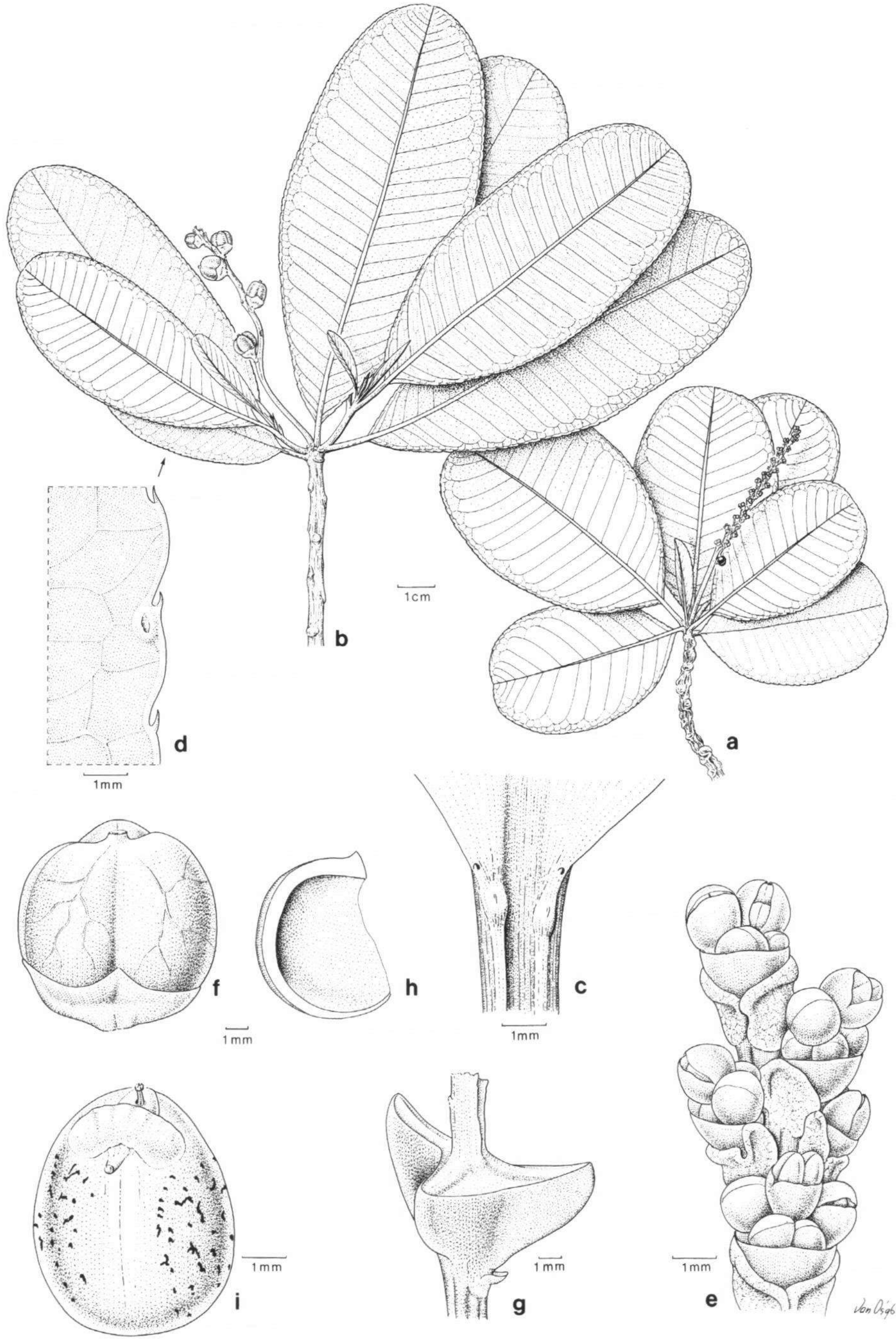
*Sapium plumerioides* Croizat, J. Arnold Arbor. 23 (1942) 507; Salvosa, Lex. Philipp. Trees (1963) 123. — Type: *Bartlett 15167* (holo A), Philippines, Babuyan Group, Dalupiri Island. Syn. nov.

Shrub to small tree, up to 10 m high, trunk 15 cm diam. *Leaves:* blade (4–)7–24 by 3–8 cm, index (1.5–)2–4, membranous and non-succulent, margin distinctly serrate, below with 5–17 glands per side, secondary and smaller veins distinct.

Distribution — Fiji (several islands of the group) and Malesia: Lesser Sunda Islands (Sumbawa, Babar, Timor), Moluccas (Seram), Philippines (Babuyan Group).



Map 6. Distribution of *Stillingia lineata* (Lam.) Müll.Arg. subsp. *pacifica* (Müll.Arg.) Steenis.


b
1 cm
a
d
1 mm
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c
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1 mm
i
1 mm
g
1 mm

Habitat & Ecology — In Malesia only known from coastal forest and coconut plantations on coral soil, but poorly known. On Fiji occurring along streams, on forest edges, in coastal thickets and on limestone cliffs. Altitude 0–300 m. Flowers on Fiji collected in Feb., July, Dec.; fruits collected in Jan., Feb., July, Dec.

Vernacular name — Philippines: loi [Tag., fide Salvosa, Lex. Philipp. Trees (1963) 123].

Note — The type of *Sapium plumerioides* is a typical flowering specimen of *S. lineata* subsp. *pacifica*. As *Stillingia* was not known for Malesia at this time, Croizat (1942) did not consider this genus, but compared the specimen only with *Excoecaria* and *Sapium* and therefore could not match it.

## 8. TRIADICA

### INTRODUCTION

*Triadica* was described by Loureiro (1790) with two species, *T. cochinchinensis* and *T. sinensis*. This concept was accepted unaltered by De Jussieu (1824). Later, however, both species had a quite different taxonomic history.

The type of *T. cochinchinensis* was re-examined only by one monographer, Müller Argoviensis (1866), and for two publications on Loureiro's herbarium, Moore (1925) and Merrill (1935). Müller Argoviensis placed the species in *Excoecaria* sect. *Parasapium*, therefore separated it from *Triadica* (see below), based on the glandular sepals of its pistillate flowers. In this case a nomen novum, *E. loureiroana*, was necessary, as Loureiro (1790) had already described *E. cochinchinensis*, a very different species. Moore (1925) and Merrill (1935) accepted it as a distinct species of *Sapium*.

Müller Argoviensis' opinion about *T. cochinchinensis* was repeated by Pax & Hoffmann (1912), Hurusawa (1954) and Kruijt (1996), although these authors separated the whole section from *Excoecaria*. Pax & Hoffmann treated it as *Sapium* sect. *Parasapium*, and Hurusawa and Kruijt as a separate genus named *Shirakia*. Pax & Hoffmann and Kruijt, although writing obviously about the same taxon as Müller Argoviensis, referred to *Sapium cochinchinense* (Lour.) Kuntze which is based on *E. cochinchinensis*, not *T. cochinchinensis*. However, in all cases the species was cited as insufficiently known, and all authors of local revisions except Gagnepain (1926, under *Sapium* without further divisions) ignored the species.

Bentham (1854) described *Stillingia discolor*. Müller Argoviensis (1863) was the first to discuss its relationships. He placed the species in *Sapium* sect. *Triadica*, effecting the combination *Sapium discolor*. Later he transferred the section *Triadica* to *Excoe-*

Fig. 6. *Stillingia lineata* (Lam.) Müll. Arg. subsp. *pacifica* (Müll. Arg.) Steenis. a. Habit of flowering plant; b. habit of fruiting plant; c. detail of leaf base, upper surface, with glands; d. detail of leaf margin, lower surface, with serration and gland; e. detail of staminate thyrse with nearly sessile flowers with fused sepals; f. fruit, unopened, with distinct woody base; g. central columella of fruit after dehiscence with carpidiophor; h. half of mericarp after septicidal and loculicidal dehiscence with pericarp of medium thickness; i. carunculate seed [a–e: *Van Steenis 18184*, L; f–i: *De Voogd 1624*, L].

*caria* (1866) and made the respective combination of *E. discolor.* Hooker (1888) returned to the classification under *Sapium* and was followed by nearly all later authors, including Airy Shaw (1972a, 1975, 1981). Only Kruijt (1996) excluded the species from *Sapium* and transferred it to *Excoecaria* again. The combination under *Triadica* was never published, as Hurusawa, who re-established *Triadica* (1954; see below), neglected this species.

Miquel (1861) described *Stillingia* (sect. *Sapium*) *lanceolaria*, based on a Malesian type. This species remained poorly known for a long time. It was cited by Müller Argoviensis (1866) as a dubious species of *Excoecaria* (which included, in his opinion, most of *Sapium*). This was repeated by Boerlage (1900) and Pax & Hoffmann (1912), but then separate from *Sapium.* Airy Shaw (1981) recognized it as identical with *Sapium discolor.*

In the present revision, *T. cochinchinensis* and *Sapium discolor* are considered to be identical, this making a name change of the quite well known *S. discolor* necessary. It is the only indigenous Malesian species of *Triadica* (see below). Chakrabarty & Gangopadhyay (1990) united '*Sapium discolor*' with *Sapium eugeniifolium* Buch.-Ham., a species from India and the Himalayan region. This effected a remarkable extension of the distribution.

*Triadica sinensis*, instead, always remained in *Triadica*, although only Webster (1994) designated it as its lectotype. Baillon (1858) and Müller Argoviensis (1863) united the species with *T. sebifera* (L.) Small; they were followed by all later authors. *Triadica sebifera* is based on *Croton sebiferus* (Linnaeus, 1753). It is indigenous to E Asia. Because it is a commercially important species, cultivated in different warmer regions of the earth for a long time, several names were applied to it, including two new generic names (*Stillingfleetia* Bojer, *Seborium* Raf.). Together with the whole of *Triadica*, it has been combined with different other genera.

After De Jussieu (1824), *Triadica* usually was considered to be a distinct part of other, but different genera. It was united as a separate section with *Stillingia* (Baillon, 1858, 1861), *Sapium* (Müller Argoviensis, 1863; Hooker, 1888; Pax, 1890; Pax & Hoffmann, 1912), or *Excoecaria* (Müller Argoviensis, 1866). Sometimes it was united with *Sapium* without infrageneric delimitation [Bentham, 1880; Webster, 1994, although Webster admitted that "further investigations may show that it (*Triadica*) should be generically separate from *Sapium*"], or with *Carumbium* (= *Homalanthus*; Kurz, 1877). Hurusawa (1954) considered *Triadica* as a separate genus, only followed by Kruijt (1996) and in the present revision.

In addition to the changing position, also the opinions about the included species varied. Characteristic for *Triadica* are the seeds with a sarcotesta attached to the central columella of the fruit, even when the pericarp has separated. Because the fruits of the type collection of *T. cochinchinensis* are immature, these characters are not visible. Therefore, the species was usually excluded from *Triadica*, and *Triadica* was sometimes considered as monotypic, only containing *T. sebifera* (Hurusawa, 1954). On the other hand, '*Sapium baccatum*' with its berries and fairly similar leaves and inflorescences was sometimes included in *Triadica*, although it does not develop a sarcotesta (Hooker, 1888; Pax & Hoffmann, 1912). The position of some extra-Malesian species (e.g., *S. rotundifolium* Hemsl.), however, still has to be evaluated, and *Triadica* probably includes more than two species.

## CHARACTERS

### Vegetative characters

The architecture of *T. cochinchinensis* (as *Sapium discolor*) has been described in some detail by Koriba (1958) and Hallé (1971). The account of Koriba was honoured with naming this type of architecture as 'Koriba's model' (Hallé et al., 1978). All ramification occurs in pseudoverticels, but the apex of the vertical trunk dies away, one of the renewal axes becomes vertical and continues the trunk; as a result the pseudomonopodial trunk grows sympodially in a zigzag manner. After a height of several metres is attained, two branches grow simultaneously, and the apical ramification appears pseudodichotomous. This may be different from other genera, but data are scarce.

The leaves are very useful for recognition of the genus. Constant characters for *Triadica*, not found in related Malesian genera, are the remarkably long petioles, the adaxial-basal and nearly globose (not disc-shaped) leaf glands (Fig. 7b) and the lowermost pair of side veins that originates strictly at the base of the blade and constitutes the basal part of the leaf margin (Fig. 7a). Additionally, the whitish (papillate or glaucous) lower leaf surface may be mentioned. The reticulate venation is shared with many related genera, but not with *Homalanthus*, which is quite similar in habit.

The leaves are also important for distinguishing the species. *Triadica cochinchinensis* is the only species with ovate-elliptic blades, whereas *T. sebifera* (and other taxa mentioned above, like '*Sapium rotundifolium*') show orbicular to broadly ovate blades. The leaf base glands are always paired in the two Malesian species, but single in '*Sapium rotundifolium*'.

### Inflorescences and flowers

Remarkable characters of the thyrses are the quite large numbers of pistillate flowers per thyrse, the comparatively long pedicels of the pistillate flowers and the combination of a large number of staminate flowers per thyrse and distinct pedicels. The number of stamens per flower is 2 or 3 (invariable in most other Malesian genera of the tribe). The species of *Triadica* show no distinguishing characters in the floral parts at all.

### Fruits and seeds

Besides some leaf characters, *Triadica* is best characterized by the very unusual fruits. The seeds are covered by a pale to white sarcotesta, unique in the tribe. Probably correlated with it as part of an endozoochorous syndrome, the seeds remain at the central columella after dehiscence of the pericarp (Fig. 7f), and the septa of the mericarps are membranous, very fragile and remain between the seeds on the plant, too. Another noteworthy feature is the fact that, if not all seeds of a fruit develop, the mature fruit will be still regularly trimerous but with empty locules. In other related genera, the abortion of seeds will result in rudimentation of locules and carpels of unequal size.

The fruits of all species of *Triadica* are very similar, even in quantitative characters. *Triadica cochinchinensis* may be distinguished by a relatively weakly developed sarcotesta that is pale but never white and often quite inconspicuous.

## BIOGEOGRAPHY AND RELATIONSHIPS

*Triadica* is most common and most diverse in E Asia, where all species occur. In this respect *Triadica* is unique in the Hippomaneae, a predominantly Neotropical tribe. *Triadica cochinchinensis*, the only indigenous Malesian taxon, occurs only in W and, rarely, C Malesia, but is most common on the SE Asian mainland (Map 7). It is probable, therefore, that Malesia was reached only by dispersal from the north.

A phylogeny of the species cannot be established at this moment. The relationships of the genus have been treated in a recent paper (Esser et al., 1998). It shows that *Triadica* is a separate branch in a group of genera close to *Sapium*, but without an obvious sister taxon. In some respects, it is most similar to *Balakata* (entire leaves with often long petioles and often whitish beneath). It must be noted, however, that the Malesian Hippomaneae are only a small part of the tribe, probably not monophyletic as a whole, and a comparison with taxa from other regions is still lacking.

## **Triadica** Lour.

*Triadica* Lour., Fl. Cochinch. ed. 1, 2 (1790) 598, 610; ed. 2, 2 (1793) 735, 748; A. Juss., Euphorb. Gen. (1824) 50; Rchb., Consp. regn. veg. (1828) 194; Hurus., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6 (1954) 315; Kruijt, Biblioth. Bot. 146 (1996) 7; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 123. — *Stillingia* sect. *Triadica* (Lour.) Baill., Etude Euphorb. (1858) 511; Adansonia 1 (1861) 351. — *Sapium* sect. *Triadica* (Lour.) Müll.Arg., Linnaea 32 (1863) 121; Hook.f., Fl. Brit. India 5 (1888) 469; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 98, f. 63; T. Post & Kuntze, Lex. Gen. Phan. (1903) 498; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 237; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 201; G.L. Webster, J. Arnold Arbor. 48 (1967) 392. — *Excoecaria* sect. *Triadica* (Lour.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1210. — Lectotype [proposed by G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 123]: *Triadica sinensis* Lour. [= *Triadica sebifera* (L.) Small].

*Stillingfleetia* Bojer, Hortus Maurit. (1837) 284, nom. nud.

*Seborium* Raf., Sylva Tellur. (1838) 63. — Type: *Seborium chinense* Raf. [= *Triadica sebifera* (L.) Small].

Trees. Monoecious. Flowering and fruiting twigs with leaves. *Indumentum* absent, although some organs are erose-ciliate. *Stipules* ovate to triangular, 0.5–2 mm long, undivided, glandless. *Leaves* alternate, but sometimes apically crowded; petiole 1–6 cm long, at least half as long as blade, usually glandless (but basilaminar glands sometimes on the petiole apex, see below); blade orbiculate to elliptic to slightly ovate, 2.5–7 cm wide, base cordate to acute to attenuate, margin entire, apex obtuse to mucronate to acuminate, above with a pair of large, nearly globose-spheroidal glands on the base (sometimes more on the petiole apex), lower surface papillate and pale to distinctly whitish-farinose, often with a row of few submarginal glands not touching the margin, secondary veins distinct, lowermost pair originating from the very leaf base and forming the basal leaf margin, with a different angle with the midrib, intersecondary veins present, smaller veins reticulate. *Inflorescences* terminal and in axils of uppermost leaves, yellowish, not compound, without sterile basal region, pistillate flowers at base of staminate part, staminate part 25–140 by 5–10 mm. *Bracts of staminate cymules* triangular, acuminate, basally with a pair of spheroidal-cylindrical glands touching the axis of the thyrse or slightly decurrent. *Staminate cymules* (3–)5–8-flowered;

bracteoles present, nearly as long as the bracts, undivided, margin slightly ciliate. *Staminate flowers* with distinct (> 2 mm long) pedicel in bud and when flowering; calyx fused for the most part with a varying number of lobes (3–6); stamens 2 or 3, filaments longer than anthers. *Pistillate flowers* with pedicel 2–10 mm long; calyx with 3, sometimes apically to completely divided sepals, glandless or sometimes with spheroidal glands at margin; ovary 3-locular, smooth; style present, disarticulating at base, stigmata 3, undivided, glandless. *Fruits* with pedicel 2–15 mm long; 3-seeded, smooth, dry, opening regularly and nearly simultaneously septicidally and loculicidally; mericarps with moderately thick pericarp, septa largely remaining at central columella, mericarps therefore hardly with septal remnants, basally without separate triangle, with one apical vascular bundle; remaining columella conspicuously alate, persistent. *Seeds* attached to the central columella for a considerable time after ripening, covered with a pale to whitish sarcotesta, without caruncle.

Distribution — Probably three or four species, all in Asia and mostly distributed in E Asia (Cochinchina, China); only one species in W Malesia up to Celebes and Palawan (Philippines).

Note — Although the genus is well-defined by its fruits and some leaf characters, the relations of some species currently included in *Sapium* still have to be examined. Especially *S. rotundifolium* Hemsl. will probably prove to belong to *Triadica.*

## KEY TO THE MALESIAN SPECIES

1a. Leaves ovate to elliptic, at least twice as long as wide . . **1. T. cochinchinensis**
b. Leaves broadly ovate, less than twice as long as wide . . . . . . . . . **2. T. sebifera**

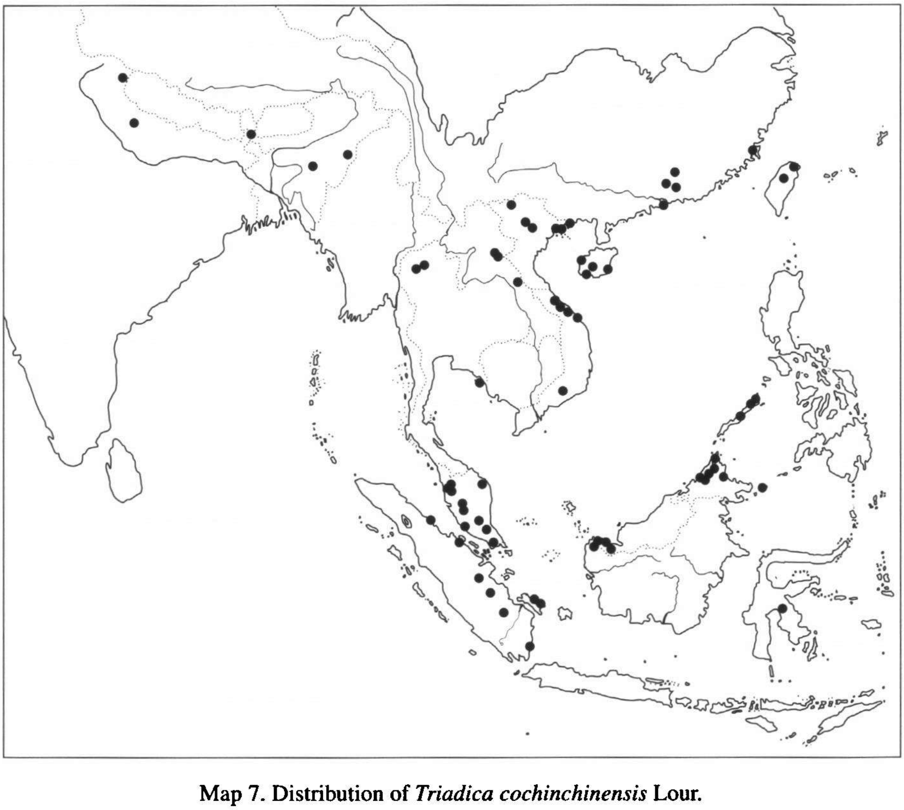
### 1. Triadica cochinchinensis Lour. — Fig. 7, Map 7

*Triadica cochinchinensis* Lour., Fl. Cochinch. ed. 1, 2 (1790) 610; ed. 2, 2 (1793) 749. — *Excoecaria loureiroana* Müll.Arg. in DC., Prodr. 15, 2 (1866) 1217, nom. nov. — *Sapium cochinchinense* (Lour.) Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 252; S. Moore, J. Bot. 63 (1925) 288; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 395, 401; Merr., Trans. Amer. Philos. Soc., n.s. 24 (1935) 241. — *Shirakia cochinchinensis* (Lour.) Hurus., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6 (1954) 318; Kruijt, Biblioth. Bot. 146 (1996) 93. — Type: *Loureiro s.n.* (holo BM; iso BM), Cochinchina.

*Stillingia discolor* Champ. ex Benth., Hook. J. Bot. Kew Gard. Misc. 6 (1854) 1. — *Sapium discolor* (Champ. ex Benth.) Müll.Arg., Linnaea 32 (1863) 121; Hook.f., Fl. Brit. India 5 (1888) 469; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 295; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 239; Ridl., Fl. Malay Pen. 3 (1924) 316; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 394, 395, 399, f. 46.2–8; Merr., Philipp. J. Sci. 30 (1926) 404; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1960; Corner, Ways. Trees Malaya 1 (1940) 276; Koriba, Gard. Bull. 17 (1958) 19, 70; Wyatt-Sm., Malay. For. Rec. 17 (1965) 113, 344; Hallé, Biotropica 3 (1971) 57, 59, f. 5; Whitmore, Tree Fl. Malaya 2 (1973) 129; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 192; C.F. Hsieh, Fl. Taiwan 3 (1977) 494; Airy Shaw, Kew Bull. 36 (1981) 341; Alph. Enum. Philipp. Euphorb. (1983) 44; Chakrab. & M.G. Gangop., J. Econ. Tax. Bot. 14 (1990) 183; 't Mannetje & Jones (eds.), Pl. Res. SE Asia (PROSEA handb.) 4, Forages (1992) 252; P.H. Hô, Câyco Viêtnam 2, 1 (1992) 355; I.M. Turner, Gard. Bull. 47 (1995) 231. — *Excoecaria discolor* (Champ. ex Benth.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1210; Kruijt, Biblioth. Bot. 146 (1996) 88. — Lectotype (proposed here): *Champion s.n.* (holo K; iso GH, K), Hongkong.

*Stillingia ? lanceolaria* Miq., Fl. Ind. Bat. Suppl. 1 (1861) 183, 461; Airy Shaw, Kew Bull. 36 (1981) 342. — *Excoecaria ? lanceolaria* (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 1221; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 296; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 170. —Type: *Teijsmann HB 549* (holo U; iso CAL, n.v.), Sumatra, Padang, Poeloe Pisang.

Shrub to tree, up to 25 m high, stem 40 cm diam., bole up to 20 m high, without buttresses. Deciduous with crown bare for 1–2 weeks. *Bark* rather smooth, not fissured, light grey to brown; inner bark granular mottled, pale to yellowish to orange. *Sapwood* pale yellow to white, soft; sapwood and heartwood little differentiated. *Stipules* 0.3–2 by 0.6–0.7 mm. *Leaves* pinkish when young, withering blood red; petiole 1–3 cm long; blade slightly ovate to elliptic, (2.5–)3.5–7 by 1–3 cm, less than half as wide as long, base cuneate to attenuate to rarely obtuse, apex obtuse to acute to acuminate, above with a pair of basal glands 1–1.5 by 0.5–0.75 mm, lower surface whitish-papillate to whitish-glaucous and with 0–3 glands per side, 0.5–1 mm diam. and (0–)0.5–1 mm distant from margin, secondary veins 9–17 pairs, angle with midrib 65–75°, arching but only indistinctly joining towards the margin, lowermost pair with angle with midrib 30–45°. *Inflorescences:* staminate part 25–50 by 7–10 mm. *Bracts of staminate cymules* 1–1.5 mm long, their glands 1–1.5 by 0.5–0.75 mm. *Staminate flowers:* pedicel 2–3 mm long, articulate near base; calyx c. 1 mm long; stamens with filaments 0.75–1



Map 7. Distribution of *Triadica cochinchinensis* Lour.

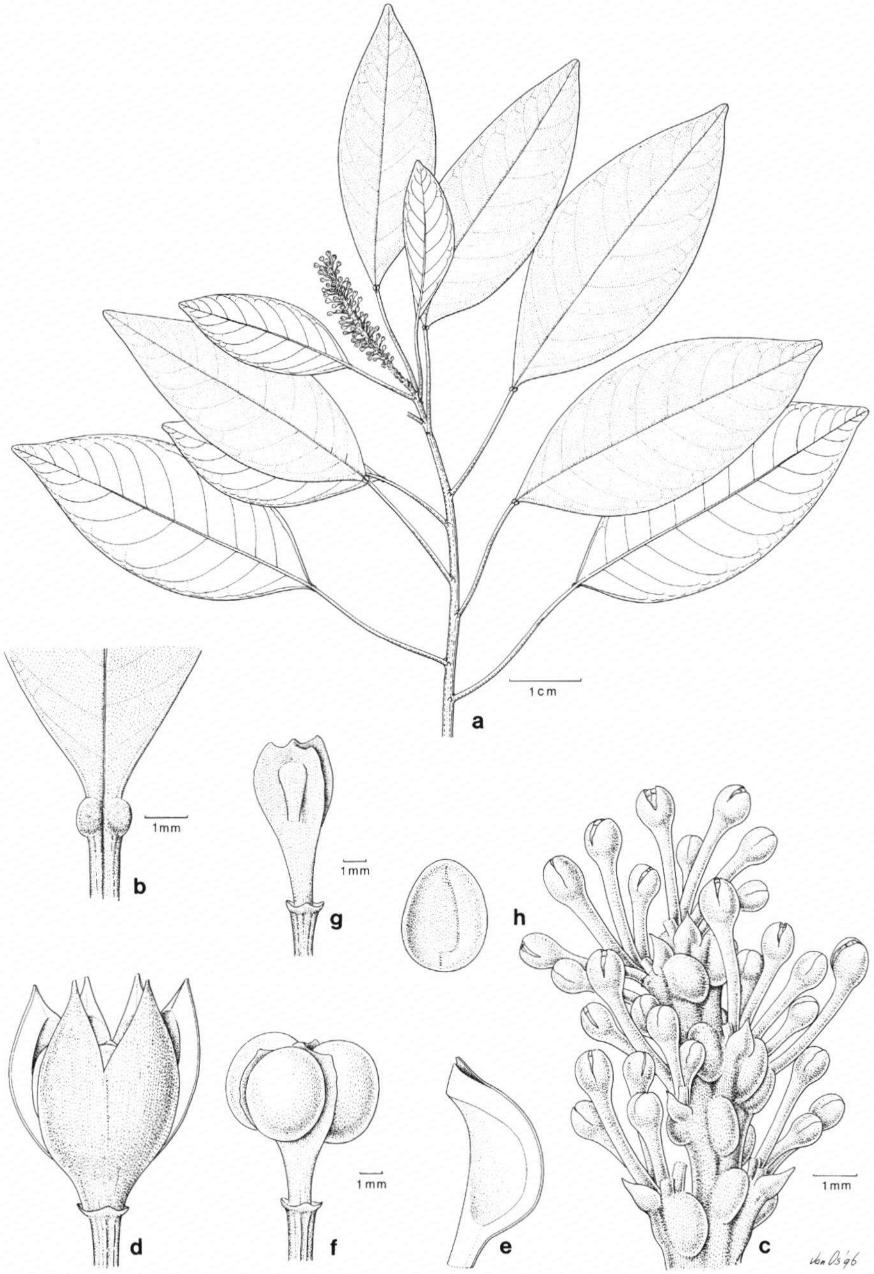


Fig. 7. *Triadica cochinchinensis* Lour. a. Habit of plant with staminate thyrse; b. detail of leaf base, upper surface, with glands; c. part of staminate thyrse with many-flowered cymules, long pedicels and partly fused sepals; d. partly opened fruit; e. half of mericarp after septicidal and loculicidal dehiscence; f. central columella of fruit with attached seeds; g. central columella of fruit without seeds; h. seed with raphe and without caruncle [a–c: *SAN (Amin et al.) 117787*, L; d–h: *SAN (Amin et al.) 123379*, L].

mm long when flowering, anthers 0.4–0.5 mm long. *Pistillate flowers* 0–13 per thyrse; pedicel 2–4 mm long; calyx 1–2 mm long, sepals rarely with basimarginal glands; style 1–3 mm long, stigmata 2–3 mm long. *Fruits:* pedicel 2.5–6 mm long; schizocarp circular in outline, 7–9 by 7–9 mm, base often clavate, slightly or not sulcate, apex rounded; pericarp 0.3–0.4 mm thick; remaining columella distinctly alate by 1.5–2.5 mm, marginally with conspicuously arching vein. *Seeds* 3.5–5 by 3.5–4.5 by 2.5–3 mm, sarcotesta pale but hardly white, brownish when dry.

Distribution — NE India, Burma, Thailand, Indochina up to Taiwan and E China (known from eight provinces: Lee, 1956), and W Malesia: Peninsular Malaysia (incl. Singapore), Sumatra, N Borneo (Sabah, Sarawak), Philippines (Palawan), and Celebes.

Habitat & Ecology — Found in primary forest, disturbed forest, young secondary forest of 5 years, and thickets, on hillsides and steep slopes, also in dry places. Soil: yellow and granitic sand. Fairly common. Altitude 10–1000 m. Flowers collected in Jan., Apr.–May, Aug.–Sept., Nov.; fruits collected the whole year through.

Vernacular names — Peninsular Malaysia: mamah pelandok. Sumatra: ludai. Borneo: sengajang, tapang lalat (Ibang).

Uses — 't Mannetje & Jones (1992) cite the species as a timber tree, additionally as minor forage plant. The wood is soft, light and not of great use (Burkill, 1935). The seed coat is poorer in palmitic acid than that of *T. sebifera*, and is therefore not used (Aziz, 1987).

Notes — 1. The combination *Sapium cochinchinense* (Lour.) Kuntze, Revis. Gen. Pl. 3 (2) (1898) 293 refers to *Excoecaria cochinchinensis* Lour., not to *T. cochinchinensis* Lour. Most subsequent authors, like Pax & Hoffmann (1912) and Merrill (1935) used it for *Triadica* (under '*Sapium*').

2. Usually all specimens from Malesia and southern Cochinchina may be distinguished from the plants of the northern part of its range (including the lectotype) by the lower surface of the leaves more distinctly whitish. The structure of the cuticular ornamentations is obviously different. The syntypes of *Stillingia discolor* represent both variants. However, a taxonomic separation cannot be corroborated. Croizat's (1940) statement that it "is a collective species with numerous local forms" probably is not justified. Chakrabarty & Gangopadhyay (1990) united the species with the Indian *S. eugeniifolium* Buch.-Ham., which had been already suggested by Hooker (1888); both taxa had been kept separate before because of differences of the leaves very similar to the differences between the two mentioned syntypes. Considering the variability of *T. cochinchinensis* over its whole range, also *Sapium laui* from Hainan, described by Croizat (1940) for slight differences of leaves and measurements, may prove to be synonymous with *T. cochinchinensis.*

## 2. **Triadica sebifera** (L.) Small

*Triadica sebifera* (L.) Small, Man. S.E. Fl. (1933) 789; Hurus., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6 (1954) 315, f. 45; Kruijt, Biblioth. Bot. 146 (1996) 89. — *Croton sebiferus* L., Sp. Pl. (1753) 1004. — *Stillingia sebifera* (L.) Michx., Fl. Bor.-Amer. 2 (1803) 213; Willd., Sp. Pl. ed. 4, 4 (1805) 588; Hassk., Cat. Hort. Bot. Bogor. (1844) 234; Baill., Étude Euphorb. Atlas (1858) pl. 7, f. 26–30; Miq., Fl. Ind. Bat. 1, 2 (1859) 413. — *Sapium sebiferum* (L.) Roxb., [Hort. Bengal. (1814) 69, nomen] Fl. Indica ed. 1832, 3 (1832) 693; Wall., Numer. List. (1847) 7972; Müll.Arg., Linnaea 32 (1863) 121; Hook.f., Fl. Brit. India 5 (1888) 470; G. Watt, Dict. Econ. Prod. India 6, 2 (1893) 472; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 295; J.J. Sm. in Koord. & Valeton, Bijdr. Boomsoort. Java 12 (1910) 613; Koord., Exkurs.-Fl. Java 2 (1912) 507; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.v (1912) 237; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1926) 394, 395, 398; Burkill, Dict. Econ. Prod. Malay Pen. 2 (1935) 1962; F.N. Howes, Kew Bull. 4 (1949) 573; K. Heyne, Nutt. Pl. Indon. ed. 3, 1 (1950) 961; Backer & Bakh.f., Fl. Java 1 (1964) 500; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 136, 192; C.F. Hsieh, Fl. Taiwan 3 (1977) 496, pl. 700. — *Seborium chinense* Raf., Sylva Tellur. (1838) 63, nomen superfl. — *Stillingfleetia sebifera* (L.) Bojer, Hort. Maurit. (1857) 284. — *Excoecaria sebifera* (L.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 1210. — *Carumbium sebiferum* (L.) Kurz, Forest Fl. Burma 2 (1877) 411, 412. — *Seborium sebiferum* Hurus., Bot. Mag. Tokyo 61 (1948) 30. — Lectotype [proposed by Radcliffe-Smith, Fl. Pakistan 172 (1986) 86]: *Osbeck s.n. in Herb. Linn. No. 1140.9* (LINN, n.v.), China, Canton.

*Triadica sinensis* Lour., Fl. Cochinch. ed. 1, 2 (1790) 610; ed. 2, 2 (1793) 749; Baill., Etude Euphorb. (1858) 512; Merr., Trans. Amer. Philos. Soc., n.s. 24 (1935) 241. — Type: *Loureiro s.n.* (holo BM, n.v.), China, 'circa Cantonem Sinarum'.

Shrub to tree, up to 8 m high. Deciduous. *Leaves:* petiole 2.5–4 cm long; blade broadly ovate to orbicular, 3.5–6.5 by 2.5–7.5 cm, more than half as wide as long, base rounded, apex acuminate, above with a pair of glands c. 0.75 mm diam., lower surface whitish-papillate and with no to few submarginal glands, secondary veins 8–10 pairs, arching and joined towards the margin, smaller veins closely and distinctly reticulate. *Inflorescences* 70–140 mm long. *Bracts:* glands c. 1 by 0.75 mm. *Pistillate flowers* 2–6 per thyrse. *Fruits:* pedicel 6–15 mm long; schizocarp c. 12 mm long, sulcate. *Seeds* 6.5–8 by 6.5–7 mm, with a white, persistent sarcotesta.

Distribution — Native to China (known from nearly all provinces: Lee, 1956) and Taiwan. For its different uses often cultivated in warmer regions and sometimes naturalizing, nowadays in the USA, N India, and Japan, in former times also grown in Indochina, and Malesia (Singapore, Bogor, Timor; compare note 2).

Habitat & Ecology — Growing well e.g. in moist soil or near waters, and thriving under a wide range of soil conditions. It is frost hardy. It flowers after three years with very fragrant flowers; the fruits take three to four months for ripening (Aziz, 1987).

Vernacular names — Java: kasoembi, kirendang (Smith, 1910).

Uses — There is a wealth of literature available concerned with cultivation and uses in regions outside Malesia, especially China, Japan, India, and the USA (e.g., Howes, 1950). The species is planted as ornamental and has positive effects when planted as shade tree in plantations of other crops, especially as the species grows very well and often tends to naturalize easily. It is also a minor timber tree, and the leaves provide a black dye. The waxy seed coat yields the 'vegetable tallow' used for candle-making and soaps in China, whereas the endosperm of the seeds provides a drying oil (Stillingia oil) with properties similar to tung oil, in its drying capacities comparable to linseed oil, but also used as an illuminant (Burkill, 1935) and for waterproofing umbrellas (Lee, 1956).

Notes — 1. *Triadica sebifera* has often been confused with species of *Homalanthus*, especially *H. populneus* (Geiseler) Pax. Airy Shaw (1975) cites some examples of erroneous records of *T. sebifera* for Malesia. *Homalanthus* species may be distinguished from *Triadica* by the remarkable large stipules, leaves with percurrent (not reticulate) tertiary venation, different adaxial leaf glands, 3-flowered staminate cymules with compressed flowers and numerous stamens, and by very different, smaller fruits with mostly two carpels, a thin and fleshy pericarp, and seeds with a reddish arilloid.

2. Although quite often cited in the literature regarding Malesia, only four collections from this region could be studied [*Horsfield s.n.*, Java (BM); *Teijsmann s.n.*, Java (P, K); *De Vriese s.n.*, Java, Bogor Bot. Gard. (L sheet no. 904.117-515); *R. Brown s.n.*, Timor (BM)]. The other localities cited were taken from the literature. Obviously, the cultivation in Malesia has been abandoned, and no records from the 20th century are available.

## SEBASTIANIA

*Sebastiania* was described by Sprengel in 1821 and named after Antonio Sebastiani, a physician and botanist of Rome who died the same year. Müller Argoviensis was the first who, in 1866, assigned a species from the Old World (including Malesia) to the genus, namely *S. chamaelea*. Later contributions to the Malesian area were few. Pax & Hoffmann (1912) described another species, *S. borneensis*, Van Steenis (1948) two more, *S. lancifolia* and *S. remota*. Airy Shaw (1960, 1974) published additional notes on *S. borneensis* (including its first illustrations), on *S. chamaelea* (1980), and useful comments on Malesian *Sebastiania* as a whole (1975).

It is becoming more and more accepted that *Sebastiania* in its actual circumscription is unnatural (compare, e.g., Webster, 1994). Indeed, *Sebastiania* s.str. ('sect. *Eusebastiania* Müll.Arg.') is strictly Neotropical and very similar to Paleotropical *Excoecaria* L. (Esser, 1994). The two genera could even be combined into one genus, as was discussed by Bentham (1878) and again noted by Airy Shaw (1980) and Esser et al. (1998). All other species of *Sebastiania*, including all Malesian ones, are still included in distinct and quite different sections; they should be assigned to different genera (*Gymnanthes* and *Microstachys*), which will be formally effected for the Malesian taxa in the present work.

### NOMINA EXCLUDENDA

1. *Sapium cochinchinense* (Lour.) Kuntze, Revis. Gen. Pl. 3 (2) (1898) 293 = ***Excoecaria cochinchinensis*** Lour.

2. *Sapium cordifolium* Roxb., Fl. Indica ed. 1832, 3 (1832) 693 = ***Alchornea mollis*** (Benth.) Müll.Arg.

3. *Sapium crassifolium* Elmer, Leafl. Philipp. Bot. 2 (1908) 485 = ***Antidesma bunius*** Spreng.

4. *Sapium subrotundifolium* Elmer, Leafl. Philipp. Bot. 3 (1910) 930 = ***Blumeodendron subrotundifolium*** (Elmer) Merr.

5. *Stillingia populnea* Geiseler, Croton. Monogr. (1807) 80 = ***Homalanthus populneus*** (Geiseler) Pax.

## ACKNOWLEDGEMENTS

This study is based on material of the herbaria A, B, BKF, BM, BR, BRI, DBN, E, FHO, FR, G, GH, HBG, K, K-WALL, L, LIV, NY, OXF, P, P-JU, P-LA, TCD, U, UC, and US. I am indebted to the directors and curators of these institutions for loans or the possibility of visits and use of their facilities. The Netherlands Organization for Scientific Research (NWO) supported the work with a grant (B 85-291), which is gratefully acknowledged. A. Gunn (LIV) provided invaluable help with types at LIV, C. Jarvis (BM) and the Linnaean Plant Name Typification Project with Linnaean types, and A. Radcliffe-Smith (K) improved the Latin diagnoses. Two anonymous reviewers made very useful comments. The staff of the Rijksherbarium, Leiden, is thanked for various support, assistance and discussions, especially M.M.J. van Balgooy, C.E. Ridsdale, and J.F. Veldkamp. Very special thanks are due to P. van Welzen for reviewing the manuscript, critical comments and manifold support. J.H. van Os is responsible for the beautiful drawings. The distribution maps were produced with the help of the COOR database (© P. van Welzen, L) and the KORT program (© B. Hansen, C).

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## IDENTIFICATION LIST

Material of *Balakata*, *Falconeria*, *Gymnanthes*, *Microstachys*, *Sapium*, *Shirakiopsis*, *Stillingia*, and *Triadica* studied (only numbered collections cited):

1-1 = *Balakata baccata*
1-2 = *Balakata luzonica*
2-1 = *Falconeria insignis*
3-1 = *Gymnanthes borneensis*
3-2 = *Gymnanthes remota*
4-1 = *Microstachys chamaelea*
5-1 = *Sapium glandulosum*
6-1 = *Shirakiopsis indica*
6-2 = *Shirakiopsis sanchezii*
6-3 = *Shirakiopsis virgata*
7-1a = *Stillingia lineata* subsp. *lineata*
7-1b = *Stillingia lineata* subsp. *pacifica*
8-1 = *Triadica cochinchinensis*
8-2 = *Triadica sebifera*

Achmad 605: 1-1; 679: 1-1; 906: 1-1; 1053: 1-1; 1203: 1-1 — Adams 3045: 4-1 — Aët (exp. Lundquist) 31: 6-1 — Ahmad bin Shukor 19: 6-1 — d'Alleizette 6567: 7-1a — Altmann 456: 4-1 — Amann 9: 4-1 — Ambriansyah 797: 3-1; 846: 6-1 — Ambriansyah & Arifin 546: 6-1; W 122: 3-1; W 495: 3-1; W 791: 3-1 — Amherst 1398 = Wallich 7797 H: 4-1; 1718 = Wallich 7966: 1-1 — Andrew 183: 4-1.

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## NOTES

V. Malecot (Paris), who currently works on the Hippomaneae of Madagascar, confirmed that indeed only one species of *Stillingia* occurs in Africa (i.e., the Mascarenes), namely *S. lineata* (pers. comm.). Now the African representatives of the genus can be considered as sufficiently well known (see p. 190–193).

Y. Tseng [Fl. Reip. Pop. Sin. 44, 3 (1997) 18–19] recently proposed *Sapium laui* Croizat as a new synonym of *Triadica cochinchinensis* (as '*Sapium discolor*'), and confirmed my suspicion (see note 2, p. 204).