



The Malesian species of *Dalechampia* (Euphorbiaceae)

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Key words

Dalechampia
Euphorbiaceae
Malesia
Plukenetieae

Abstract *Dalechampia* is a mainly South American genus of generally climbing shrubs with usually sharp stiff trichomes in some of the inflorescence parts. The bisexual inflorescences are very condensed and subtended by two, often showy, large bracts. The three pistillate flowers are separate from the staminate subinflorescence (both groups with their own bracts). The staminate subinflorescence contains groups of staminodial-like bractlets that provide resin for female bees or fragrance for male bees. In west Malesia (Sumatra and Java) one indigenous species is found, the climbing *D. bidentata*, and occasionally cultivars of the subshrub *D. spathulata*.

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INTRODUCTION

Linnaeus (1753) introduced the genus based on a name by Plumier. At present c. 118 species are known, occurring worldwide in tropical areas with an emphasis on South America (Govaerts et al. 2000). Webster (1994, 2014) and Radcliffe-Smith (2001) classified *Dalechampia* in subfamily *Acalyphoideae* Beilschm. tribe *Plukenetieae* (Benth.) Hutch. subtribe *Dalechampiinae* (Müll.Arg.) G.L.Webster, because of the special inflorescence (2-bracteate capitate pseudanthia) and pollen type. The tribal classification is confirmed in the backbone *Euphorbiaceae* phylogeny of Wurdack et al. (2005); *Dalechampia* Plum. ex L. is part of clade A8, the *Plukenetieae*. In the phylogeny of Cardinal-McTeague & Gillespie (2016) the monogeneric *Dalechampiinae* form indeed a clade, sister to the *Plukenetieae*, which comprises the other lianaceous genera in the *Euphorbiaceae*.

The bisexual inflorescences are proterogynous, the basal pistillate subinflorescences are receptive first. The inflorescences are most typical for *Dalechampia*, they are very contracted pseudanthia (inflorescences mimicking flowers). The single, axillary (to terminal) inflorescences are covered by two subopposite bracts, with at their base at both sides a bracteole (homologous with leaves and stipules, respectively). These big bracts were considered to be typical for *Dalechampia*, but recently the non-related genus *Weda* was described (Van Welzen et al. 2021), where the two species also have these big bracts. Inside the involucre bracts there is a basal cyme of three pistillate flowers surrounded by its own bracts or a bract and 2 small bracteoles. Above it is the staminate subinflorescence, also surrounded by bracts, which comprises several staminate flowers and staminodial-like groups of bractlets. The homology of the bractlets is still uncertain, but they may be derived from inflorescences (comment by a reviewer). The

bractlets provide resin for bees, collected by female bees and used to build nests (but a shift in pollinators to fragrance collecting male bees occurred in *D. spathulata*, see there under Ecology). Most *Dalechampia* species have sharp trichomes in some parts of the inflorescence, which is a general feature in most other lianaceous genera in the *Plukenetieae*.

Baillon (1858) divided the genus into three sections (A (pistillate disc present, ovaries 3- or 4-locular), B (leaves divided, stigmas distinct, on top of ovary) and C = *Cremophyllum* (Scheidw.) Baill. (leaves simple, with stipellae; stigmas hidden in a cavity)). Baillon's sections B and C are section *Eudalechampia* of Müller Argoviensis (1866; invalid name for the autonym, sect. *Dalechampia*), which contains all but one species. Baillon's section A conforms with section *Champadelia* of Müller Argoviensis (1866) and only comprises *D. houlettiana* Baill. (the only species with a floral disc and according to Webster & Armbruster (1991) clearly not Euphorbiaceous, but probably a species of *Cissus*, *Vitaceae*). Pax (1890) maintained the sections of Müller, and in Pax & Hoffmann (1931) this was extended to 13 sections based on presence/absence of a disc, margin of sepals (entire or pectinate) and division of the leaves. In the most recent classification of Webster & Armbruster (1991) this was reduced to six sections, whereby one section (*Dalechampia*) had five subsections; Armbruster (1996) added a seventh section. Of the two species (sometimes) present in Malesia, *D. bidentata* Blume likely belongs to section *Scandentes* Pax & K.Hoffm. (no disc, divided sepals, lobed leaves) in the classification of Pax & Hoffmann (1931) and section *Dalechampia* subsect. *Dalechampia* of Webster & Armbruster (1991), while the cultivated *D. spathulata* (Scheidw.) Baill. is classified in sect. *Cremophyllum* (no disc, entire sepals). The most recent phylogeny of *Dalechampia* (Armbruster et al. 2009) does not discuss an infrageneric classification, though likely various clades may support sections.

Purpose of this contribution is to review the species present in the Malay Archipelago, thus revising them for the Flora Malesiana project (www.nationaalherbarium.nl/euphorbs).

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MATERIALS AND METHODS

Herbarium material in Naturalis Biodiversity Center (abbreviated L and U) in The Netherlands was used to revise the Malesian material. Fresh inflorescences of *D. spathulata* were donated by the Hortus botanicus, Leiden University (no. HBL20150165), and the analysis and drawing of all structures contributed greatly to the understanding of the rather condensed and complex inflorescences. As most herbarium specimens only comprise few inflorescences and the analysis of them is quite destructive, we refrained from analysing the complete inflorescence of *D. bidentata*.

The morphology was studied with stereo-binocular microscopes (Zeiss Discovery.V8). Type specimens studied are marked with an ! in the text and those seen as photo via <https://plants.jstor.org/> marked with an *.

RESULTS AND DISCUSSION

In Malesia only a single indigenous species is found, *D. bidentata*. Occasionally, *D. spathulata* is grown as an ornamental. Both species are easy to identify, *D. bidentata* is a climber with deeply trilobate, ovate leaves, while *D. spathulata* is a subshrub with entire, obovate leaves. There are also differences in the inflorescences: in *D. spathulata* the pistillate part is surrounded by a bract and two much smaller and narrower bracteoles, in *D. bidentata* the pistillate cyme is surrounded by two bracts, of which the lower is 3-lobed. The pistillate sepals in *D. bidentata* have long glandular trichomes perpendicular to the margin; in fruit the sepals enlarge considerably and the glandular trichomes become stiff side-branches (giving the sepals a pectinate appearance) and the sepals become densely covered with stiff, sharp, glochidiate trichomes that provide a very hostile impression to the infructescences (the infructescences of *D. spathulata* remain attractive, no great enlargement of the sepals and no masses of sharp trichomes). With the staminate subinflorescences there is a difference in the resin or fragrance secreting glands. In *D. spathulata* the fragrance emitting glands are in groups of different sizes, small near the flowers, much bigger groups away from the flowers, within the groups the organisation of the glands seems random; all groups are more or less parallel to the axis of the flowers. In *D. bidentata* there is less variation in the size of the groups, but these are perpendicular to the axis of the flowers and the resin producing glands are parallel to each other (appearing lamellate).

TAXONOMIC PART

Dalechampia Plum. ex L.

Dalechampia Plum. ex L. (1753) 1054, (1754) 473; A.Juss. (1824) 55; Baill. (1858) 485; Miq. (1859) 417; Müll.Arg. (1866) 1232; Benth. in Benth. & Hook.f. (1880) 330; Hook.f. (1888) 467; Pax (1890) 67; Pax & K.Hoffm. (1919) 3; Gagnep. (1926) 344; Pax & K.Hoffm. (1931) 151; Hurus. (1954) 293; Backer & Bakh.f. (1963) 492; Airy Shaw (1972) 251, (1975) 6; Armbr. (1988) 303; G.L.Webster & Armbr. (1991) 137; G.L.Webster (1994) 95; Philcox (1997) 176; Armbr. (1994) 302; L.J.Gillespie & Armbr. (1997) 14; Govaerts et al. (2000) 547; Radcl.-Sm. (2001) 262; S.S.Larsen (2005) 226; G.L.Webster (2014) 154. — *Dalechampia* Plum. ex L. sect. *Eudalechampia* Müll.Arg. (1866) 1233, nom. inval. — Type: *Dalechampia scandens* L. *Cremophyllum* Scheidw. (1842) 23. — Type: *Cremophyllum spathulatum* Scheidw. (= *Dalechampia spathulata* (Scheidw.) Baill.). [*Rhopalostylis* Klotzsch ex Baill. (1865) 317, nom. inval., in synonymy, non H.Wendl. & Drude (Arecaceae). — Based on: *Rhopalostylis buettnerioides* Klotzsch ex Baill. (= *Dalechampia micrantha* Poepp.).] *Dalechampia* Plum. ex L. sect. *Champadelia* Müll.Arg. (1866) 486. — Type: *D. houllettianum* Baill. (perhaps not *Euphorbiaceae*, see above). *Megalostylis* S.Moore (1916) 250. — Type: *Megalostylis poeppigii* S.Moore (= *Dalechampia micrantha* Poepp.).

Perennial herbs to erect or usually twining shrubs, monoecious. *Indumentum* of simple soft and stiff sharp trichomes, sometimes in parts glandular trichomes. *Stipules* rather persistent, relatively large, with basal glands inside. *Leaves* spiral, simple and unlobed to palmatifid to trifoliate to palmate, petiolate, base often with 2 (stipelliform) glands adaxially, margin entire to usually serrate or dentate, especially in upper half, with at lower surface erect glands; basally often palmately veined, lobes penninerved, secondary veins looped and closed near margin. *Inflorescence* axillary or terminal, solitary, pseudanthial, bisexual, bilaterally partite (staminate and pistillate flowers separated), subtended by a pair of usually sessile, subopposite, often showy involucre bracts, entire to serrate to 3-lobate, each with a pair of stipules; basally the pistillate flowers, present as a contracted, usually 3-flowered dichasium inserted above the lower involucre bract and subtended by a bract and 1 or 2 fused upper bracteoles; staminate part terminal, apparently inserted between pistillate cyme and upper involucre bract, pleiochasium of 5 (or 7) sessile, generally 3-flowered cymes with bracts next to a mass of fused, triterpenoid resin secreting bractlets, often lamellate. *Flowers* symmetric, pedicellate, petals and disc absent. *Staminate flowers*: pedicel usually articulate halfway; receptacle convex or column-like; sepals 4–6, valvate, recurving at anthesis, stamens (8 or) 10–30 (–100), filaments basally connate into a column, anthers with 2 thecae, opening via latrorse lengthwise slits; pistillode absent. *Pistillate flowers* subsessile, but pedicels elongating in fruit; sepals 5–12, entire or divided, imbricate, entire or pinnatifid; ovary 3- or (4-)locular; 1 ovule per locule; style long, apically broadened, stigmatic tissue at tip of style to extending down to sometimes 3/4 of style. *Fruit* a 3- or (4-)lobed capsule, dehiscent into 2-valved cocci; often subtended by an accrescent calyx, often armed with stiff trichomes; valves thin, woody; columella persistent. *Seeds* subglobose, without caruncle, smooth.

Distribution — About 118 species (Govaerts et al. 2000), mostly American (Neotropics), central and southern Africa, Madagascar, S and SE Asia, and West Malesia. In Malesia one species and one occasionally cultivated species.

KEY TO THE SPECIES

1. Leaves deeply trilobate, lobes ovate; petiole 2 cm or more long. Pistillate sepals enlarging in fruit to 25 mm long, pectinate, densely set with sharp trichomes. — Wild 1. *D. bidentata*
1. Leaves unlobed, blade ovate; petiole less than 2 cm long. Pistillate sepals hardly enlarging in fruit, less than 6 mm long, not pectinate, with short soft trichomes outside and along margin. — Cultivated 2. *D. spathulata*

1. *Dalechampia bidentata* Blume — Fig. 1

Dalechampia bidentata Blume (1825) 632; Miq. (1859) 417; Müll.Arg. (1866) 1243; J.J.Sm. (1910) 531, 756; Pax & K.Hoffm. (1919) 31; Backer & Bakh.f. (1963) 493; Airy Shaw (1969) 121, (1972) 251; Govaerts et al. (2000) 549; S.S.Larsen (2005) 227, plate XII: 2. — *Dalechampia bidentata* Blume var. *genuina* Pax & K.Hoffm. (1919) 32, nom. inval. — Lectotype (designated here): Blume 691 (lecto L (L.2212090!)), [Indonesia,] Java; see note 1. [*Croton acerrimus* Reinw. ex Blume (1823) 104, nom. nud.] *Dalechampia bidentata* Blume var. *yunnanensis* Pax & K.Hoffm. (1919) 32. — Syntypes: A. Henry 12354 (A00047585*, K00959098*, US00096455*), China, Yunnan, Szemao.

Twining herb; stems 1.5–6 m long, with thinly distributed, shortly appressed trichomes, flowering branches 1.7–2 mm diam. *Stipules* narrowly ovate, falcate, 4.5–15 by 2–4 mm, apex acute, subglabrous, especially inside. *Leaves*: petiole ± round in transverse section, adaxially shallowly grooved, 2–15 cm long, basally and apically pulvinate, and often twisted/curved at

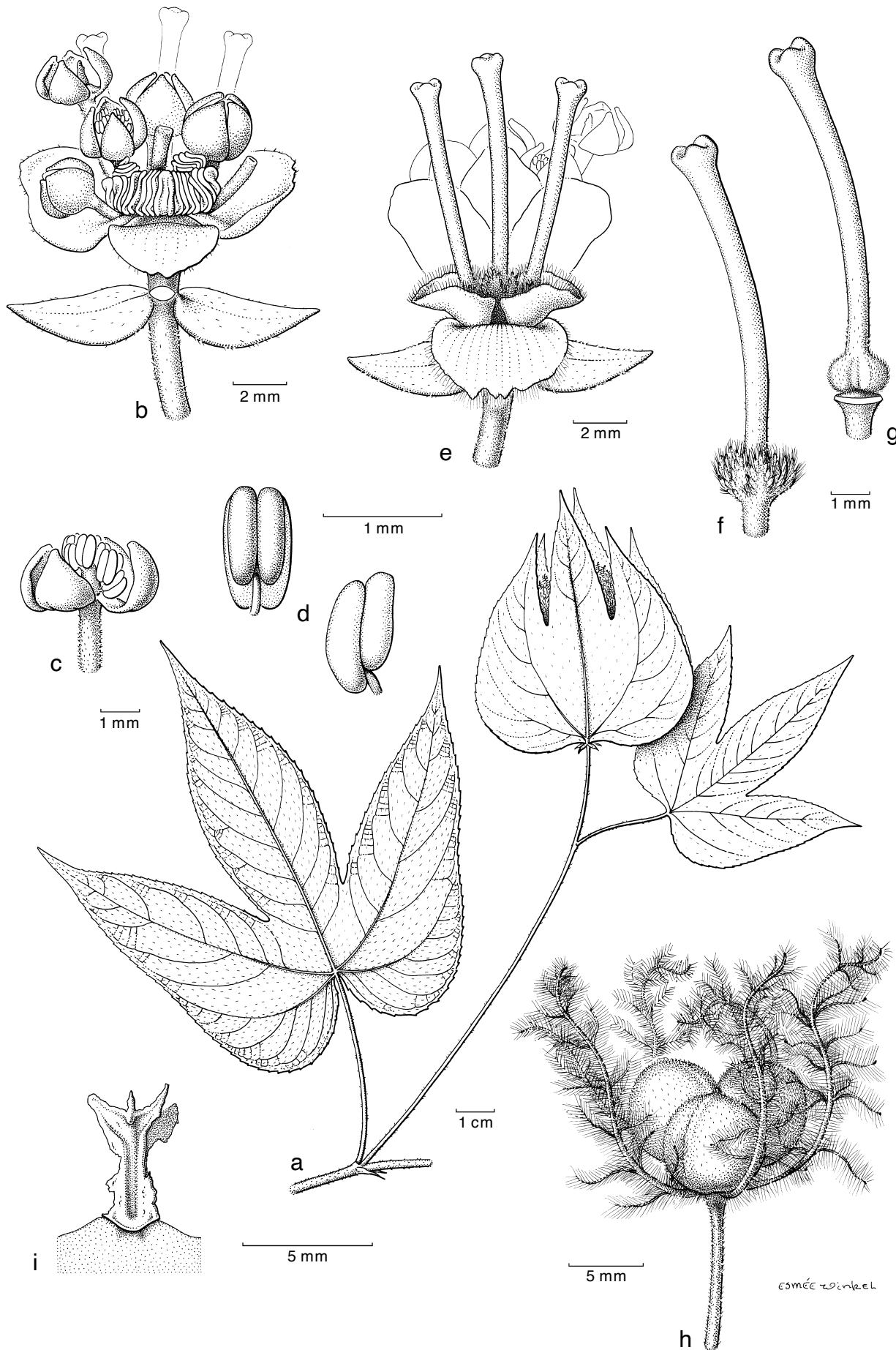


Fig. 1 *Dalechampia bidentata* Blume. a. Habit with two leaves (lower two) and an inflorescence of which only two bracts visible, at base of bracts bracteoles; b. inflorescence with bracts removed, showing still two bracteoles, staminate part visible surrounded by bracts and with glandular staminodial bractlets in front, in background pistillate part; c. opening staminate flower; d. anthers; e. pistillate part of same inflorescence with three bracts visible around the 3-flowered cyme; f. pistillate flower; g. pistillate flower with calyx removed; h. fruit with extended sepals and extended glandular trichomes ('side branches') covered with stinging trichomes; i. columella (a–g: Middleton, Suddee & Hemrat 1607; h, i: Van Harreveld HT 4422; all L). — Drawn by Esmée Winkel.

lower pulvinus, shortly sericeous with simple trichomes; stipellae ovate, 1.3–6 by 0.7–1 mm, with pedicelled glands basally inside, outside hairy, (sub)glabrous inside; blade deeply 3- (or 5-)lobate, ovate, 4–21 by 6–22 cm, 0.7–0.9 times longer than wide, papyraceous when dry, symmetric, base deeply emarginate, margin indistinctly serrate, flat, teeth bent towards apex, ending in gland, apices acuminate, upper surface dark green, lower surface lighter green, both sides with short appressed trichomes especially on venation, glabrescent, sometimes an occasional long sharp hair present; basally 5-nerved with between nerves abaxially roof-like domatia, lobes penninerved, with 12 or 13 veins per side in midlobe (counting from junction), looped and closed near margin, higher nerves reticulate, side-lobes with two major veins of which lower short; midlobe ovate to elliptic, 9–14.8 by 2.2–3.8 cm (length measured from connection with petiole), symmetric, side lobes asymmetrically ovate, 8.3–13.4 by 2.5–4.6 cm. *Inflorescence* solitary, axillary (see note 3); peduncle 3.3–19.5 cm long, subglabrous, halfway often a small(er), often caducous leaf leaving persistent stipules and axillary bud; involucre bracts sessile, subequal, ovate, 3-lobed, 4–6.8 by 2–6.5 cm, margin entire but with glandular trichomes (appearing as serrate), inside subglabrous, outside sparsely hairy, 5- or 7-nerved, with 3 acute lobes, basally with several stalked glands; basally each bract with 2 bracteoles, obliquely ovate, to 10 by 4 mm long, with at attachment inside several stalked glands, apex acute. *Pistillate part* basally with two pale green bracts, ovate, lower one 3-lobed, c. 6 by 15 mm, the subopposite higher bract c. 10 by 5 mm, apex 2-lobed; pistillate flowers 3, cymose, on short, 1.5–2 mm long pedicels; sepals 8–12, in two rows, ovate-triangular, c. 1.5 by 0.5 mm, completely short hairy, margin with long glandular, hairy trichomes with a c. 1.4 mm long stalk, and c. 0.3 mm long gland; ovary ovoid, slightly 3-lobed, c. 1.3 by 1.3 mm, densely short hairy, 3-locular; style 8–11.8 mm long, cylindrical, hairy, apex slightly widened into stigma, stigma somewhat 3-lobed, becoming convex discoid later. *Staminate part* only present in young inflorescences, caducous, on a c. 2.5 mm pedicel above the group of pistillate flowers, sturdy, broadening towards apex, with a few short appressed trichomes; on top 4 bracts in two rows, outer 2 larger, ovate, c. 6 by 4.5, apex a bit erose, completely slightly hairy with short appressed trichomes; staminate flowers 7–10, light green, pedicel up to 10 mm long, with abscission zone in upper third, slightly hairy; sepals 4 or 5, ovate, 2–3.3 by 1.5–1.8 mm, recurved but upper bent inwards, apex acute with apical gland, both sides shortly sparsely hairy; androphore c. 2 mm long, free filaments 0.5–0.7 mm long, anthers c. 25, ellipsoid, c. 1 by 0.7 mm, with 1 theca larger than the other; staminodial bractlets below flowers, at one side of flowers, in tight groups with anther-like parts parallel. *Fruits*: pedicels elongating to 18 mm long, longest with the median flower; sepals elongating to 25 by 1.5 mm, becoming \pm pectinate as glandular trichomes elongate to c. 5 mm long, the glandular tips disappear, the sharp trichomes covering the sepals become stiff and elongate up to c. 1.5 mm long; stigma in fruit 2 \times broader than style, disc-shaped. *Fruits* 3-lobed, c. 13 by 6 mm, densely shortly hairy; columella c. 4.5 mm high, top widened into 3 wings of c. 2 mm long. *Seeds* 3–5 mm diam, white and reddish brown marmorated.

Distribution — China (Yunnan), Myanmar (Tavoy = Dawei District), Laos (?), Thailand (South-Western, South-Eastern, Peninsular), *Malesia*: Sumatra, Java.

Habitat & Ecology — Evergreen forest, edge of primary forest, secondary forest with bamboo; once recorded from limestone. Altitude: 90–1200 m. Flowering: May, August, November, December; fruiting: January, May, July, August, October to December. For pollination information see Armbruster et al. (2011).

Vernacular names — Java: Areuj kakapasan (Smith 1910; *Bakhuizen van den Brink* 2346), Aroi Kekapasan (Miquel 1859) or Aroy Kakapassang (Blume 1825) (Sundanese); Oedoe lada, Patjahan (Smith 1910).

Notes — 1. The best fruiting material (no flowering material) that could be attributed to Blume (and not Herb. Blume, which are generally specimens from a later date) has been selected as lectotype.

2. On Java the leaf lobes of many specimens are more slender than in other areas; normally the species is found at altitudes up to 800 m, but *Koorders* 35784 from Java is from 1200 m and has much smaller leaves.

3. The inflorescence seems to develop axillary, with then in the lower third to halfway there is a leaf (often smaller than the other leaves, generally caducous), which shows that it is in fact a side branch with a terminal inflorescence. The whole side branch is here considered to be the peduncle.

2. *Dalechampia spathulata* (Scheidw.) Baill. — Fig. 2

Dalechampia spathulata (Scheidw.) Baill. (1858) 487; Backer & Bakh.f. (1963) 493; Armbr. (1988) 309. — *Cremophyllum spathulatum* Scheidw. (1842) 24. — Type: Not indicated, described from plants introduced from Brazil in 1839 and cultivated and flowering in Bruxelles in 1841 (Armbruster 1988). *Dalechampia roezliana* Müll.Arg. (1866) 1233. — *Dalechampia roezliana* Müll.Arg. var. *rosea* Müll.Arg. (1866) 1233, nom. inval., not homonym. — Lectotype (designated here): *Roezl s.n./Ortgies s.n.* (lecto G [G317251*]), Mexico, Veracruz, Sontecomapan. Müller did not describe a variety that could be considered a homonym, but only under var. *rosea* a reference to Roezl is given.

Dalechampia roezliana Müll.Arg. var. *viridis* Müll.Arg. (1866) 1234. — Type: *Hort. Van Houtte/Ortgies s.n.* (holo G [G317252*]), cultivated in hortus Ghent: Van Houtte.

Dalechampia roezliana Müll.Arg. var. *alba* W.Bull. (1875) 557. — Type: Not indicated.

Dalechampia spathulata (Scheidw.) Baill. var. *alba* G.Nicholson (1885) 439. — Type: Not indicated (may be based on the former name, but no reference to it).

Shrublet, erect, to 80 cm high, stem simple or sparsely branched; flowering branches 2–2.5 mm diam, somewhat flattened, indumentum of more or less adpressed, long and/or short trichomes, glabrescent. *Stipules* falcately ovate, 9–13.5 by 3.5–5.5 mm, base broad, convex on stem, margin entire, apex acute, rather persistent, outside either short or some long adpressed trichomes, venation distinct, parallel. *Leaves*: petiole completely pulvinate, 0.3–1.5 cm long, above flattened, short or long appressed hairy, sometimes glabrescent; blades spathulate-obovate, 9.7–26 by 3.7–8.8 cm, 2.4–3.7 times longer than wide, papery, symmetric, tapering towards the sometimes slightly widened, narrowly, shallowly, emarginate base, seldom widened into small lobes, with two small, upright adaxial glands at connection with petiole, margin subentire to laxly serrate or crenate, especially in wider part, teeth with a glandular erect yellowish tooth abaxially, flat to slightly revolute, apex acuminate and mucronate, surfaces drying dark brown or greenish above, lighter underneath; on both sides venation distinct, glabrous or hispid trichomes along midrib, glabrescent, second order veins 12–20 per side till apex, bent upwards and closed near margin, tertiary order veins subscalariform to reticulate, higher orders reticulate. *Peduncle* shortly sericeous. *Bracts* white to pink: lower bract ovate, c. 4.7 by 3.5 cm, base broadly attenuate, margin serrate, teeth ending in upward pointing glands, apex acute, very short trichomes along margin and on nerves on both sides, very strongly 3-nerved basally; basally on both sides a bracteole, recurved, falcately ovate, c. 10 by 5.5 mm, base one side much longer, touching other bracteole, margin entire, apex acute, venation \pm parallel, especially midrib distinct, margin and outside with few trichomes, inside glabrous; upper

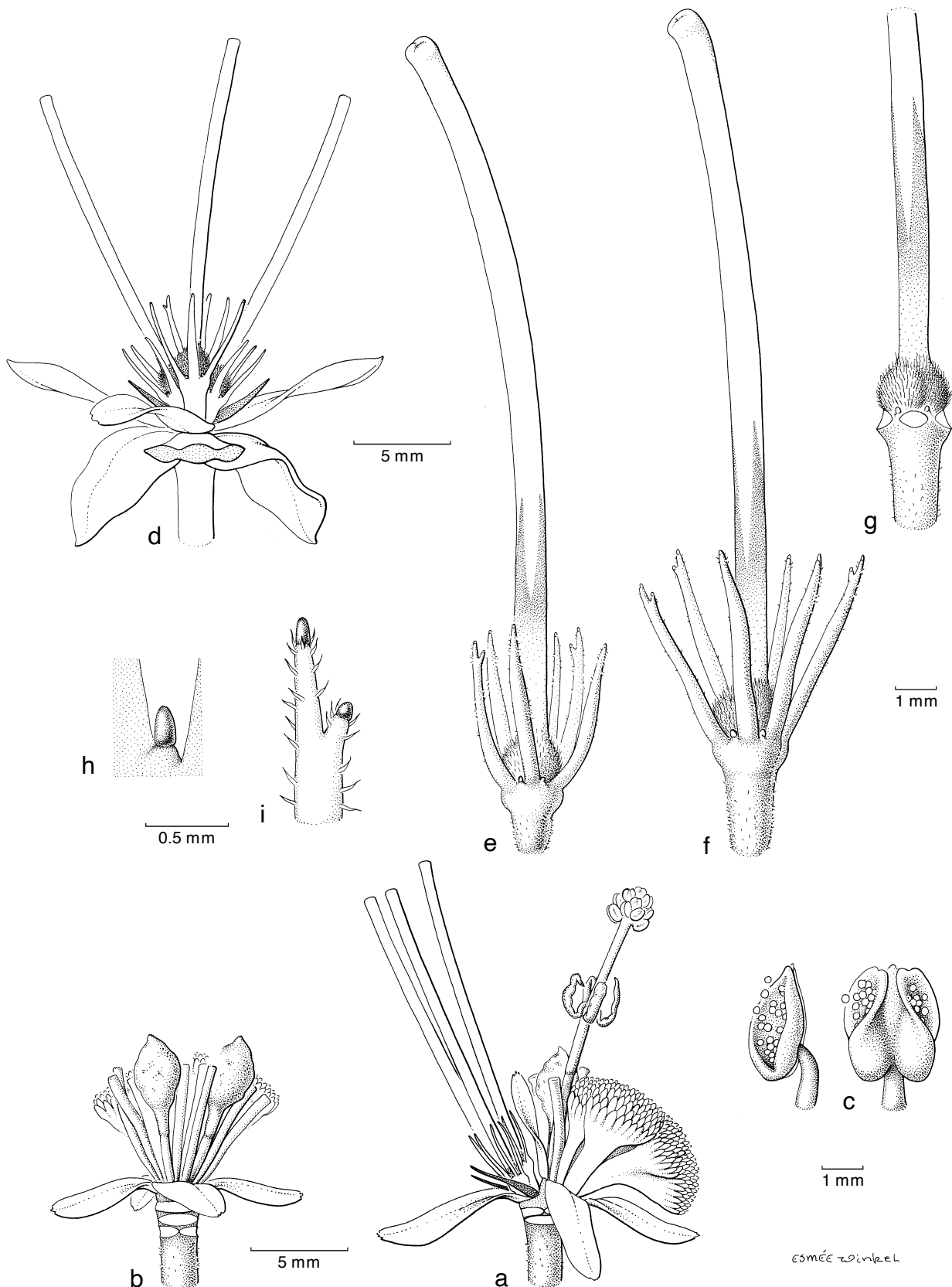


Fig. 2 *Dalechampia spathulata* (Scheidw.) Baill. a. Inflorescence with pistillate part (left) and staminate part (right, one staminate flower flowering, also showing dense groups of sterile staminodial bractlets; 2 bracts and 4 bracteoles to inflorescence removed); b. staminate part of inflorescence, flowers either caducous or in bud, in background glandular staminodial bractlets; c. anthers; d. pistillate part of inflorescence (2 bracts to the inflorescence removed, scar of one visible, 4 bracteoles of both bracts visible, 2 pointing downwards, 2 in back, bract, pointing to front, and small triangular bracteoles to pistillate flowers visible, cyme of 3 pistillate flowers); e. lateral pistillate flower; f. central pistillate flower; g. hairy ovary and basal part of style with two differently coloured parts (sepals removed); h. gland between sepals; i. glands at tip of sepals (based on fresh material from Hortus botanicus, Leiden University, no. HBL20150165). — Drawn by Esmée Winkel.

bract idem, c. 4.2 by 4.2 mm; bracteoles falcately ovate, c. 9.5 by 4 mm, mainly only margin hairy. *Pistillate part*: bract to pistillate flowers ovate, c. 9 by 5.3 mm, symmetric, margin entire, slightly shortly hairy, apex rounded, slightly 2- or 3-serrate; venation indistinct; bracteoles narrowly triangular, c. 4.8 by 0.7 mm, margin entire, slightly hairy; floral parts often with stinging *Urticaceae*-like trichomes, a thicker capillary basal part and a narrower point. *Pistillate flowers* 3 in a cyme; petioles c. triangular in transverse section, that of central flower c. 2.3 mm long, those of side-flowers c. 1 mm long, shortly hairy, sturdy, gradually widening towards apex; sepals 6, in 2 rows, long triangular, erect, apex ending in gland, outer slightly longer or shorter but always broader than inner, c. 5.3 by 0.9 mm, inner c. 5.2 by 0.7 mm, margin sometimes with a single serration at one side ending in a glandular tip, outside and margin hairy with soft trichomes, inside glabrous; erect glands in between sepals, c. 0.5 mm long, sometimes growing into short, sepal-like organs; ovary 3-locular, 3-lobed, c. 1.2 mm high by 1.7 mm wide, with long hispid trichomes, style to 17.3 mm long, hairy, slightly triangular in transverse section, in basal third with long triangular darker green surfaces, stigmatic apex slightly bent, circular, forming 3 only slightly raised knobs, not thickened. *Staminate part* on c. 4 mm long peduncle, broadening upwards, very sturdy, somewhat triangular, hairy; bracts 4, old, upright, ovate to somewhat obovate, 5–7.3 by 4–5 mm, outward and margin subglabrous; staminate flowers c. 9, petiole c. 7.8 mm long, upper part above abscission zone slightly thicker; sepals 4, long-ovate, c. 5.3 by 1.8 mm, valvate, apex ending in a gland, pinkish, outside and margin somewhat hairy; androphore c. 4 mm long, round in transverse section, hairy, white, free filament part c. 0.3 mm long, thin, anthers c. 12, subbasally attached, elliptic to somewhat triangular, c. 0.6 by 0.4 mm, bent downward and opening with seemingly 2 lengthwise slits with an indusium-like side, back of anther quite hard; staminodial bractlets many, stems 4.5–6.5 mm long, slender near flowers, then with a single bright yellow, shiny, apical gland, c. 0.8 mm long, further from flowers much thicker and with many apical glands. *Fruits* 3-lobed, c. 0.5 cm high by 0.8–1 cm wide, containing 3 globose seeds.

Distribution — South Mexico to Peru. *Malesia*: occasionally cultivated on Java (Backer & Bakhuizen van den Brink f. 1963).

Habitat & Ecology — Edge of somewhat disturbed rain forest. Flowering: March, August to November; fruiting: March, October. Altitude: c. 100 m. A shift in pollinators occurred, *D. spathulata* is not pollinated by female bees collecting resin, but by male *Eulaema* (Euglossinoid) bees, which use the fragrance-emitting monoterpenes of the staminate glands as an odorant (Armbruster & Webster 1979, Armbruster 1988). The staminate glands do not contain resin.

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REFERENCES

- Airy Shaw HK. 1969. Notes on Malesian and other Asiatic Euphorbiaceae. CXIII. *Dalechampia bidentata* in South-East Asia. Kew Bulletin 23: 121.
- Airy Shaw HK. 1972. The Euphorbiaceae of Siam. Kew Bulletin 26: 191–363.
- Airy Shaw HK. 1975. The Euphorbiaceae of Borneo. Kew Bulletin, Additional Series 4: 1–245.
- Armbruster WS. 1988. A new species, section, and synopsis of *Dalechampia* (Euphorbiaceae) from Costa Rica. Systematic Botany 13: 303–312.
- Armbruster WS. 1994. Early evolution of *Dalechampia* (Euphorbiaceae): insights from phylogeny, biogeography, and comparative ecology. Annals of the Missouri Botanical Garden 81: 302–316.
- Armbruster WS. 1996. Cladistic analysis and revision of *Dalechampia* sections *Rhopalostylis* and *Brevicolumnae* (Euphorbiaceae). Systematic Botany 21: 209–235.
- Armbruster WS, Gong YB, Huang SQ. 2011. Are pollination “syndromes” predictive? Asian *Dalechampia* fit neotropical models. American Naturalist 178: 135–143.
- Armbruster WS, Lee J, Badwin BG. 2009. Macroevolutionary patterns of defense and pollination in *Dalechampia* vines: Adaptation, exaptation, and evolutionary novelty. Proceedings of the National Academy of Sciences of the United States of America 106 (43): 18085–18090.
- Armbruster WS, Webster GL. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11: 278–283.
- Backer CA, Bakhuizen van den Brink Jr RC. 1963. Flora of Java 1. Noordhoff, Groningen.
- Baillon HE. 1858. Étude Générale du Groupe des Euphorbiacées. Librairie de Victor Masson, Paris.
- Baillon HE. 1865. Species Euphorbiacearum. Euphorbiacées Américaines 1. *Adansonia* 5: 305–360.
- Bentham G, Hooker JD. 1880. Genera Plantarum 3, 1. Reeve & Co., Londini.
- Blume CL. 1823. Catalogus van eenige der merkwaardigste zoo in- als uitheemse gewassen te vinden in 's Lands Plantentuin te Buitenzorg. Ter lands drukkerij, Batavia.
- Blume CL. 1825. Bijdragen tot de Flora van Nederlandsch Indië 12. Ter lands drukkerij, Batavia.
- Bull W. 1875. New plants. The Gardeners' Chronicle, n.s. 3: 557.
- Cardinal-McTeague WM, Gillespie LJ. 2016. Molecular phylogeny and pollen evolution of Euphorbiaceae tribe Plukenetieae. Systematic Botany 41: 329–347.
- De Jussieu A. 1824. De Euphorbiacearum Generibus medicisque earumdem viribus tentamen. Didot Junioris, Parisiis.
- Gagnepain F. 1926. Euphorbiaceae. In: Lecomte MH (ed), Flore Générale de l'Indo-Chine 5: 229–673. Masson & Cie, Paris.
- Gillespie LJ, Armbruster WS. 1997. A contribution to the Guianan Flora: *Dalechampia*, *Haematosomon*, *Omphalea*, *Pera*, *Plukenetia*, and *Tragia* (Euphorbiaceae) with notes on subfamily Acalyphoideae. Smithsonian Contributions to Botany 86: 1–48.
- Govaerts R, Frodin DG, Radcliffe-Smith A. 2000. World checklist and bibliography of Euphorbiaceae (with Pandaceae) 2. The Royal Botanic Gardens, Kew.
- Hooker JD. 1888. The Flora of British India 5. Reeve & Co., London.
- Hurusawa I. 1954. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen in weiteren Sinne. Journal of the Faculty of Science, University of Tokyo, Section III, Botany 6: 209–342.
- Larsen SS. 2005. *Dalechampia*. In: Chayamarit K, Van Welzen PC (eds), Euphorbiaceae (genera A–F). In: Santisuk T, Larsen K (eds), Flora of Thailand 8, 1: 226–228. The Forest Herbarium, Bangkok.
- Linnaeus L. 1753. Species Plantarum 2. *Impensis Laurentii Salvii*, Holmiae.
- Linnaeus L. 1754. Genera Plantarum, ed. 5. *Impensis Laurentii Salvii*, Holmiae.
- Miquel FAW. 1859. Flora van Nederlandsch Indië 1, 2. Fleischer, Lipsiae.
- Moore S. 1916. *Alabastra diversa* – part xxvi. The Journal of Botany (British and Foreign) 14: 249–257, 281–291.
- Müller (Argoviensis) J. 1866. Euphorbiaceae. In: De Candolle ALPP (ed), Prodrum Systematis Naturalis Regni Vegetabilis 15, 2: 189–1286. Victoris Masson et filii, Parisiis.
- Nicholson G. 1885. The illustrated dictionary of gardening 1. Upcott, London.
- Pax F. 1890. Euphorbiaceae. In: Engler A, Prantl K (eds), Die natürlichen Pflanzenfamilien 3, 5: 1–119. Engelmann, Leipzig.
- Pax F, Hoffmann K. 1919. Euphorbiaceae – *Dalechampiae*. In: Engler A (ed), Das Pflanzenreich IV.147.xii. Engelmann, Leipzig.
- Pax F, Hoffmann K. 1931. Euphorbiaceae. In: Engler A, Harms H (eds), Die natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233. Engelmann, Leipzig.
- Radcliffe-Smith A. 2001. Genera Euphorbiacearum. Royal Botanic Gardens, Kew.
- Philcox D. 1997. Euphorbiaceae. In: Dassanayake MD, Fosberg FR (eds): A revised handbook to the Flora of Ceylon 11. Balkema Publishers, Rotterdam.
- Scheidweiler M. 1842. Notice sur quelques nouveaux genres et espèces de plantes. Bulletins de l'Académie Royale des Sciences et Belles-lettres de Bruxelles 9: 19–26.
- Smith JJ. 1910. Euphorbiaceae. In: Koorders SH, Valetton T (eds), Bijdrage no. 12 tot de kennis der boomsoorten op Java. Mededeelingen uitgaande van het Departement van Landbouw 10: 9–637. Kolff & Co., Batavia.
- Van Welzen PC, Arias Guerrero S, Arifiani D, et al. 2021. Weda, a new genus with two new species of Euphorbiaceae-Crotonoideae from Halmahera (North Maluku, Indonesia) and phylogenetic relationships of the Australasian tribe Ricinocarpeae. Journal of Systematics and Evolution 59 (5): 1000–1017.

- Webster GL. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* 81: 33–144.
- Webster GL. 2014. Euphorbiaceae. In: Kubitzki K (ed), *The families and genera of vascular plants* 11: 51–216. Springer, Heidelberg, etc.
- Webster GL, Armbruster WS. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). *Botanical Journal of the Linnean Society* 105: 137–177.
- Wurdack KJ, Hoffmann P, Chase MW. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcl* and *trnL-F* DNA sequences. *American Journal of Botany* 92: 1397–1420.

IDENTIFICATION LIST

- 1 = *Dalechampia bidentata* Blume
2 = *Dalechampia spathulata* (Scheidw.) Baill.
- Backer 3804: 1 – Bakhuizen van den Brink Jr. 2200: 1 – Bakhuizen van den Brink Sr. 2346: 1 – Blume 691: 1.
- Forbes 2677: 1.
- Geesink, Hattink & Phengkai 6941: 1.
- Iboet 500: 1.
- Kerr 9612: 1 – Koorders 23544: 1; 23752: 1; 31174: 1; 35784: 1 – Kulju & Co 56: 2.
- Larsen 9418: 1 – Larsen & Larsen 33808: 1 – Lörzing 4120: 1.
- Middleton, Suddee & Hemrat 1607: 1.
- Poilane 21666: 1.
- Van Harreveld HT 4422: 1 – Ventura 21402: 2.
- Webster & Armbruster 20899: 2.
- Zollinger 3772: 1.