Blumea 70, 2026: 125–151
www.ingentaconnect.com/content/nhn/blumea

RESEARCH ARTICLE

https://doi.org/10.3767/blumea.2026.70.02.01

Revision of the genus *Croton* (*Euphorbiaceae*) for Java and the Lesser Sunda Islands (Indonesia and Timor-Leste)

L. van Duijn[1,2,*], H.-J. Esser[3], I. Pacheco[4], P. Silveira[4], P.C. van Welzen[1,2,*]

Keywords
Croton
Crotonoideae
Euphorbiaceae
Indonesia
Java
Lesser Sunda Islands
Taxonomic revision

Abstract The *Croton* species (*Euphorbiaceae*) from Java and the Lesser Sunda Islands (Indonesia, Timor Leste) are revised. In total 16 species were recognized, 12 species for Java, and 11 for the Lesser Sunda Islands (overlapping in seven species); included are four species new to science, *C. brevipetiolatus* (W Java and SE Borneo), *C. pseudoverticillatus* (Lesser Sunda Islands: Flores), *C. sumbensis* (Lesser Sunda Islands: Sumba, Flores, Timor), and *C. tetraglandulosus* (Java). Various lectotypes are indicated.

Citation: van Duijn L, Esser HJ, Pacheco I, Silveira P & van Welzen PC. 2026. Revision of the genus *Croton* (*Euphorbiaceae*) for Java and the Lesser Sunda Islands (Indonesia and Timor-Leste). Blumea 70 (2): 125–151. https://doi.org/10.3767/blumea.2026.70.02.01.
Effectively published online: 8 January 2026.

INTRODUCTION

Croton L. has been widely recognized as a complex and enormously diverse genus, containing over 1200 species, and exhibiting a range in habits like trees, shrubs, annual or perennial herbs, and some lianas (Frodin 2004, Berry et al. 2005, van Ee et al. 2011, Arévalo et al. 2017, Haber et al. 2017). Around two-thirds of the species can be found in the Neotropics and in Madagascar, and the remaining third, approximately 450 species (Berry et al. 2017), in the Palaeotropics up to the Pacific Islands (van Ee et al. 2011). In Malesia *Croton* is generally present and the estimated amount of species is c. 100 (comment van Welzen) comprising widespread species and endemics. General characters of *Croton* are clear to milky (or red(dish) coloured) latex; conspicuous stellate to lepidote trichomes; one or more pairs of basal, petiolar and/or laminar abaxial extrafloral nectaries; spike-like or raceme-like, terminal or subterminal thyrsoid inflorescences usually with pistillate flowers at the base and staminate flowers at the top; actinomorphic flowers with five sepals that are fused at the base, staminate flowers usually with five free petals, pistillate flowers very rarely with petals, anthers inflexed and introrsely inverted until anthesis; inaperturate pollen (Webster 1994, 2014, Radcliffe-Smith 2001, Berry et al. 2005, Haber et al. 2017, Thaowetsuwan et al. 2020, 2024); exceptions may occur, but not on Java (central island in the south of Indonesia, with the highest population of all of Indonesia) and the Lesser Sunda Islands (LSI; islands east of Java, comprising the provinces Bali, Nusa Tenggara Barat and Nusa Tenggara Timur, and the country Timor-Leste).

Croton belongs to the family *Euphorbiaceae*, subfamily *Crotonoideae*, which is divided into 12 tribes (Webster 1975, 1994, 2014, Radcliffe-Smith 2001, Berry et al. 2005). However, molecular evidence suggests that the subfamily and several of its tribes are not monophyletic (Wurdack et al. 2005). On the other hand, the tribe *Crotoneae* seems to be a well-supported clade containing the genera *Croton*, *Astraea* Klotzsch, *Acidocroton* Griseb., *Brasiliocroton* P.E.Berry & Cordeiro, *Sagotia* Baill., and *Sandwithia* Lanj. *Croton* contains most of the tribe's diversity. Even though the clade *Crotoneae* itself seems to be well supported, molecular analysis of nuclear and chloroplast genomes nevertheless shows different phylogenetic positions for the genera within the clade (Silva et al. 2020).

The circumscriptions of some *Croton* species are not stable yet, and new revision work not only recognises new species (e.g., Beyer et al. 2023 for tropical Asia), but also synonymises names. The general consensus in the literature divides the genus into approximately 40 sections (Webster 1993) and four subgenera (van Ee et al. 2011). There are only a few large-scale studies, like the world-wide synopsis of *Croton* species by Webster (1993), presently outdated. Research focused more often on specific groups or sections like arborescent New World *Croton* clades (Riina et al. 2010), *Barhamia* (Klotzsch) Baill. (Burilli et al. 2025), *Cleodora* (Klotzsch) Baill. (Caruzo &

[1] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; Corresponding author emails: lauravanduijn@ziggo.nl, peter.vanwelzen@naturalis.nl.

[2] Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA Leiden, The Netherlands.

[3] Botanische Staatssammlung München, Menzinger Strasse 67, 80638 München, Germany.

[4] Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal.

Cordeiro 2013, Riina et al. 2018), *Cyclostigma* Griseb. (Riina et al. 2009), and *Geiseleria* (A. Gray) Baill. (Riina et al. 2021), or areas like Australia (van Ee et al. 2015), the Cerrado in Brazil (da Silva et al. 2015), Michoacán in Mexico (Steinmann 2021), India (Chakrabarty & Balakrishnan 1997 ('1992')), Sumatra (Beyer et al. 2023), Thailand (Esser 2005), and China (Li & Esser 2008). As most species reside in the Neotropics, most studies have only focused on this area (van Ee et al. 2011). There are, however, some publications that treat species from the Old World, especially Madagascar, for it holds a third of the Old World species (Berry et al. 2017). A few others include species from Thailand (Esser & Chayamarit 2001, Esser 2002, 2010), Peninsular Malaysia (Esser & Veldkamp 2008), or Sumatra (Beyer et al. 2023).

Croton for Java was revised by Backer & Bakhuizen van den Brink (1963), who recognised six species: *C. argyratus* Blume, *C. caudatus* Geiseler, *C. glabrescens* Miq., *C. hirtus* L'Hér., *C. oblongus* Burm.f., and *C. tiglium* L. In his checklist for the *Euphorbiaceae* of central Malesia (Sulawesi, Lesser Sunda Islands, Moluccas in Indonesia) Airy Shaw (1982a) mentioned nine *Croton* species for the Lesser Sunda Islands (LSI) of which three have an uncertain status: *C. argyratus*, *C. cascarilloides* Raeusch., *C.* cf. *caudatus*, *C.* cf. *glabrescens*, *C.* cf. *montis-silam* Airy Shaw, *C. oblongus*, *C. prunifolius* Airy Shaw (an illegitimate name, currently accepted as *C. coccymelophyllus* Radcl.-Sm. & Govaerts), *C. tiglium*, and *C. tomentellus* F.Muell. Additionally, recent findings suggest two species new to the area, likely *C. adumbratus* Croizat (Esser & Veldkamp 2008), which appeared to be distinguishable from *C. argyratus*, and the introduced *C. bonplandianus* Baill., native to South America, for Java (Anshori et al. 2020). However, the occurrence of *C. adumbratus* on Java and the LSI is not yet proven (Esser & Veldkamp 2008). This study extends upon Beyer et al. (2023) to further revise and classify the *Croton* species of Southeast Asia, focusing on Java and the LSI.

MATERIAL AND METHODS

Morphological characters of the material from Naturalis Biodiversity Center, Leiden, The Netherlands (L; for herbarium abbreviations see Thiers continuously updated) were inspected using a Zeiss stereo microscope. The species delimitations were based on constant differences in morphology between groups of specimens. Important characters for species delimitation were habit, indumentum, stipules, size, shape, and margin of the leaf blade, extrafloral leaf nectaries and (when present) colleters (glands generally on the teeth of the leaf serrations), venation, inflorescences, flowers, capsules, and seeds. As already shown by Beyer et al. (2023), leaf morphology varied widely within species, but was sometimes useful for species delimitation. The identification key is mostly based on vegetative characters, so that it can be used for identidification of sterile or incomplete specimens.

For correct naming of the species, the types of the species were checked. Types physically seen are indicated with an exclamation mark (!), other types were inspected through high resolution pictures found on the Global Plants website of JSTOR (https://plants.jstor.org/) or via local online databases of herbaria, and these are indicated with an asterkis (*). When an herbarium houses several duplicates of a specimen, or if no collector number exists, a barcode or QR code is given as a unique identifier to separate the individual sheets.

Distributions, elevations, habitats, and data on ecology were summarized from specimen labels, and when present on the labels also added were descriptive data (e.g., habit, colours), vernacular names, and possible uses.

RESULTS

Four species are proposed as new (*C. brevipetiolatus*, *C. pseudoverticillatus*, *C. sumbensis*, and *C. tetraglandulosus*); see the identification key and diagnoses under the species for the typical characters.

Croton oblongus is a very problematic name (e.g., Beyer et al. 2023) and it is not recorded for Java and the LSI, but specimens previously identified as such were mainly found to be *C. laevifolius* Blume; other specimens appeared to be *C. brevipetiolatus* (newly described here), *C. scalaeus* Beyer, and *C. sumbensis* (newly described here). See also the discussion below.

For Java, 12 species are now recorded: *C. argyratus*, *C. bonplandianus* (observation by Anshori et al. 2020), *C. brevipetiolatus* (newly described here), *C. cascarilloides*, *C. caudatus*, *C. glabrescens*, *C. hasskarlianus* Müll.Arg., *C. hirtus*, *C. laevifolius*, *C. scaleus*, *C. tetraglandulosus* (newly described here), and *C. tiglium*. *Croton brevipetiolatus*, *C. cascarilloides*, *C. hasskarlianus*, *C. laevifolius*, *C. scaleus*, and *C. tetraglandulosus* are new additions for the flora of Java. *Croton hasskarlianus* and *C. laevifolius* were already known from literature to exist on Java (Miquel 1859), but were combined by Backer & Bakhuizen van den Brink (1963) under the name *C. oblongus*.

For the LSI, 11 species are now known: *C. adumbratus*, *C. argyratus*, *C. bonplandianus*, *C. cascarilloides*, *C. caudatus*, *C. glabrescens*, *C. laevifolius*, *C. pseudoverticillatus* (newly described here), *C. sumbensis* (newly described here), *C. tiglium*, and *C. tomentellus*. Of the nine species mentioned by Airy Shaw (1982a), several appeared to be incorrect identifications or the species were absent from LSI. *Verheijen 3442* (L), identified as *C.* aff. *montis-silam*, represents *C. adumbratus*. *Croton coccymelophyllus* (under the superfluous name *C. prunifolius*) appeared to be absent from LSI and is perhaps only present in New Guinea (Daan Curwiel pers. comm.). *Croton oblongus* is not recorded for the LSI (see below), and specimens identified as such were mainly *C. laevifolius*, but also the new species *C. sumbensis*. Thus, there are five new additions to the *Croton* flora of the LSI: *C. adumbratus*, *C. bonplandianus*, *C. laevifolius*, *C. pseudoverticillatus*, and *C. sumbensis*.

DISCUSSION

Species concepts

Two of the four new species were previously determined as *C. oblongus*. This is a consequence of the overly short description and too general plate by Burman (1768) for that

name; they fit almost every Asian *Croton* species (Corner 1939, Beyer et al. 2023). Burman's type collections are in G (Taxonomic Literature II online: https://www.sil.si.edu/DigitalCollections/tl-2/browse.cfm?vol=1#page/461), but during a previous visit to G and search in the Burman herbarium there, one of us, HJE, was not able to trace original material. Also, their database (https://www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en) does not show a type for *C. oblongus*. The plate can perhaps be considered the type, but should then be accompanied by the designation of an epitype to make the species interpretable. A better solution might be to suppress the name (nomina utique rejicienda; Art. 56 in Turland et al. 2025), in particular because the name has been used for several different species which notably blurred the taxonomy of SE Asian *Croton*. Unfortunately, a study that encompasses the Indian or Sri Lankan species was beyond the scope of this study. Like with Beyer et al. (2023), we found that most specimens identified as *C. oblongus* were *C. laevifolius*. The remaining specimens were still very variable and, like mentioned in Beyer et al. (2023), some of these forms appeared to be new species: *C. brevipetiolatus*, *C. scalaeus* (see Beyer et al. 2023), and *C. sumbensis*. The key presented here and the one in Beyer et al. (2023) will help to identify so-called *C. oblongus* material, but in areas like Borneo, the Philippines, Sulawesi, the Moluccas, and New Guinea there are almost certainly other undescribed species among the specimens.

Croton brevipetiolatus (newly described below) shows variation. The specimens were originally identified as *C. oblongus*, and morphologically they most closely resemble *C.tetraglandulosus* (newly described below), but there are no double extrafloral nectaries visible. The defining characters of *C. brevipetiolatus* are their relatively thick petioles, short inflorescences, and a semi-pubescent indument abaxially.

The material of Java, identified as *Croton glabrescens*, comprised two individuals that deviated from the type material (checked on https://plants.jstor.org/). *Backer 17863* (L) had two sets of extrafloral nectaries, and the abaxial side was set with stellate trichomes (unlike *C. glabrescens*). The other, *Zollinger 3805* (L), also had trichomes on the abaxial leaf side similar to those of *Backer 17863*, but a single set of extrafloral nectaries on the secondary veins. Together, these are here described below as a new species, *C. tetraglandulosus*, which can be characterised by the presence of usually a double set of glands, long and thin petioles, chartaceous leaf blade, and a semi-pubescent indument abaxially.

De *Voogd 2244* (L), from Sumba in the LSI, previously identified as *C. oblongus*, resembled *C. coccymelophyllus* very closely. However, the extrafloral nectaries are abaxial, laterally on the petiole instead of on the midrib and the inflorescence is subglabrous instead of with scattered trichomes. As such, this specimen was assigned to a new species, *C. sumbensis*, described below. A paratype of *C. prunifolius* (an illegitimate later homonym, now *C. coccymelophyllus*), *Kostermans 22064* (L), was mentioned by Airy Shaw (1978b: 57) for the LSI (Flores). However, this species is limited to New Guinea and has different basal extrafloral nectaries than the LSI material. *Kostermans 22064* also appeared to be the new species *C. sumbensis*.

Another specimen, formerly also identified as *C. prunifolius*, was from the island of Wetar (*Elbert 4637*, L) and it is the type of *Croton elbertii* Airy Shaw (*holo K*, iso L), but Wetar is politically part of the Moluccas, and it will be treated in another publication (Curwiel et al. in prep.). This specimen has stalked basal extrafloral nectaries laterally on the petiole, which were not observed in the type material.

The presence of *C. tomentellus*, which was indicated for both Java (Backer & Bakhuizen van den Brink 1963) and the LSI (Airy Shaw 1982a), could only be confirmed for the LSI. One of the individuals identified as *C.* cf. *tomentellus* (*Schmutz 844*, L), differed from the lectotype and represents a new species, *C. pseudoverticillatus*, see below, having as defining characters abaxial basal extrafloral nectaries on the very base of the midrib, and a much less dense indument (versus extrafloral nectaries on the petiole and a much denser indument, the abaxial leaf surface not visible, in *C. tomentellus*).

Croton adumbratus was found to be present on the LSI, but not on Java, which is in line with the findings of Esser & Veldkamp (2008). However, it was previously not confused with *C. argyratus* but with *C. montis-silam*. The material in the LSI has smaller leaves then the more western collections.

IMPORTANT CHARACTERS FOUND IN THE *CROTON* SPECIES OF JAVA AND THE LESSER SUNDA ISLANDS

Habit

All native species of *Croton* are woody, and grow as trees, shrubs, or climbers (*C. caudatus*). The bark is smooth, but often with fissures during the drying process; the colour ranges from dark reddish brown on young twigs to light brown or grey on older branches. The two introduced species, *C. bonplandianus* and *C. hirtus*, are annual herbs. *Croton hirtus* was recently also recorded as introduced for Sumatra (Beyer et al. 2023).

Indumentum

The indumentum consists of sessile stellate trichomes with free radii (Fig. 1b, c) or often radii in one plain with a central (larger) porrect radius, or flat lepidote trichomes with partially (sublepidote) to completely fused radii (Fig. 2b, c) (terminology following Pinto-Silva et al. 2023). Simple trichomes can be found in the floral parts of the plant, like on the apices of the floral bracts, sepals, or petals. The trichome coverage on plant parts varies between densely pubescent (no epidermis visible) to glabrous. Younger parts of the plant are often more densely covered. The trichome size and shape are important characters to separate species, but these can differ on various plant parts.

Leaves

All *Croton* specimens from Java and the LSI have simple leaves that are alternately placed or pseudo-verticillate when separated by very short internodes. Each leaf has a distinct petiole, which is grooved above, and often has an upper and lower pulvinus. Trichome coverage on the petiole varies between species from glabrous to pubescent. Leaf shape, base and apex are very variable. The leaf blade is in most cases thin, or in rare cases subcoriaceous (C. *brevipetiolatus*,

C. scalaeus). The margin is entire to serrate, and the teeth are mostly tipped by colleters (simple glands). In the case of *C. caudatus*, the margin has stalked extrafloral nectaries (see also next paragraph) between the serrae. The venation is mainly penninerved or triplinerved (*C. caudatus*, *C. glabrescens*, *C. hirtus*, *C. tiglium*), higher order veins are reticulate and more visible in the less hairy species. The secondary veins are looped and closed near the margin.

Extrafloral nectaries

The *Croton* species in this study have several nectary structures in the leaves, of which the extrafloral nectaries at the base of the leaves are the most obvious ones (for terminology of the secreting stuctures see Vitarelli et al. 2015). Number, shape, size, and location vary between species, but often also within a species, even within a single specimen. The variation is smaller in the latter case. The extrafloral nectaries can be flat (not raised), sessile (slightly raised) or with a small stalk. They are usuallly in pairs, but there can be two (C. *tetraglandulosus*; Fig. 5c) or more pairs and they can be found laterally on the petiole, laterally on the abaxial midrib, on the leaf margin near the base or abaxially on the leaf base close to but not on the midrib.

Inflorescences and flowers

All native *Croton* species have bisexual axillary or terminal thyrsoid inflorescences of which the cymules are reduced. Inflorescences therefore resemble a raceme, in which each flower node (cymule) has a separate bract and bracteoles, the latter often being much shorter than 1 mm. Pistillate flowers can be found basally in the inflorescence. Generally, there is a single pistillate flower per node, but it is rarely accompanied by one or two staminate flowers in bud. Staminate flowers are found apically with up to four flowers per node. This part usually falls off when the fruits ripen. Flowers have five sepals, which are fused at the base, and five free petals in the staminate flowers. Variation in this number is only seen in *C. laevifolius*. Whereas staminate flowers have fully developed petals, in pistillate flowers they are often absent or reduced. Typically, the stamens in staminate flowers are bent inwards in bud and straightened in full flower. Pistillodes and staminodes are absent. The style is in most cases absent, and the stigma is divided into three arms, each apically again split once, or twice in *C. cascarilloides*. Characters most important for separating species are the shape, size and indument of the sepals and petals.

Styles and stigmas

Our definition of the style is the united part on top of the ovary, which is often absent (stigmas sessile). The arms (three in the Malesian *Croton* species) are considered to be the stigmas, also the forking ends. There is a difference between stigma and stigmatic tissue, the latter are the structures that receive the pollen, they can only be locally present on the stigmas, like with species of *Homalanthus* A.Juss., they can cover the complete upper surface, like the branched papillae in species of *Mallotus* Lour., or the upper surface can be smooth and glabrous, not being indicative of any stigmatic tissue, like in Malesian *Croton*. According to Riina (pers. comm.) the stigmatic tissue in *Croton* is on the tips of the stigmas.

Fruits and seeds

Fruits are generally capsular with a hard pericarp. The capsules are globose or obovoid. Sizes differ between species. Each fruit has three locules with a single seed per locule. Seeds are often ellipsoid, but globose in *C. laevifolius*. The seeds are dry, smooth and generally glabrous, except subglabrous in *C. caudatus*. A small apical caruncle is often present.

TAXONOMIC TREATMENT

Croton L.

Croton L. (1753) 1004; (1754) 435; A.Juss. (1824) 28; Baill. (1858) 349; Müll.Arg. (1866) 512; Benth. (1880) 293; Hook.f. (1887) 385; Gagnep. (1925) 256; Pax & K.Hoffm. (1931) 83; Backer & Bakh.f. (1963) 475; Airy Shaw (1968) 374; (1969) 69; (1971) 514; (1972a) 241; (1972b) 78; Whitmore (1973) 84; Airy Shaw (1974a) 310; (1974b) t. 3712; (1975) 89; (1978a) 387; (1978b) 55; (1980a) 614; (1980b) 65; (1981a) 283; (1981b) 604; (1982a) 14; (1982b) 379; (1983) 17; Thin (1986) 28; G.L.Webster (1994) 111; Radcl.-Sm. (2001) 320; Esser (2005) 189; G.L.Webster (2014) 169, fig. 39. — *Croton* L. sect. *Eucroton* Baill. (1858) 354, nom. inval. — *Croton* L. sect. *Croton*: G.L.Webster (1993) 805. — Lectotype (designated by Small 1913: 454): *Croton tiglium* L.

Tridesmis Lour. (1790) (540,) 576. — Lectotype (designated here by Esser): *Tridesmis tomentosa* Lour. (= *Croton crassifolius* Geiseler).

Brachystachys Klotzsch (1843a) 47. — Type: *Brachystachys hirta* (L'Hér.) Klotzsch (= *Croton hirtus* L'Hér.).

Tiglium Klotsch (1843b) 418. — *Croton* L. sect. Tiglium (Klotzsch) Baill. (1858) 361. — Type: *Tiglium officinale* Klotzch (= *Croton tiglium* L.).

For all synonymous genera see Radcliffe-Smith (2001).

(Descriptions of all species based on the specimens from Java and LSI unless indicated otherwise.) Trees, shrubs, climbers, or herbs, monoecious; latex colourless or red. *Bark* smooth, older branches light brown or grey, young twigs dark reddish brown. *Indumentum* consisting of stellate to lepidote trichomes mixed with simple trichomes on floral structures. *Stipules* linear to triangular; persistent to caducous. *Leaves* simple, alternate or pseudo-verticillate; petiole grooved above, upper and lower pulvini often present; blade symmetric, chartaceous to subcoriaceous; base variable; basal extrafloral nectaries 1 (or 2) abaxial pairs, sessile to stalked, on the very apex of the petiole, very base of the midrib, or on the lamina near the base; margin entire to serrate, colleters often present at end of teeth, sometimes also extrafloral nectaries between the serrae (*C. caudatus*); adaxially and abaxially densely pubescent to glabrous, younger leaves often with a denser indument; venation mainly penninerved, sometimes triplinerved, secondary veins looped and closed near margin, higher order veins reticulate. *Inflorescenses* thyrsoid with reduced cymules, sulcate, axillary or terminal, bisexual, rarely unisexual; basally pistillate flowers, often single per node, rarely accompanied by one or two staminate flowers; apically staminate flowers, up to 4 flowers per node. *Flowers* pedicelled; sepals 5, fused at the base; petals 5, free, but often absent or reduced in pistillate flowers; disc glands 5; receptacle lanate. Staminate flowers stamens (10–)11(–33), anthers 2-thecate, inflexed when in bud, opening introrse with lengthwise slits; pistillode absent. *Pistillate flowers* ovary globose to oblate, 3-locular, single ovule per locule, pubescent, style most often absent,

stigma divided into three arms, apically each split once, rarely twice, glabrous, stigmatic tissue not obvious. *Fruits* capsular, globose to obovoid, with a hard pericarp. *Seeds* ellipsoid, rarely globose, glabrous to rarely with scattered trichomes, small caruncle present.

Between 1200 and 1300 species (Govaerts et al. 2000) occurring pantropically, but mainly found in the Neotropics (2/3 of species) and Madagascar. Twelve species on Java, eleven in the Lesser Sunda Islands.

IDENTIFICATION KEY TO *CROTON* SPECIES OF JAVA AND THE LESSER SUNDA ISLANDS

1. Herbs to subshrubs (stems herbaceous except sometimes the base woody) 2
1. Woody climbers, shrubs, trees 3

2. Stellate trichomes with long radii, without central porrect radius. Leaf margin with colleters at teeth apices, serration simple; blade 1.9–3.6(–4.3) times longer than wide. Fruits obovoid . . . . . .3. *C. bonplandianus*
2. Stellate trichomes with short radii except for the long central porrect radius. Leaf margin without colleters at teeth apices, serration double; blade (1–)1.2–1.8 times longer than wide. Fruits globose . . . . . .9. *C. hirtus*

3. Abaxial leaf indumentum dense, epidermis not visible . . .4
3. Abaxial leaf indument absent or far less dense, epidermis visible 6

4. Radii of stellate trichomes more than 40. Inflorescences 0.5–1 cm long. Stigmas divided twice (4 end parts per branch) . . . . . .5. *C. cascarilloides*
4. Radii of stellate trichomes less than 30. Inflorescences 2.6–29.4 cm long. Stigmas divided ones (2 end parts per branch) 5

5. Stipules 1–3.7 by 0.3–0.4 mm. Leaf blades 2.3–3.6 times longer than wide, base obtuse or narrowly subcordate. Fruits 5–7 mm high . . . . . .1. *C. adumbratus*
5. Stipules 10–15(–18) by 1–1.4 mm. Leaf blades 1.4–2.7 times longer than wide, base obtuse to rounded with the very base cordate. Fruits 12–14 mm high . . .2. *C. argyratus*

6. Climber. Leaves with stalked marginal extrafloral nectaries between serrae . . . . . .6. *C. caudatus*
6. Shrubs or trees. Leaves without extrafloral nectaries between serrae, sessile colleters can be present on tip of serrae 7

7. Leaf extrafloral nectaries sometimes in two pairs: one pair on the petiole, other on the base of the secondary veins; when one pair of extrafloral nectaries, then on the base of the basal secondary veins . . . . . .14. *C. tetraglandulosus*
7. Leaf extrafloral nectaries present as one pair, laterally on the base of the midrib, or laterally at the top of the pedicel, or on the margin of the blade near the base 8

8. Leaf extrafloral nectaries on margin of blade near the base . . . . . .15. *C. tiglium*
8. Leaf extrafloral nectaries laterally on the apex of the petiole or laterally on the basal part of the midrib 9

9. Trichomes stellate, free radii in all directions 10
9. Trichomes (sub)lepidote (radii partly or completely connected) or stellate (radii free), in one plain, when stellate often with one porrect radius 12

10. Mature leaf blades adaxially semi-pubescent and abaxially pubescent to densely pubescent . . . . . .16. *C. tomentellus*
10. Mature leaf blades adaxially glabrous or scattered trichomes, abaxially scattered trichomes 11

11. Petioles 1.8–6.5 cm long; leaf blades 8.4–16 by 3.2–6.4 cm . . . . . .7. *C. glabrescens*
11. Petioles 0.8–1.8 cm long; leaf blades 2.3–6.2 by 1.5–2.9 cm . . . . . .11. *C. pseudoverticillatus*

12. Trichomes mainly stellate in one plain on branches, usually with a porrect radius (absent in *C. sumbensis*), radii can be partly fused (sublepidote) 13
12. Trichomes mainly (partly) lepidote on branches, radii in one plain, partly (sublepidote) to completely fused (lepidote) 15

13. Leaf blades abaxially with (densely) scattered trichomes to semi-pubescent . . . . . .4. *C. brevipetiolatus*
13. Leaf blades abaxially glabrous but with scattered trichomes when young 14

14. Trichomes porrect-stellate, radii can be partly fused (sublepidote). Stipules (3.9–)5–7.2 mm long. Leaf blade margin entire to serrulate — Java, Borneo, Sulawesi, Lesser Sunda Islands (Flores) . . . . . .10. *C. laevifolius*
14. Trichomes flat-stellate, radii free. Stipules c. 3 mm long. Leaf blade margin serrulate — Lesser Sunda Islands (Sumba, Flores, Timor) . . . . . .13. *C. sumbensis*

15. Stipules 1.4–1.9 mm long. Leaf blades 3.7–4.5 times as long as wide, base attenuate, margin serrulate with colleters — Java (Madura Island) . . . . . .8. *C. hasskarlianus*
15. Stipules 3.4–6.7 mm long. Leaf blades 1.7–2.4 times as long as wide, base obtuse, margin subentire with colleters — Sumatra, W Java, Borneo . . . . . .12. *C. scalaeus*

1. *Croton adumbratus* Croizat

Croton adumbratus Croizat (1942b) 495; Esser & Veldkamp (2008) 167, f. 1a–c; Beyer et al. (2023) 8, fig. 2, 3a–c. — Holotype: *Griffith s.n.* '*Malacca*' (holo GH [00047509]!; iso CAL n.v., CGE n.v., K [K000959164, K000959165]*, L [L 0233476, L 0233442]!, M [M-0241965]!, P [P00623698]*), Malacca.

Croton argyratus auct. non Blume: Müll.Arg. (1866) 526, p.p.; Hook.f. (1887) 385, p.p.; Ridl. (1924) 260, p.p. ('*argyratum*'); Whitmore (1973), 85, p.p.

Croton erythrostachys auct. non. Hook.f.: Airy Shaw (1981a) 284, p.p.; Govaerts et al. (2000) 449, p.p.

Croton montis-silam auct. non Airy Shaw: Airy Shaw (1982a) 14.

(Description partly based on Sumatran specimens: Beyer et al. 2023.) Shrubs or trees; young twigs densely pubescent, hardly glabrescent; older branches glabrous. *Bark* fissured when dried, otherwise smooth, brownish yellow. *Indumentum* consisting of flat, sessile, (sub)lepidote trichomes, 0.2–0.3 mm diameter, 20–30 radii; abaxially on leaves silvery or yellowish-brown to a darker caramel colour with a dark brown centre; on venation, petioles, inflorescences, and young twigs caramel-coloured to brown with a dark brown centre; adaxially on leaves hyaline with a yellowish centre. *Stipules* linear-triangular, 1–3.7 by 0.3–0.4 mm, densely pubescent, caducous. *Leaves* alternate; petiole (0.6–)1.1–2.9 cm long, grooved above, slightly sulcate, densely pubescent, lower pulvinus 2–3 mm long, upper pulvinus not obvious; blade ovate to elliptic, 5.2–10 by 1.8–4.2 cm, 2.3–3.6 times longer than wide, base obtuse or narrowly subcordate, basal extrafloral nectaries laterally on the very base of the main vein, flat, c. 0.25 mm diameter, margin entire, apex acute to acuminate, adaxially glabrous except when young with scattered lepidote trichomes, abaxially epidermis not visible, completely covered by lepidote trichomes with dark brown centres distinctly visible as dots, overall a reddish brown appearance, venation visible as dark brown lines, penninerved, adaxially visible up to third order, sunken, abaxially visible up to second order, raised, secondary veins 6–9 pairs up to apex. *Inflorescences* terminal, up to 3 per node, (3.7–)5.1–7.9 cm long, sulcate, densely pubescent; basally pistillate flowers single per node; apically staminate flowers 1 (or 2) per node; bracts triangular, 0.7–0.8 by c. 0.5 mm, densely pubescent; bracteoles linear, densely pubescent. *Staminate flowers* c. 3 mm diameter; pedicel c. 1.5 mm long, densely pubescent; sepals 5, triangular, c. 1.6 by 1.2 mm, outside densely pubescent, inside glabrous; petals 5, obovate, c. 2 by 0.9 mm, outside and inside glabrous, margin ciliate with long, simple yellowish trichomes; receptacle lanate; disc glands orange; stamens c. 11, filaments c. 2.1 mm long, anthers c. 0.7 by 0.7 mm. *Pistillate flowers* c. 2.2 mm diameter; pedicel c. 0.8 mm long, densely pubescent; sepals 5, elliptic, c. 2.2 by 1 mm, longer than the ovary, outside densely pubescent, inside with scattered trichomes; petals absent; ovary globose, c. 1.7 by 1.5 mm, densely pubescent, style c. 0.4 mm long, densely pubescent, stigmas c. 1.5 mm long, apically once divided till c. 0.4 mm from the base, with scattered trichomes. *Fruits* globose, 5–7 mm high by 6–7 mm diameter, slightly sulcate, densely pubescent, apex sunken; pericarp c. 0.3 mm thick; columella 5–7 mm long. *Seeds* ellipsoid, flattened, 5–7 by 4–5 mm, glabrous, with a small caruncle.

Distribution — *Malesia*: Malay Peninsula incl. Singapore, Sumatra, Borneo (Kalimantan Barat), Sulawesi, Lesser Sunda Islands (Flores).

Habitat & Ecology —Primary and secondary lowland forests. Altitude: 0–750 m, often on sandstone but also on limestone hills. Flowering: March–April, July–August, October–November; fruiting: March, July, October (Esser & Veldkamp 2008, Beyer et al. 2023).

Notes — Several specimens from the Lesser Sunda Islands were found to belong to *C. adumbratus*. One (*Verheijen 3442*, L) was originally identified as *C.* aff. *montis-silam*. *Croton montis-silam* has leaf blades 3.6–4 times longer than wide, base rounded and rarely subcordate, trichomes colouring lower leaf surface whitish and the trichomes have a distinct reddish-brown dot, versus leaf blades 2.3–3.6 times longer than wide in *C. adumbratus*, base obtuse to subcordate, trichomes on the abaxial leaf side colouring the leaf dark reddish brown.

The Sunda specimens have much smaller leaves (leaf blades up to 10 cm long) than generally found in west *Malesia* (leaf blades 9–21 cm long).

2. *Croton argyratus* Blume

Croton argyratus Blume (1826) 602 (‘*argyratum*’); Müll.Arg (1866) 526; Hook.f., (1887) 385; J.J.Sm. (1910) 336; Merr. (1921a) 336; (1923) 425; Ridl. (1924) 260, p.p. (‘*argyratum*’); Gagnep. (1925b) 277; Merr. (1926) 381; (1929) 156; Burkill (1935) 688; M.R.Hend. (1939) 70; Backer & Bakh.f. (1963) 476; Airy Shaw (1972a ‘1971’) 243; Whitmore (1973) 85; Airy Shaw (1975) 90; (1976) 385; (1980a) 616; (1981a) 284; (1982a) 14; (1983) 17; Corner (1988) 283, text-fig. 81; Chakrab. & N.P.Balakr. (1997 ‘1992’) 22, fig. 1, map 1; Esser (2005) 193, fig. 45, plate X: 2; Esser & Veldkamp (2008) 169, fig. 1d–f; Chakrab. (2019) 629; Beyer et al. (2023) 8, fig. 3d–f. — *Croton argyratus* Blume var. *genuinus* Müll.Arg. (1866) 526, nom. inval. — *Oxydectes argyrata* (Blume) Kuntze, (1891) 611. — Lectotype (designated by Esser & Veldkamp 2008: 169): *Blume s.n.* (lecto L [L0233566]!; possible isolecto A [AS00106971]!, BM [BM000630468]! as no. 230, P n.v.), Indonesia, Java. Airy Shaw (1980a) appointed Blume s.n. (BO) ‘in sylvis montium calcareorum Provinciarum occidentalium Javae’ as type, but that text is copied from Blume (1825), and does not appear as such on labels, therefore no specific specimen was mentioned and thus no lectotypification).

Croton bicolor Roxb. [(1814) 69, nom. nud.], (1832) 680. — *Oxydectes bicolor* (Roxb.) Kuntze (1891) 611. — Lectotype (designated by Chakrabarty & Balakrishnan 1997 ‘1992’: 22): *Icones Roxburgianae 2558* (lecto CAL (2561 on drawing); isolecto K (2551 on drawing)), Indonesia, Sumatra, probably Bengkulu, Fort Marlborough.

Croton zollingeri Miq. (1859) 381. — Lectotype (designated by Beyer et al. 2023: 8): *Zollinger 963-Z* (lecto U [U 007936]! as *Unknown s.n.*; isolecto A [A0010017]!), Indonesia, Java.

Croton argyratus Blume var. *hypoleucus* Müll.Arg. (1864) 483; (1866) 526. — Lectotype (designated by Esser & Veldkamp 2008: 169): *Motley 758* (lecto K [K000959191]!), Borneo, Banjarmasin.

Croton argyratus Blume var. *hypoleucus* Müll.Arg. (1864) 483; (1866) 526. — Lectotype (designated by Esser & Veldkamp 2008: 169): *Motley 758* (lecto K [K000959191]!), Borneo, Banjarmasin.

Croton argyratus Blume var. *brevipes* Müll.Arg. (1866) 527. — Lectotype (designated by Esser & Veldkamp 2008: 169): *Zollinger 3212* (lecto G-DC [G00311485]!; isolecto A [A00047510]!, G [G00434384]!, [G00434386]!), Indonesia, Java.

Croton argyratus Blume var. *gracilis* Müll.Arg. (1866) 527. — Lectotype (designated by Esser & Veldkamp 2008: 169): *Zollinger 3809* (lecto G-DC [G00311486]*; isolecto BM [BM000630468]!, CAL [CAL0000023639]*, G [G00434385]!, W [1889-0074726]!), Indonesia, Bali.

Croton budopensis Gagnep. (1922 ‘1921’) 549. — Syntypes: *Poilane 793* (A [A00099663], K [K000959154], P [P00120308]), Cochinchine, Prov. de Thu-dau-mot, Budop.

Croton maieuticus Gagnep (1925a) 463. — Syntypes: *Poilane 10237* (K [K000959155]*, P [P00120328, P00610257, P00610258]*) [Vietnam,] Annam, Prov. Quang-tri, Dent du Tigre.

Croton pilargyros Croizat (1942b) 372. — Lectotype (designated here): *Brass 8062* (lecto A [A00047525]*; isolecto BM [BM000951462]*, BRI [BRI-AQ0342508]*), British New Guinea [Papua New Guinea], Lower Fly River, east bank opposite Sturt Island.

Croton avellaneus Croizat (1942b) 498. — Type: *BS* (Ramos & Edaño) 43977 (holo A [A00047539]!; iso BM!, G!, W [1930-0001714]!), Philippines, Sulu.

Trees, up to 30 m high, to 30 cm diameter; young branchlets densely pubescent, hardly glabrescent; older branches glabrous. *Bark* smooth, pale yellowish or grey; lenticellate, young bark fissured when drying out; living bark c. 1 cm thick, beefy red outside, dirty white inside for c. 3 mm. *Indumentum* consisting of flat, sessile, stellate trichomes, 0.2–0.3 mm diameter, 18–28 free to partially fused radii, central porrect radius sometimes short (stems and leaves) or long (on stems); on stems, inflorescences and abaxial venation reddish-brown to yellowish brown trichomes; leaf trichomes with mostly hyaline radii with some reddish brown ones, and a brown centre mixed with a few reddish-brown radii; simple yellowish trichomes on bracts and bracteoles. *Stipules* linear, 10–15(–18) by 1–1.4 mm, pubescent on both sides, caducous. *Leaves* alternate; petiole grooved above, 1.4–15.8 cm long, slightly sulcate, densely pubescent, lower pulvinus 2–7 mm long; blade ovate to elliptic, 6.1–19.5 by 3.2–10.4 cm, 1.4–2.7 times longer than wide, base obtuse to rounded with the very base cordate, basal extrafloral nectaries abaxially lateral on the very base of the main vein, flat, (0.5–)0.7–0.8(–0.9) mm diameter, margin entire, apex acuminate, adaxially nearly glabrous, trichomes mainly on venation, abaxially completely and densely pubescent, lamina not visible, venation penninerved, adaxially sunken, abaxially raised, on both sides visible up to third order, secondary veins 7–9 pairs up to apex. *Inflorescences* terminal, sulcate, up to 4 per node, densely pubescent, often one long bisexual to 29.4 cm long, and up to 3 small unisexual inflorescences, 1–2 cm long, seemingly only with staminate flowers, the long inflorescence matures first; basally (2–)5–13(–25) pistillate flowers, 1 per node, occasionally with 1 or 2 staminate flowers, apically usually 3 staminate flowers per node. *Staminate flowers* c. 4.8 mm diameter; bracts ovate to triangular, 0.7–1.1 by 0.3–0.6 mm, outside lanate, inside subglabrous; bracteoles triangular, outside lanate, inside subglabrous; pedicel 2.1–4.4 mm long, densely pubescent; sepals 5, ovate, c. 2.2 by 1.7 mm, outside densely pubescent, inside glabrous, margin ciliate with long, simple hyaline trichomes; petals 5, obovate, 2.5–2.9 by 0.8–0.9 mm, covered with simple hyaline trichomes, outside and inside thinly lanate, margin basally with shorter trichomes than apically; receptacle lanate, disc glands 5; stamens 10–11, filaments 2.5–2.9 mm long, anthers 0.8–0.9 by 0.4–0.5 mm. *Pistillate flowers* 4.8–7.5 mm diameter; bracts ovate, 1.5–1.8 by c. 1.1 mm, apex bilobed, hispid; bracteoles triangular, hispid; pedicel 2.7–5.5 mm long, densely pubescent; sepals 5, elliptic, 3.7–3.8 by 2.5–2.6 mm, much longer than ovary, outside densely pubescent, inside with scattered trichomes; petals absent; ovary globose, c. 2.7 by 2.7 mm, densely pubescent, style c. 0.3 mm long, densely pubescent, stigmas c. 5 mm long, apically divided once to 2.6–3.2 mm from base, flattened with a groove on the upper side along the middle up to the apical division, pubescent below. *Fruits* obovoid to globose, faintly 3-lobed, 1.2–1.4 cm high by 1.4–1.5 cm diameter, densely pubescent, stigmas caducous; columella 1.2–1.4 cm long. *Seeds* ellipsoid, flattened, c. 11 by 8 by 5 mm, glabrous, with a very small caruncle.

Distribution — SE Asia (Thailand, Andaman and Nicobar Islands); *Malesia*: Peninsular Malaysia, Sumatra, Java, Borneo, Philippines, Sulawesi, Lesser Sunda Islands (Bali, Lombok), Moluccas. Also recorded for Andorra (Europe), but likely introduced or misnamed.

Habitat & Ecology — Heterogenous primary forest to secondary vegetation. Loam soil, as well as on calciferous or sandy soil. Altitude: 10–1000 m. Flowering and fruiting the whole year through (Smith 1910)

Uses — Wood for housing. Lamp oil from the seeds (Smith 1910).

Vernacular names — Java: Djarakan, Huru dangdang, Leprak, Parengpeng, Paskapason, Perkoso, Tapen, Tapen kebo, Tjalik angin, Walik, Walik angin, Walik lar (Smith 1910).

Notes — Pistillate flower sizes might be bigger than the size measured in this paper, because the sepal lobes were probably young, often not yet folded outwards but still covering the ovary.

3. *Croton bonplandianus* Baill.

Croton bonplandianus Baill. (1864) 339 (‘*bonplandianum*’); Croizat (1940) 573; Radcl.-Sm. (1986) 43; Chakrab. & N.P.Balakr. (1997 ‘1992’) 31; Esser (2005) 195, plate X: 3. — *Oxydectes bonplandiana* (Baill.) Kuntze (1891) 610. — Lectotype (designated by Berry et al. 2017: 24) : *Bonpland s.n.* (P [P00623061]*, isolectotype P [P00623060]*), Argentina, Prov. de Corrientes.

Croton sparsiflorus Morong (1893) 221; Burkill (1914) 235. — *Oxydectes sparsiflora* (Morong) Kuntze (1898) 289. — Lectotype (designated here by Esser, indicated by Valduga, *Croton* Pampas grasslands 2021: 48): *Morong 940* (lecto NDG [NDG29229]!; isolecto NY [NY00262958]!, PH [PH00007339]*, US [US00997749]*), Paraguay, Pilcomayo River (the thesis of Valduga, an online publication, lacks an ISBN number and is, therefore, not effectively published, see Art. 29.1 in Turland et al. 2025).

Herbs, c. 40 cm tall; stem slightly sulcate; young branchlets densely pubescent, glabrescent; latex red. *Indumentum* consisting of stalked, stellate trichomes, 0.31–0.53(–0.57) mm in diameter, 9–16(–20) radii on leaves and veins, 16–28 radii on stems, radii pointing downward, sometimes flat; hyaline radii with centre yellowish brown. *Stipules* linear, 1–2.4 by c. 0.4 mm, trichomes on both sides, early caducous. *Leaves* petiole grooved above, (1.2–)3.8–5.8(–9) mm long, covered with scattered trichomes, more densely so when young; blade ovate, 3–4.7 by 0.7–2 cm, 1.9–3.6(–4.3) times longer than wide, base obtuse, basal extrafloral nectaries abaxially on lamina, sessile, in many cases absent, 0.6–1 mm in diameter, margin once serrate, apices of serrae with colleters, apex acute, adaxial side glabrous, abaxial side subglabrous, trichomes only on the veins, venation scalariform, adaxially visible to first order, sunken, abaxially visible up to second order, raised, second order veins 11–12 pairs up to apex. *Inflorescences* terminal, sulcate, with scattered trichomes, 4.2–5.1 cm long when pistillate flowers finished blooming, 13.2–15.2 cm long when fruits ripe; basally up to 9 pistillate flowers, single per node, apically staminate flowers up to 4 per node; bracts ovately triangular, 0.7–0.9 by c. 0.4 mm, glabrous, margin ciliate with simple hyaline trichomes; bracteoles caducous.

Staminate flowers 2–2.6 mm in diameter; pedicel 1.2–1.6 mm long, glabrous; sepals linear-ovate, c. 2 by 0.8 mm, glabrous, apex truncate with short, simple, hyaline trichomes, midrib slightly darker in colour, margin in the upper part hyaline; petals linear-obovate, c. 2 by 0.5 mm, hyaline, lanate in the lower half, apex rounded; receptacle glabrous, disc glands 5; stamens c. 17, filaments c. 1.8 mm long, anthers 0.5–0.6 mm long. *Pistillate flowers* 1.4–2.3 mm diameter; pedicel 0.8–1 mm long, glabrous, sometimes basally glands of 0.5–0.7 mm diameter; sepals triangular, c. 1.8 by 0.8 mm, glabrous, midrib slightly lighter in colour on the outside, margin ciliate with white simple trichomes; petals reduced to small white orbital structures; receptacle glabrous; ovary densely pubescent, style absent, stigmas c. 2 mm long, apically divided to c. 1 mm from base, glabrous, flat with groove in the middle up to the division. *Fruits* obovate, slightly 3-lobed, c. 6 mm high by 4.7 mm diameter, covered with scattered trichomes; columella c. 4.9 mm long, with 3 pronounced apical lobes (see note 2). *Seeds* ellipsoid, one side slightly flattened, c. 4.4 by 2.2 by 1.7 mm, glabrous, ridge along the sides, indented line over the belly; caruncle very distinct.

Distribution — Originally from South America, now introduced in tropical Africa, Southeast Asia, and *Malesia*: Malay Peninsula (incl. Singapore), Java, Borneo, Sulawesi, Lesser Sunda Islands (Timor-Leste).

Habitat & Ecology — Primarily in the seasonal dry tropics. Weed in disturbed areas like the banks of sewage ponds, roadsides, and abandoned lands or in upper tidal areas (Anshori et al. 2020).

Notes — 1. *Croton bonplandianus* is an introduced species in the Lesser Sunda Islands, noticed first by Anshori et al. (2020) on Java.

2. *Croton bonplandianus* is part of section *Adenophylli* Griseb. A typical character for this subgenus is the presence of the three pronounced apical lobes on the columella (Riina et al. 2009: 366, as section Cascarilla; see also van Ee et al. 2011: 800).

4. *Croton brevipetiolatus* Duijn, sp. nov. — Fig. 1

Croton brevipetiolatus: petiole relatively short, thick (0.8–3.5 cm by 1–2 mm); abaxial leaf surface with a semi-pubescent indument; inflorescenes short and thin (1.6–5 cm by mostly ≤ 1 mm). It used to be confused with *C. laevifolius*, but can easily be recognized by the semi-pubescent indument at the abaxial side of the leaf, instead of being (sub)glabrous. The relatively short and thick petioles and short and thin inflorescences separate this species from *C. tetraglandulosus*, which has long and relatively thin petioles (2.1–4.1 cm by, c. 1 mm or less) and long inflorescences (14.9–16.2 cm by 1–2 mm). — Type: *S.H. Koorders 39520* (holo L [L.2203863]!), Indonesia, Java, Prov. Preanger. Paratypes: *J. van Borssum Waalkes 595* (L [L.2203792]!), Indonesia, Pulau Panaitan, near westerly Tg. Kadam; F.W. Junghuhn '97' (L [L.2203866]!), Indonesia, Java; *S.H. Koorders 25559* (L [L.2203869]!), Indonesia, Java, Prov. Preanger; *S.H. Koorders 26287* (L [L.2203869]!), Indonesia, Java, Prov. Preanger; *S.H. Koorders 32845* (L [L.2203868]!), Indonesia, Java, Prov. Preanger; *E. Kuswata Kartawinata 1443* (L [L.2203667]!), Indonesia, Borneo, Tanah mearh, Lempake; *McDonald & Afriastini 3388* (L [L.2212604]!), Indonesia, West Java, Ujung Kulon Reserve, summit of Gunung Cibinua; Ramlanto 32 (L [L.2203668]!), Indonesia, Borneo, Wanariset, Balikpapan.

Shrubs or small trees, 2–4 m tall, branching midway up, candellaber growth; young branchlets pubescent, early glabrescent, older branches glabrous. *Bark* smooth with a silvery shine, older branches yellowish, young branchlets reddish brown. *Indumentum* consisting of flat stellate trichomes with a short central porrect radius, 0.2–0.5 mm diameter, radii (9–)13–25, hyaline to yellowish brown with a brown centre on leaves and inflorescences, reddish brown on branches and petioles. *Stipules* linear to linear triangular, 1–5.3 by 0.2–0.4 mm, (late) caducous to persistent, pubescent to scattered trichomes. *Leaves* alternate or pseudo-verticillate; petiole 0.8–3.5 cm by 1–2 mm, grooved above, with scattered trichomes, young petioles pubescent, early glabrescent, upper pulvinus 2–6 mm long, lower pulvinus 3–6 mm long; blade obovate to elliptic, (3–)11–17.4(–21.9) by 3.6–7.3 cm, 2–3.7 times longer than wide, subcoriaceous, base attenuate to rounded, basal extrafloral nectaries laterally at the very base of the main vein or very apex of the petiole, sometimes seemingly on the lamina, (0.2–)0.4–1 mm diameter, subsessile or with a short, 0.1–0.3(–0.4) mm long stalk, margin entire to serrulate, with colleters, in young leaves accompanied by one or two simple trichomes, apex attenuate to acuminate, adaxially glabrous, abaxially with (densely) scattered trichomes to semi-pubescent, pubescent when young but early glabrescent, venation penninerved, visible up to third order, adaxially main vein slightly sunken, other veins raised, secondary veins 5–12 pairs up to apex. *Inflorescences* terminal or axillary, 1.6–5 cm long and mostly ≤ 1 mm thick, sulcate, up to 2 per node, subglabrous; flowers white; basally up to 4 pistillate flowers; apically up to 3 staminate flowers per node; bracts triangular, 0.6–1.2 by 0.3–0.4 mm, with scattered trichomes to glabrous; bracteoles linear-triangular, with scattered trichomes to glabrous. *Staminate flowers* c. 4.2 mm diameter; pedicel 1.4–3.8 mm long, glabrous; sepals 5, ovate to oblong, outside subglabrous to scattered trichomes, inside glabrous, apically with a tuft of hyaline simple trichomes; petals 5, obovoid, c. 1.8 by 1.2 mm, glabrous but with some long simple trichomes at the base, margin slightly lighter in colour, apex ciliate; receptacle lanate; disc glands 5; stamens 11, filaments c. 1.3 mm long, anthers c. 1 by 0.8 mm. *Pistillate flowers* 3–4.5 mm diameter; pedicel 1.3–2 mm long in flower, to 4 mm long in fruit, densely pubescent to scattered trichomes; sepals ovate to oblong, 1.7–2.5 by 1.1–1.3 mm, as long as to much longer than the ovary, outside with scattered trichomes, inside glabrous, with a tuft of simple hyaline trichomes at the apex; petals absent or reduced to linear appendages; receptacle not visible; ovary oblate, 1.2–1.6 by 1.7–2.2 mm, densely pubescent with hyaline or reddish brown trichomes, style absent, stigma 2.9–3.9 mm long, split into two to 0.6–1 mm from base. *Fruits* globular, c. 6 mm high by 6 mm diameter, copper-furfuraceous at inception, yellow-green at maturity, dehiscing loculicidally via groove, covered with scattered trichomes, either brown or hyaline with brownish centre; columella 4–6 mm long. *Seeds* globular, c. 4.4 by 4 by 4.8 mm, glabrous, ecarunculate.

Distribution — *Malesia*: Java (Gunung Burangrang, Pulau Panaitan, Ujung Kulon reserve, Preanger), Borneo (Tanah merah, Wanariset).

Habitat & Ecology — Common understory shrub in primary forest; sandy clay soil.

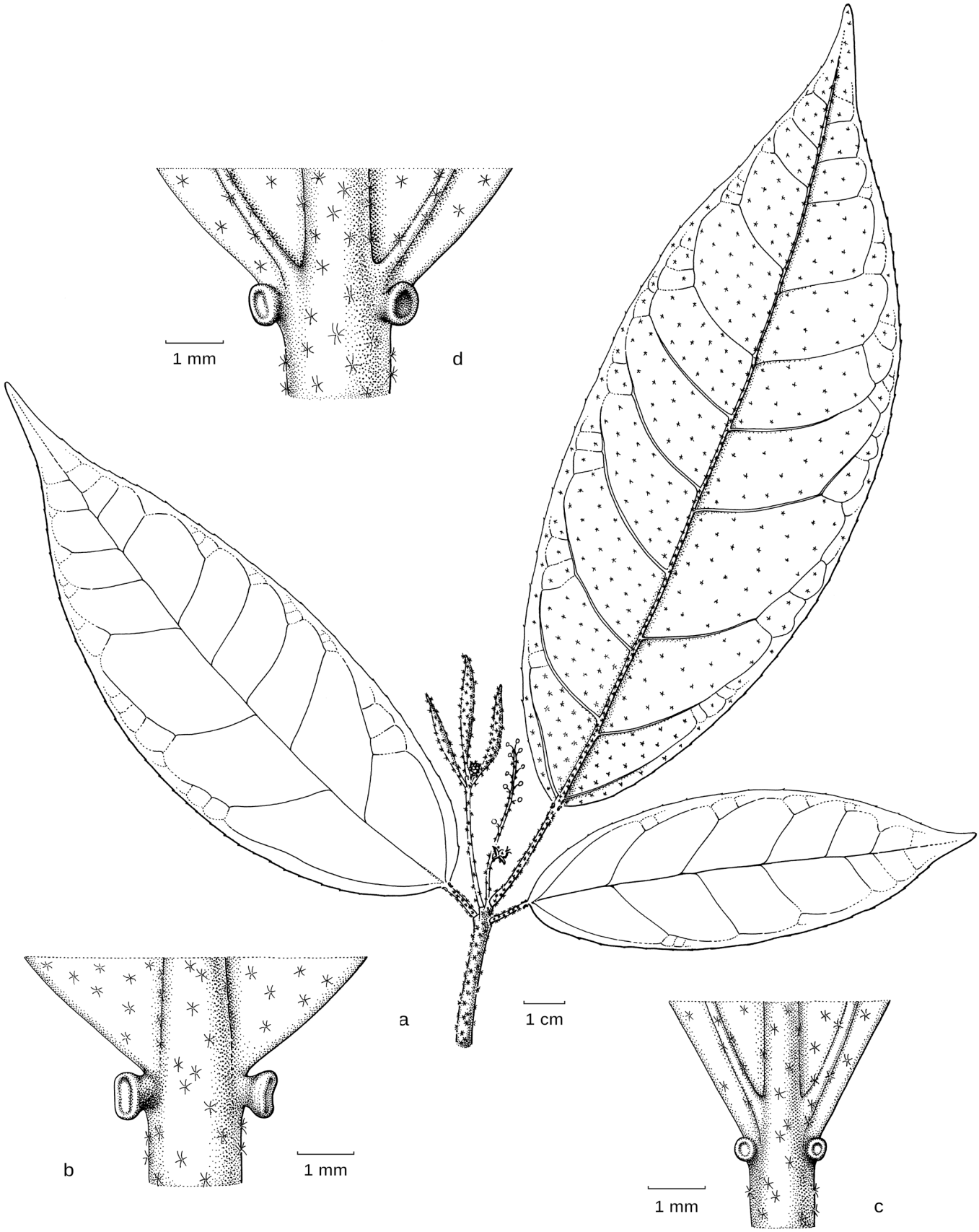

Fig. 1 *Croton brevipetiolatus* Duijn – **a.** Habit, **b.** Abaxial stellate hairs and extrafloral nectaries; **c.** Idem; **d.** Idem (a: *Koorders 39520*, L.2203863; b: *Koorders 26559*, L.2203867; c. *van Borssum Waalkes 595*, L.2203792). Illustration by Esmée Winkel.

Notes — 1. Most buds of the staminate flowers are eaten from the inside.

2. The seeds measured were indented at the bottom and likely still immature, the real sizes of the seeds might be larger.

3. The variation in leaf characters, stipules, basal extrafloral nectaries and trichome colour is very large. The stipules vary in length per specimen, 2–2.5 mm long in *Koorders 2628*, 3–5 mm in *Koorders 2628*. For three individuals (*Koorders 26287, McDonald & Afriastini 3388, van Borssum Waalkes 595*) the diameter of the basal extrafloral nectaries is 0.5 mm or less, while for the others it is 0.6 mm or bigger. The location of the basal extrafloral nectaries varies between 'on the petiole', 'on the main vein' or 'on the lamina', even within a single specimen (*McDonald & Afriastini 3388*). The leaf blades can be obovate with an acute to attenuate base (*Junghuhn 97, McDonald & Afriastini 3388, van Borssum Waalkes 595*), elliptic with a round base (*Koorders 32845, 39520*), or ovate to elliptic with a round base (*Koorders 26287, 25559*). The leaves of *McDonald & Afriastini 3388* and *van Borssum Waalkes 595* dried to a pale yellow and had hyaline trichomes with a brown centre abaxial, where almost all other specimens dry to a brown-green shade and have yellowish brown to brown trichomes. In the pistillate flowers, the ovary can be covered by reddish brown stellate trichomes (*Koorders 32845*) or yellowish white trichomes (*Koorders 39520*). Two specimens featured a columella, c. 4 mm long in *McDonald & Afranisti 3388* and c. 6 mm long in *Koorders 39520*.

5. *Croton cascarilloides* Raeusch.

Croton cascarilloides Raeusch. (1797) 280; Merr. (1934) 60; (1935) 234; Croizat (1942a) 46; Airy Shaw (1963) 344; (1972a '1971') 244; Whitmore (1973) 84; Airy Shaw (1975) 91; (1981a) 284; (1982a) 14; (1983) 18; Esser (2005) 197; P.T.Li & Esser (2008) 260; Beyer et al. (2023) 10. — *Croton punctatus* Lour. (1790) 581 ('*punctatum*'), nom. illeg., non Jacq. (1787); Müll.Arg. (1866) 565; Gagnep. (1925) 290. — Lectotype (first step designation, herbarium, by Merrill 1935; second step, sheet: Beyer et al. 2023): *Loureiro s.n.* (lecto BM [BM000926610]!; isolecto BM [BM000926609]!), Cochinchine (= southern Vietnam).

Croton polystachyus Hook. & Arn. (1838) 270, nom. illeg., non Spreng. (1826: 868). — Type: *Beechey s.n.* (holo K [K000959133]*), Loo Choo Islands (Ryukyu Islands). Hooker & Arnott refer to Willdenow (meaning Sprengel) with a question mark, but as *C. polystachus* Spreng. (not *polystachyus*!) is from Brazil, the name is here considered as the introduction of a new name/species.

Croton cumingii Müll.Arg. (1865) 101; (1866) 566; Craib (1911) 463; (1912) 190; Merr. (1923) 426; Ridl. (1924) 261; Gagnep. (1925) 264; M.R.Hend. (1939) 30, 70. — *Oxydectes cumingii* (Müll.Arg.) Kuntze (1891) 611. — Lectotype (designated by Beyer et al. 2023: 10): *Cuming 1384* (lecto G [G00434383]!; isolecto A [00099662] packet!, BM [BM000926594]!, E!, G-DC [G00311739]!, GOET [GOET003339, GOET003340, GOET003341]!, K [K0009591761, K000959177]!, KIEL!, L [L0016148, L0062226, L0062227] L0062228]!, NY n.v., W 3 sheets!), Philippines, Luzon, Prov. Albay.

Croton cumingii Müll.Arg. var. *angustifolius* Gagnep. (1925) 264. — Lectotype (designated by Beyer et al. 2023: 10): *Poilane 1725* (lecto A [A00105618]!; isolecto A [A[00105617 p.p.]!, BM!, E [E00327461]!, K!, NY [00452493]!), Vietnam, Prov. Thanh-hoa, à La-han.

Croton pierrei Gagnep. (1922 '1921') 558; (1925) 265. — Lectotype (designated by Beyer et al. 2023: 10): *Pierre 6233* (lecto P [P00109484]!; isolecto A [00072716]!, BM [000551499]*, as Pierre s.n., E [E00327460]!, G [G00358191]*, as *Pierre s.n.*, GH [00099664]!, NY [00262986]!, as *Pierre s.n*, P [P00109485]!), Cochinchine, Prov. de Ty-ninh, Mont Deonba (perhaps also in K (K000959153)*, as *Pierre s.n*., but locality missing).

Croton cascarilloides Raeusch. var. *pilosus* Y.T.Chang (1983) 171. — Type: *Z.X. Zhang & S.L. Wang 4051* (holo KUN n.v.), China, Guangxi..

Shrubs, to 2 m tall; young branchlets pubescent, hardly glabrescent. *Bark* dark grey; outer bark slightly fissured. *Indumentum* consisting of flat, sublepidote trichomes, 0.4–0.6 mm diameter, adaxially on leaves, often on the smaller side, radii 40–54, or adaxially 28–39; radii hyaline with a yellowish-brown to reddish brown centre, sometimes several reddish-brown radii. *Stipules* linear-triangular, 1.4–2 by 0.5–0.8 mm, densely pubescent, caducous. *Leaves* alternate to pseudo-verticillate apically; petiole 1.4–3.4 cm long, grooved above, slightly sulcate, densely pubescent; blade ovate to obovate, 6.9–14.8 by 3–6.9 cm, 1.9–3 times longer than wide, base cuneate to obtuse, the very base subcordate, extrafloral nectaries laterally on the very base of the midrib, flat, rarely seemingly on the lamina near the very base of the midrib and slightly raised, 0.5–0.8 mm diameter, margin entire, apex acute to attenuate, adaxially scattered trichomes, abaxially completely covered with trichomes, lamina not visible, several trichomes with reddish brown radii distinctly visible as dots, overall a silvery yellowish appearance, venation penninerved, visible up to third order adaxially, slightly raised and midrib slightly sunken, visible up to second order abaxially, midrib highly raised, second order slightly raised, secondary veins 8–10 pairs up to apex. *Inflorescences* terminal, 0.4–1 cm long, up to 3 per node, densely brownish pubescent; flowers very few, densely pubescent; bracts triangular, 1.5–3 by 1–1.5 mm, densely pubescent on both sides, caducous. *Staminate flowers* c. 4 mm diameter; pedicel 0.5–1.5 mm long, densely pubescent; sepals triangular-ovate, c. 2 by 1.5 mm, completely pubescent silvery brown to dark brown; petals oblong, c. 2 by 1 mm, glabrous outside, lanate on margin and apex; stamens 11–16, free, filaments c. 1.5 mm long, anthers c. 1 by 0.5 mm. *Pistillate flowers* c. 5 mm diameter; pedicel 1.5–3 mm long, densely pubescent; sepals elliptic, 2–3 by 1–2 mm, densely pubescent outside, larger than ovary; petals absent; ovary globose, c. 1.5 by 2 mm, densely pubescent, styles less than 0.5 mm long, stigmas 3–3.5 mm long, divided twice to 1–2 mm from apex. *Fruits* obovoid, deeply 3-lobed, almost as 3 individual capsules, 5–6 by 6–6.5 mm, sulcate, apex pressed inwards, densely pubescent; pericarp inside with scattered trichomes; columella 4–5 mm long. *Seeds* ellipsoid, 4.5–5.5 by c. 4 mm, slightly flattened, very rough, glabrous except for a few stellate trichomes near the attachment, with a small caruncle.

Distribution — Myanmar, Laos, China (South-Central, Southeast, Hainan), Vietnam, Taiwan, Japan (Ryukyu Islands), Thailand, *Malesia*: Peninsular Malaysia, Sumatra, Borneo, Java (Kangean Island), Philippines, Sulawesi.

Habitat & Ecology — In primary dry evergreen or mixed evergreen/deciduous forest, bamboo-hardwood forest, secondary forest, on rocky slopes, hills, also along streambanks, usually shaded. Grows on limestone, sandstone, or clayey substrates. Altitude: 0–600 m. Flowering and fruiting the whole year through (Beyer et al. 2023).

Notes — The material did not have mature inflorescences and the specimens were collected from very young plants. The descriptions of staminate and pistillate flowers, fruits, and seeds are adapted from Beyer et al. (2023).

6. *Croton caudatus* Geiseler

Croton caudatus Geiseler (1807) 73; Müll.Arg. (1866) 599; Hook.f. (1887) 388; S.Moore (1925) 100; J.J.Sm. (1910) 352; Merr. (1921a) 336; (1923) 425; Gagnep. (1925) 286; Burkill (1935) 689 (‘*caudatum*’); Backer & Bakh.f. (1963) 477; Airy Shaw (1972a ‘1971’) 245; Whitmore (1973) 85; Airy Shaw (1975) 92; (1981a) 284; Chakrab. & N.P.Balakr. (1997 ‘1992’) 37, map 2; Philcox (1997) 94; P.I.Forst. (2003) 372, fig. 8; Esser (2005) 198; P.T.Li & Esser (2008) 262; Chakrab. (2019) 3629; Beyer et al. (2023) 11, fig. 2b, 4. — *Croton caudatus* Geiseler var. *genuinus* Müll.Arg. (1866) 599, nom. inval. — *Croton caudatus* Geiseler var. *caudatus*: Kurz (1877) 375. — *Oxydectes caudata* (Geiseler) Kuntze (1891) 611. — Lectotype (designated by Chakrabarty & Balakrishnan 1997 ‘1992’): *Rottler s.n.* (lecto C [C10011161]!), India orientalis.

Croton racemosus Burm.f. (1768) 206 (‘306’), suppressed name. — Lectotype (designated by Esser 2001: 1211): *Anonymous (Herb. Houttuyn) s.n.* (lecto G!), Sri Lanka.

Croton aromaticus Gaertn. (1790) 119 (‘*aromaticum*’), nom. illeg., non L. (1753). — Type: Not indicated.

Croton denticulatus Blume (1826) 603 (’*denticulatum*’), nom. illeg., non Geiseler (1807); Miq. (1861) 180, 452. — Lectotype (designated by Beyer et al. 2023: 11): *Unknown s.n.* (lecto L [L.2210974]!), (Indonesia, Java,) Nussa Kambang.

Croton drupaceus Roxb., [(1814) 69, nom. nud. (‘*drupaceum*’)] (1832) 683 (‘drupaceum’). — Lectotype (designated by Chakrabarty 2019: 3629): *Roxburgh s.n.* (BM [BM000951447]*).

Croton malvifolius Griff. (1848) 200. — Lectotype (designated by Beyer et al. 2023: 11): *Griffith 2518* (lecto BM [BM000951453]*), Boutan (= Bhutan).

Croton sumatranus Miq. (1859) 381. — *Oxydectes sumatrana* (Miq.) Kuntze (1891) 613. — Lectotype (designated by Beyer et al. 2023: 11): *Zollinger s.n.* (lecto U [U007934]!), Indonesia, Sumatra, Lampong (fragment). Another fragment, Zollinger 642 (A [00047516]!) was also indicated as duplicate, but Zollinger 642 is the type collection of C. *caudatus* var. *oblongifolius* (see next).

Croton caudatus Geiseler var. *denticulatus* Müll.Arg. (1866) 599. — Lectotype (designated by Beyer et al. 2023: 11): *Hooker & Thomson s.n.*, s.d. (holo G-DC [G00311925]*), Assam.

Croton caudatus Geiseler var. *oblongifolius* Müll.Arg. (1866) 600. — Lectotype (designated by Beyer et al. 2023: 11): *Zollinger 642* (lecto G-DC [G00311913]*; isolecto A [A00047516*, A00106972!], L [L0234052]!, G-DC [G00311912, G00311921, G00434381, G00434382]!), Indonesia, Java.

Croton caudatus Geiseler var. *hispidus* Hook.f. (1887) 389 (‘*hispida*’). — Type: not indicated.

Croton caudatus Geiseler var. *ruminatus* Hook.f. (1887) 389 (‘ruminata’). — Lectotype (designated by Beyer et al. 2023: 11): *Griffith s.n.*, 1845 (lecto K [K000246831]*), India, Khasia Hills.

Croton caudatus Geiseler var. *globosus* Hook.f. (1887) 389 (‘*globosa*’). — Type: not indicated.

Croton caudatus Geiseler var. *tomentosus* Hook.f. (1887) 389 (‘*tomentosa*’). — Lectotype (designated by Beyer et al. 2023: 11): *Griffith s.n.* (lecto K [K000246826]*), India, Assam.

Croton caudatus Geiseler var. *malaccanus* Hook.f. (1887) 389 (‘*malaccana*’); Ridl. (1924) 259. — Lectotype (designated by Beyer et al. 2023: 11): *Griffth KD 4775* (lecto CAL [CAL0000023572]*; isolecto: K [K000246829 without number, K000246830 without number, K000959168 without number, K000959169 without number, K000959170]*, M [M-0241964]!, G-DC [G00311922]!, GH [GH00099677]! without number, [GH00100129]! without number, W!, ZT!), Myanmar. Other syntype: *Maingay KD 1376* (CAL [CAL0000023573]*, GH [00047511]!, L [L0233998]!, P!), Malaysia.

Croton caudatus Geiseler var. *harmandii* Gagnep. (1925) 286. — Lectotype (designated by Beyer et al. 2023: 11): *Couderc s.n.* (P [P00610256]*), Cambodia, Vat-Preah.

Croton caudatus Geiseler var. *obovoideus* N.P.Balakr. & Chakrab. (1985 ‘1983’) 190, fig. 1. — Type: *Sebastine 25343A* (holo MH, n.v.; isotypes MH [MH00001136, MH00001133, MH00001135, MH00001134]*), India, Kerala, Kottayam Dist., Velara.

Croton laccifer auct. non L.: Airy Shaw (1972a ‘1971’) 248.

Lianas or straggling shrubs, up to 4 m high; young branchlets densely pubescent, slowly glabrescent. *Bark* silvery grey to yellowish brown to purplish brown, smooth to lenticellate; young twigs yellowish brown or light green, smooth to slightly ribbed; latex reddish. *Indumentum* consisting of stellate trichomes, either flat with a long central porrect radius or with radii pointing in all directions, (0.2–)0.3–0.5 mm diameter and (3–)6–9 radii on leaves, 0.2–0.3 mm diameter and (7–)9–15 radii on branches, petioles and inflorescences light or yellowish brown. *Stipules* linear, 4.6–8.3(–11) by 0.6–1.2 mm, slightly to densely pubescent, caducous, side lobe absent or at ⅓ up from the base, caducous. *Leaves* alternate; petiole grooved above, 1.8–5.7 cm long, densely pubescent, lower pulvinus 4–5 mm long, upper pulvinus indistinct or (3–)8–10 mm long; blade ovate to elliptic, 5.8–14.7 by 2.3–7 cm, (1.2–)1.4–2.6(–3.3) times longer than wide, base obtuse to rounded with the very base subcordate, basal extrafloral nectaries stalked, laterally on very base of main vein or petiole, 1–2(–3) pairs, 0.5–0.7(–1) mm diameter, stalk 0.5–1.2 mm long, margin biserrate to lowly serrate, marginal extrafloral nectaries in between teeth with a stalk and a disc, 0.3–0.4 mm high, disc 0.2–0.3 mm diameter, colleters present at tip of serrae, apex acuminate, adaxially with scattered trichomes, abaxially slightly to densely pubescent, but densely pubescent on veins, venation slightly triplinerved, adaxially up to third order slightly raised, abaxially distinctly raised, secondary veins c. 4 pairs up to apex. *Inflorescenses* ribbed, 4.2–22 cm long, 1–3 per node; basally up to 10 pistillate flowers, single per node, seldom mixed with staminate flowers; apically staminate flowers up to 3(–4) per node; bracts elongate-triangular, c. 3.5 by 0.3 mm, pubescent outside, with scattered trichomes inside. *Staminate flowers* c. 7 mm diameter; pedicel 3.5–6.5 mm long, densely pubescent; sepals ovate-triangular, c. 2.5 by 2.7 mm, midrib distinct, outside densely pubescent, inside glabrous, margin with hyaline simple trichomes; petals obovate, c. 3 by 1.2 mm, outside glabrous, inside glabrous except basally simple hyaline trichomes, margin ciliate with simple trichomes, disc lobes not visible; stamens c. 33, glabrous, filaments c. 3.5 mm long, anthers c. 0.8 by 0.4 mm. *Pistillate flowers* c. 7 mm diameter; pedicel c. 2.5 mm long, densely hairy; sepals ovate-triangular, c. 3.6 by 2.5 mm, midrib distinct, outside slightly covered with stellate trichomes, inside with simple trichomes, apically a tuft of hyaline simple trichomes; petals reduced, linear, up to 0.6 mm long; disc not visible; ovary globose, densely pubescent with large dark yellowish brown trichomes, style absent, stigmas

3, 3.2–4.7 mm long, completely divided, flat, glabrous. *Fruits* globular, 2.1–2.4 cm high, 2.1–2.3 cm diameter, densely pubescent with stellate and simple trichomes, a single raised longitudinal line over each locule; columella c. 13 mm long. *Seeds* ellipsoid flattened, 11–13 by 8.3–8.5 by 5–6 mm, glabrous, sometimes thinly covered with stellate trichomes; caruncle indistinct.

Distribution — Bangladesh, Assam, Nepal, Bhutan, India, Sri Lanka, Bangladesh, Myanmar, Laos, China (South-Central), Vietnam, Thailand, Cambodia, *Malesia*: Malay Peninsula, Sumatra, Java, Christmas Island, Borneo, Philippines, Sulawesi; Australia (Queensland).

Habitat & Ecology — In peat swamp forest, deciduous and evergreen forest, secondary forests and thickets, along rivers and streams. Altitude: 0–700 m. Flowering and fruiting the whole year through (Beyer et al. 2023).

Vernacular names — Java: Ki-hukupu, Merangan (Smith 1910)

7. *Croton glabrescens* Miq.

Croton glabrescens Miq. (1859) 382; J.J.Sm. (1910) 347; Backer & Bakh.f. (1963) 476; Airy Shaw (1982a) 14. — Lectotype (designated here): *Zollinger 2702* (lecto A [A00047513]!; isolecto A [A00100140]!, G [G00434378]!, U [as Anonymous s.n., U 0007935]!), Java, Nusa Baron.

Trees; young branchlets thinly pubescent. *Bark* dark brown with a silvery shine, ridged, slightly fissured. *Indumentum* consisting of stellate trichomes, 0.15–0.32 mm diameter, 20–30 radii in multiple directions, light or yellowish brown to off-white, centre often a darker yellowish brown; flat trichomes with a central porrect radius and 8–20 radii, mostly found on leaf surfaces. *Stipules* linear, 0.7–2.3 by c. 0.3 mm, with scattered trichomes to pubescent, trichomes with free radii, caducous. *Leaves* alternate, apically often pseudo-verticillate, light green after drying; petiole 1.8–6.5 cm long, grooved above, with scattered trichomes, basal pulvinus c. 3 mm long; blade oblong, sometimes ovate, 8.4–16 by 3.2–6.4 cm, 1.7–2.8 times longer than wide, base rounded, rarely obtuse, with the very base cuneate, basal extrafloral nectaries sessile to stalked, lateral on the very apex of the petiole or on the very base of the midrib, 0.6–0.9 mm diameter when sessile or slightly stalked, then 0.3–0.5 mm diameter, stalk 0.1–0.3 mm long, margin serrulate, slightly wavy, with colleters sometimes accompanied by a single hyaline simple trichome, apex acute to attenuate, adaxially glabrous, when young with scattered trichomes, abaxially glabrous or with a few trichomes, when young with scattered trichomes, venation penninerved, sometimes slightly triplinerved, adaxially visible up to second order, slightly sunken, abaxially visible up to fourth order, slightly raised, secondary veins 7–9 pairs up to apex. *Inflorescences* terminal or axillary, 4.4–5.4 cm long, sulcate, semi-pubescent; basally up to 8 pistillate flowers, single per node, rarely accompanied by a single staminate flower; apically staminate flowers, single per node; bracts linear-triangular, 0.8–1.2 by 0.2–0.5 mm, pubescent; bracteoles linear, semi-pubescent. *Staminate flowers* 3–3.5 mm diameter; pedicel 1.5–2.7 mm long, semi-pubescent; sepals 5, ovate-triangular, c. 1.4 by 0.8 mm, glabrous, apex with simple trichomes; petals 5, ovate-triangular, c. 1.7 by 0.6 mm, glabrous, apex with simple trichomes; disc not visible; stamens c. 11, filaments c. 1.8 mm long, anthers c. 0.5 by 0.4 mm. *Pistillate flowers* 2.5–3.5 mm diameter; pedicel 1–1.7 mm long, pubescent; sepals 5, linear-triangular, c. 1.6 by 0.8 mm, glabrous, apically margin with simple trichomes; petals absent or reduced to orbicular or linear structures, c. 1.8 by 0.6 mm, glabrous, margin ciliate with simple trichomes; disc not visible; ovary oblate, c. 2 by 1.5 mm, densely pubescent, 3-lobed, style absent, stigmas c. 2.3 mm long, once divided to c. 0.6 mm from base, glabrous. *Fruits* 4.5–6 mm high, with scattered trichomes; columella c. 4.5 mm long. *Seeds* ellipsoid flattened, c. 4 by 0.9 by 0.9 mm, glabrous, caruncle present.

Distribution — *Malesia*: Malay Peninsula, Java, Lesser Sunda Islands (Bali, Flores).

Habitat & Ecology — Forest remnants. Altitude: 5–500 m. Flowering: August – October. Fruiting: November (Smith 1910).

Vernacular name — Java: Kapsan (Smith 1910).

8. *Croton hasskarlianus* Müll.Arg. — Fig. 2

Croton hasskarlianus Müll.Arg. (1866) 573. — *Oxydectes hasskarliana* (Müll.Arg.) Kuntze (1891) 611. — Lectotype (designated here by Esser): *Zollinger 1779* (lecto L [L.2203793]!; isolecto G-DC [G00311766]!, W [W 1889-0024654, W 1889-0024655]!), Indonesia, Island Madura.

Woody plants; young branchlets with scattered trichomes. *Bark* longitudinally fissured, smooth, silvery grey. *Indumentum* consisting of flat, stellate to sublepidote trichomes with occasionally a central porrect radius, (0.25–)0.28–0.37(–0.45) mm diameter, whitish with a caramel-coloured centre, radii 14–29; radii fused on the branches, and less so on the leaves. *Stipules* linear, 1.4–1.9 by 0.2–0.3 mm, pubescent. *Leaves* alternate or pseudo-verticillate; petiole 0.9–2.6 cm long, basal pulvinus c. 2 mm long, with scattered trichomes but pubescent at the base; blade elliptic, 10–14.6 by 2.2–3.2 cm, 3.7–4.5 times longer than wide, base attenuate, basal extrafloral nectaries sessile, flat, laterally on the very apex of the petiole, sometimes seemingly on the very base of the midrib, 0.6–0.9 mm diameter, margin serrulate, with colleters, apex acute or attenuate, adaxially glabrous, abaxially with very few trichomes, venation penninerved, adaxially up to second order slightly raised, abaxially up to third order slightly raised, midrib obviously raised, secondary veins c. 9 up to apex. *Inflorescences* terminal, sulcate, c. 7.6 cm long, semi-pubescent; basally up to 3 pistillate flowers. *Staminate flowers* not seen; bracts triangular, c. 0.5 by 0.3 mm, with one or two trichomes, apex with simple hyaline trichomes; bracteoles triangular, with one or two trichomes, apex with simple hyaline trichomes. *Pistillate flowers* too few to dissect; c. 3.3 mm diameter; bracts and bracteoles caducous; pedicel c. 1.3 mm long, with scattered trichomes; sepals ovately triangular, c. 1.5 by 0.9 mm, outside with scattered trichomes, inside glabrous, apex with tuft of hyaline simple trichomes; ovary c. 1.5 by 2 mm, pubescent with reddish brown trichomes, style c. 0.2 mm long, stigma size unknown, split into two to c. 0.6 mm from base. *Fruits* and *seeds* not seen.

Distribution — *Malesia*: Java (Madura Island).

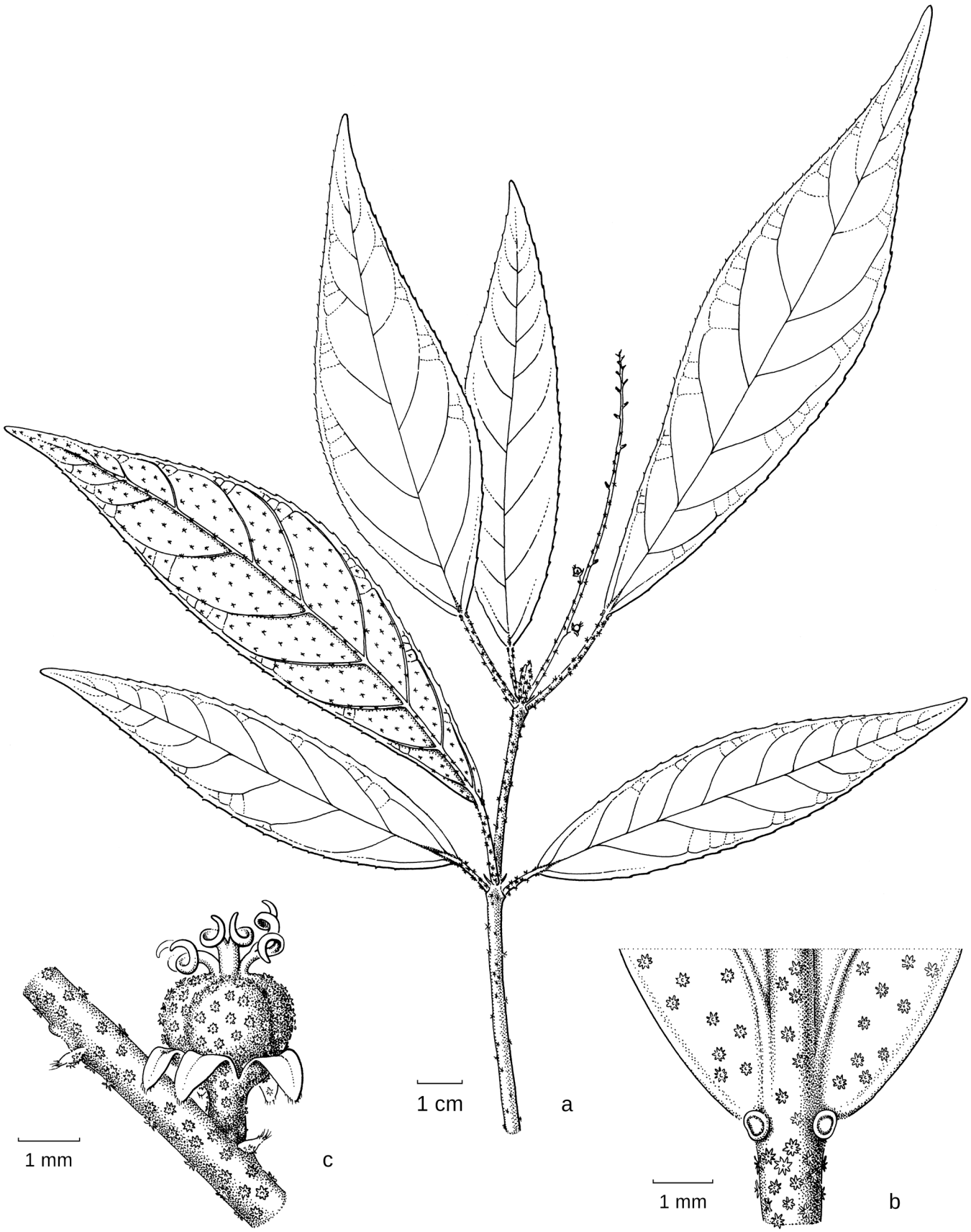

Fig. 2 *Croton hasskarlianus* Müll.Arg. – **a.** Habit; **b.** Abaxial lepidote trichomes and extrafloral nectaries; **c.** Pistillate flower (*Zollinger 1779*, L.2203793). Illustration by Esmée Winkel.

Notes — This species is only represented by a single flowering collection. Staminate flowers, fruits, and seeds therefore remain undescribed. Also, as the label lacks any information the habit was uncertain.

9. *Croton hirtus* L'Hér.

Croton hirtus L'Hér. (1784) 17, t. 9; Sinclair (1956) 1, fig. 1; Backer & Bakh.f. (1963) 476; G.L.Webster & D.G.Burch (1968) 262; Whitmore (1973) 84; Philcox (1997) 88; Esser (2005) 206; Beyer et al. (2023) 15. — *Podostachys hirta* (L'Hér.) Klotzsch (1841) 194 (see note). — *Brachystachys hirta* (L'Hér.) Klotzsch (1843a) 47. — *Croton glandulosus* L. var. *hirtus* (L'Hér.) Müll.Arg. (1866) 684; Airy Shaw (1981a) 284; Chakrab. & N.P.Balakr. (1997 '1992') 48. — *Oxydectes glandulosa* (L.) Kuntze var. *hirta* (L'Hér.) Kuntze (1891) 614. — *Croton glandulosus* L. subsp. *hirtus* (L'Hér.) Croizat (1948) 401. — Type: *Richard s.n.* (holo P [P00623551]*; iso P [P00623550]*), French Guiana, cultivated in Paris. [For other synonyms see Plants of the World Online (http://www.plantsoftheworldonline.org/).]

Herbs to sub-shrubs, 30–70(–100) cm tall, whole plant disappearing quickly after fruiting; young parts pubescent, glabrescent; latex red. *Bark* smooth to grooved, off-white with a silvery shine. *Indumentum* whitish to yellowish porrect-stellate trichomes; on stems 0.5–1.4 (excluding the porrect radius) mm diameter, flat, 9–13(–17) radii of unequal length, central porrect radius 1.3–2.2 mm long; on inflorescences and abaxial side of leaves 0.3–0.6 mm diameter, radii 9–13(–17), pointing in all directions; on adaxial side of leaves c. 0.2 mm diameter, radii 1–5, central porrect radius (0.17–)0.25–1.1 mm long, some with enlarged whitish base, mostly near margin, sometimes also present abaxially. *Stipules* linear, 3.2–5.1 by 0.2–0.25 mm, late caducous, with scattered trichomes. *Leaves* alternate; petiole flattened, 0.4–3.9 cm long, hispid, bigger trichomes yellowish, smaller ones whitish; blade ovate, 3.2–4.2 by 2.3–3.6 cm, (1–)1.2–1.8 times longer than wide, leaves near the base of the plant bigger with petioles longer than leaves near the top of the plant, base rounded to cuneate, sometimes oblique, basal extrafloral nectaries stalked laterally on petiole, disc 0.2–0.33 mm diameter, stalk 0.5–1.1 mm long, not obviously present on every leaf, sometimes of unequal length, margin serrate to biserrate, apex acute, adaxially and abaxially hispid, trichomes bigger on the veins, venation triplinerved, visible up to third order, raised, secondary veins 4–7 pairs up to apex. *Inflorescences* terminal or axillary, up to 3 per node, 1.5–2.4 cm long, slightly sulcate, pubescent; basally (3–)6–9 pistillate flowers, single per node; apically staminate flowers; bracts linear, 1.3–2.6 by 0.2–0.4 mm, two stalked glands (colleters) at ½–⅔, a few scattered trichomes, 1–2 long simple trichomes at the apex; bracteoles linear, 1.2–4.2 mm long, split into two glands with occasionally a middle lobe, glabrous. *Staminate flowers* c. 2 mm diameter; pedicel 0.8–0.9 mm long, pubescent; sepals 5, ovoid to triangular, c. 1.1 by 0.7 mm, dark brown, outside pubescent, inside glabrous, apically a tuft of small simple trichomes; petals 5, obovoid, c. 1.3 by 0.5 mm, apically truncate, glabrous except margin ciliate with simple long trichomes near the base and shorter ones near the apex; receptacle lanate; disc glands 5; stamens c. 11, filaments c. 0.7 mm long, anthers c. 0.4 by 0.3 mm. *Pistillate flowers* c. 2.5 mm diameter; pedicel c. 1.8 mm long, densely pubescent; sepals 5, obovoid to linear, 2–2.6 by c. 0.1 mm, apex attenuate to acuminate, outside pubescent, inside glabrous, lower half dark brown, upper half whitish, margin near apex with a few simple trichomes; petals reduced, triangular, white; ovary globose, pubescent, style absent, stigmas completely divided, c. 2.3 mm long, slightly flattened, adaxially covered by stigmatic papillae of which some are apically bent. *Fruits* capsular, subglobose, slightly 3-lobed, 3.2–3.6 mm high by 3.4–3.8 mm diameter, sparsely covered with trichomes, style and stigma late caducous; columella 2.5–2.9 mm long. *Seeds* ellipsoid-flattened, 2.8–3.2 by 2–2.3 by 1.4–1.5 mm, glabrous, black, longitudinal groove abaxially; caruncle distinct.

Distribution — Originally from central and southern America, introduced to west and central Africa and S, SE Asia, and *Malesia*: Malay Peninsula, Sumatra, Java, Borneo, New Guinea.

Habitat & Ecology — Sandy beaches near high water mark, along roadsides, rivers, and in grasslands; typical for somewhat nutrient poor soils. Sometimes in secondary forests (Pulau Lankawi, *Soepadmo & Suhaimi 256*). Altitude: 1–500 m.

Vernacular Names — Malaysia (Pulau Langkawi): Maman (*Soepadmo & Suhaimi 256*); Java: Kloebloem (*Coert 1258, 1815*).

Note — Klotzsch (1841), when making the combination *Podostachys hirta*, did not give a reference to the basionym (see Art. 41.1; Turland et al. 2025), which would make the name invalid. However, based on Art. 41.4 (Turland et al. 2025) the name can be considered as a valid new combination by Klotzsch based on circumstantial evidence, because it was published before 1 January 1953 and an original specimen in M, annotated by Klotzsch, is present. This information was not known yet by Beyer et al. (2023) and they, therefore, treated the name as an invalid nomen novum.

10. *Croton laevifolius* Blume

Croton laevifolius Blume (1826) 603 ('*laevifolium*'); Müll.Arg. (1866) 619; J.J.Sm. (1910) 341; Merr. (1921a) 337; Corner (1939) 294; Whitmore (1973) 85; Beyer et al. (2023) 16. — Lectotype (designated by Beyer et al. 2023: 16): *Blume 1473* (lecto L [L.2203878]!; isolecto L [L. 2203879]!), Indonesia, Java.

Croton diadenus Miq. (1861) 451 description, 180 vernacular name ('*diadenum*'). — Type: *Teijsmann HB 3499* (holo U [U 0001893]!; likely iso G-DC (without number) [G00312289]!), Indonesia, Bangka, prope Djebus.

Croton korthalsii Müll.Arg (1866) 527. — Type: *Korthals s.n.* (holo L [L.2203684]!), Indonesia, Borneo.

Mallotus minahassae Koord. (1898) 626. — Lectotype (designated by Beyer et al. 2023: 16): *Koorders 196453* (lecto L [L.2203657]!), [Indonesia,] Celebes, Prov. Minahasa, Menado, 1895.

Croton oreoborneicus Croizat (1942b) 496. — Type: *Agama 568* (holo A [A00047515]!), British North Borneo [= Sabah].

Croton oblongus auct. non. Burm.f: Merr. (1921b) 361 ('*oblongum*'); (1929) 156, p.p.; Backer & Bakh.f. (1963) 476, p.p.; Airy Shaw (1975) 94, p.p.; (1981a) 285, p.p.; (1982a) 15, p.p.; Govaerts et al. (2000) 449, p.p.

Treelets (Beyer et al 2023); young twigs with scattered trichomes, soon glabrescent; buds and petioles of young leaves pubescent. *Bark* yellowish to greyish brown, young twig dark reddish brown to yellowish; glabrous, smooth but with several lenticels. *Indumentum* consisting of porrect-stellate

or sublepidote trichomes, 0.1–0.3(–0.4) mm diameter, radii (7–)13–22(–28), free to partially fused; whitish to yellowish cream often with a darker yellowish centre. *Stipules* linear, (3.9–)5–7.2 by c. 0.6 mm, late caducous to persistent, pubescent to semi-pubescent, trichomes sublepidote. *Leaves* alternate to apically pseudo-verticillate, brown when dried; petiole grooved above, 1.5–5.5 cm long, with scattered trichomes to glabrous, lower pulvinus 0.3–0.4 cm long, upper pulvinus 0.2–0.3 cm long; blade elliptic, 7.2–19 by 3.1– 6.4 cm, 1.9–3.6 times longer than wide, base obtuse to rounded, basal extrafloral nectaries sessile to stalked, laterally on the very apex of the petiole, 0.5–0.7 mm diameter, stalk 0.1–0.5 mm long, margin entire to serrulate, if serrulate then with colleters on teeth, apex acute to acuminate, adaxially glabrous, abaxially glabrous or with scattered trichomes when young, venation penniveined, adaxially visible up to second order, abaxially up to third order, raised on both sides, secondary veins 7–10 pairs up to apex. *Inflorescences* terminal and subapically axillary, (1–)2–5 per node, sulcate, (sub)glabrous, (3.3–)6.5–10.8 cm long; basally up to 17 pistillate flowers, often single per node, rarely accompanied by 1–2 staminate flowers, apically 1–2 staminate flowers per node, sometimes staminate flowers on separate glabrous inflorescences; bracts triangular, 0.5–1.4 by 0.3–0.6 mm, glabrous except simple trichomes at the apex; bracteoles linear, glabrous except simple trichomes at the apex. *Staminate flowers* 3–3.5 mm diameter; pedicel 1.3–3.3(–8) mm long, glabrous; sepals 5, ovate, c. 1.6 by 1.3 mm, glabrous except a tuft of simple trichomes at the apex; petals 5, elliptic to obovate, 1.6–2.1 by 0.7–0.9 mm, apex truncate, glabrous outside, long hyaline simple trichomes at the bottom inside, apex margin with simple trichomes; receptacle lanate; disc glands 5; stamens 11, filaments 1.8–3 mm long, anthers 0.7–1.1 by 0.5–0.9 mm. *Pistillate flowers* 3.5–4 mm diameter; pedicel 1.1–2.7 mm long in flower, up to 4 mm long when fruit bearing, (sub)glabrous; sepals 5(–7), ovate-triangular, c. 1.3 by 0.8–1.1 mm, subglabrous, longer than ovary, with a tuft of simple trichomes at the apex; petals 6, reduced to either a linear structure or a white orbital structure; receptacle lanate; disc glands 5(–6); ovary oblate, 0.7–1.6 mm high by 1–2.1 mm diameter, yellowish pubescent, style c. 0.1 mm long, stigmas 0.9–2.2 mm long, split into two to 0.3–0.6 mm from base. *Fruits* oblate to globose, distinctly 3-lobed, 4–5.8 mm high by 0.4–1 cm diameter, with scattered trichomes, stigma not caducous; columella c. 4.5 mm long. *Seeds* globose, c. 5 mm diameter, glabrous, ecarunculate or with a small caruncle.

Distribution — *Malesia*: Malay Peninsula incl. Singapore, Sumatra, W Java, Borneo, Sulawesi, Lesser Sunda Islands (Sumba, Flores).

Habitat & Ecology —Primary or secondary forest. Clayey or sandy soil or granitic sand. Altitude: 500–1000 m. Flowering: August–January, April; fruiting: January–May (Smith 1910, Beyer et al. 2023).

Notes — According to Corner (1939) *C. laevifolius* is phenotypically diverse, and not a synonym of *C. oblongus*. Material identified as *C. oblongus* appeared to represent multiple species, as was the case with the *C. oblongus* specimens from Sumatra (Beyer et al. 2023). *Croton oblongus* is a species difficult to interpret, perhaps the name should be suppressed, just as *Croton racemosus*, another name by Burman (1768).

11. *Croton pseudoverticillatus* Duijn, sp. nov. — Fig. 3a–c

Resembling *C. tomentellus* in overall appearance. *Croton pseudoverticillatus* differs in having a less dense indument, the lamina of the leaves is abaxially visible, just as the bark on the young twigs, giving these plant parts a much less yellowish colour (the colour of the trichomes) than it does in *C. tomentellus*. The extrafloral nectaries at the leaf base at the very base of the main vein for *C. pseudoverticillatus*, whereas those of *C. tomentellus* at the very apex of the petiole. — Type: *E. Schmutz 844* (holo L [L.2212174]!), Indonesia, Lesser Sunda Islands, W. Flores, Nggoer. Patatype: *E. Schmutz 1889* (L [L.2211344]!), Lesser Sunda Islands, W. Flores, Look.

Woody plants; young branchlets pubescent, glabrescent. *Bark* smooth, silvery brown; second year wood glabrescent. *Indumentum* pubescent to scattered, stellate trichomes, 0.1–0.3 mm diameter, 8–16 radii, leaves adaxially and especially abaxially covered by larger trichomes of 0.4–0.6 mm diameter with 7–13(–22) radii in all directions, yellowish brown, sometimes hyaline. *Stipules* linear, 1.3–2.3 by 0.2–0.4 mm, pubescent, caducous. *Leaves* at apices of branches pseudo-verticillate; petiole grooved above, 0.8–1.8 cm long, with scattered trichomes; blade elliptic, 2.3–6.2 by 1.5–2.9 cm, 1.4–2.7 times longer than wide, base rounded or cuneate, basal extrafloral nectaries stalked, 0.4–0.5 mm diameter, stalk c. 0.2 mm long, laterally at the base of the midrib, margin serrulate, colleters at apices of teeth, apex acute, adaxially and abaxially with scattered trichomes, densely pubescent when young, venation penniveined, adaxially visible up to second order, slightly sunken, abaxially visible up to third order, slightly raised, secondary veins 5–8 pairs up to apex. *Inflorescences* terminal, up to 14 cm long, sulcate, with scattered trichomes; in lower half up to 11 pistillate flowers, this part 2.1–4.3 cm long, apically staminate flowers; bracts linear-triangular, 1.1–1.3 by c. 0.3 mm, with scattered trichomes outside; bracteoles linear, up to 0.4 mm long. *Staminate flowers* c. 5.3 mm diameter; pedicel c. 5 mm long, round, apically few stellate trichomes; sepals 5, ovate-triangular, 1.8–2.3 by 1.1–1.2 mm, outside few trichomes; petals 5, obovate, c. 2.3 by 1.2 mm, with simple, lanate trichomes along the top margin and the margins of the basal part on the inside; disc glands 5; receptacle lanate, stamens c. 11, filaments c. 1.7 mm long, basally broader and with long lanate trichomes, anthers c. 0.6 b by 0.5 mm. *Pistillate flowers* 2.8–3.2 mm diameter; pedicel 1.1–2 mm long, with scattered trichomes; sepals 5, triangular, 1.4–1.5 by 0.8–1 mm, outside with scattered trichomes, inside glabrous, apex with simple trichomes; petals 5 vestiges with long simple trichomes at base; disc 5 glands; ovary globose, slightly 3-lobed, 1.3–1.5 mm high by 1.7–2 mm diameter, densely pubescent, style absent, stigmas c. 1.5 mm long, glabrous, divided into two to c. 0.6 mm from base. *Fruits* unknown. *Seeds* unknown.

Distribution — *Malesia*: Lesser Sunda Islands (endemic to west Flores); only known from two specimens.

Habitat & Ecology — Mangrove area. Altitude: 1–10 m.

Notes — The specimens were originally identified as *C. tomentellus*, but they have a much less dense indument on

bark and leaf laminas, the trichomes and leaves also slightly smaller, and the trichomes have less radii. The leaf blades are slenderer, especially the bigger ones, 1.4–2.7 times longer than wide instead of 1.6–2.1 as in *C. tomentellus*. Most importantly, the extrafloral nectaries at the base of the leaf are on the very base of the midrib and 0.4–0.5 mm in diameter, instead of on the very apex of the petiole and 0.6–0.7 mm in diameter.

12. *Croton scalaeus* J.Beyer

Croton scalaeus J.Beyer in J.Beyer et al. (2023) 17, fig. 5. — Type: *Haviland & Hose 1846* (holo L [L.2212508]!; iso L [L.2212509]!), Malaysia, Sarawak, 1st division, Kuching, 22 Feb. 1952.

Woody plants; young twigs with scattered trichomes, sulcate. *Bark* smooth, young twigs reddish brown. *Indumentum* consisting of flat lepidote to sublepidote trichomes,

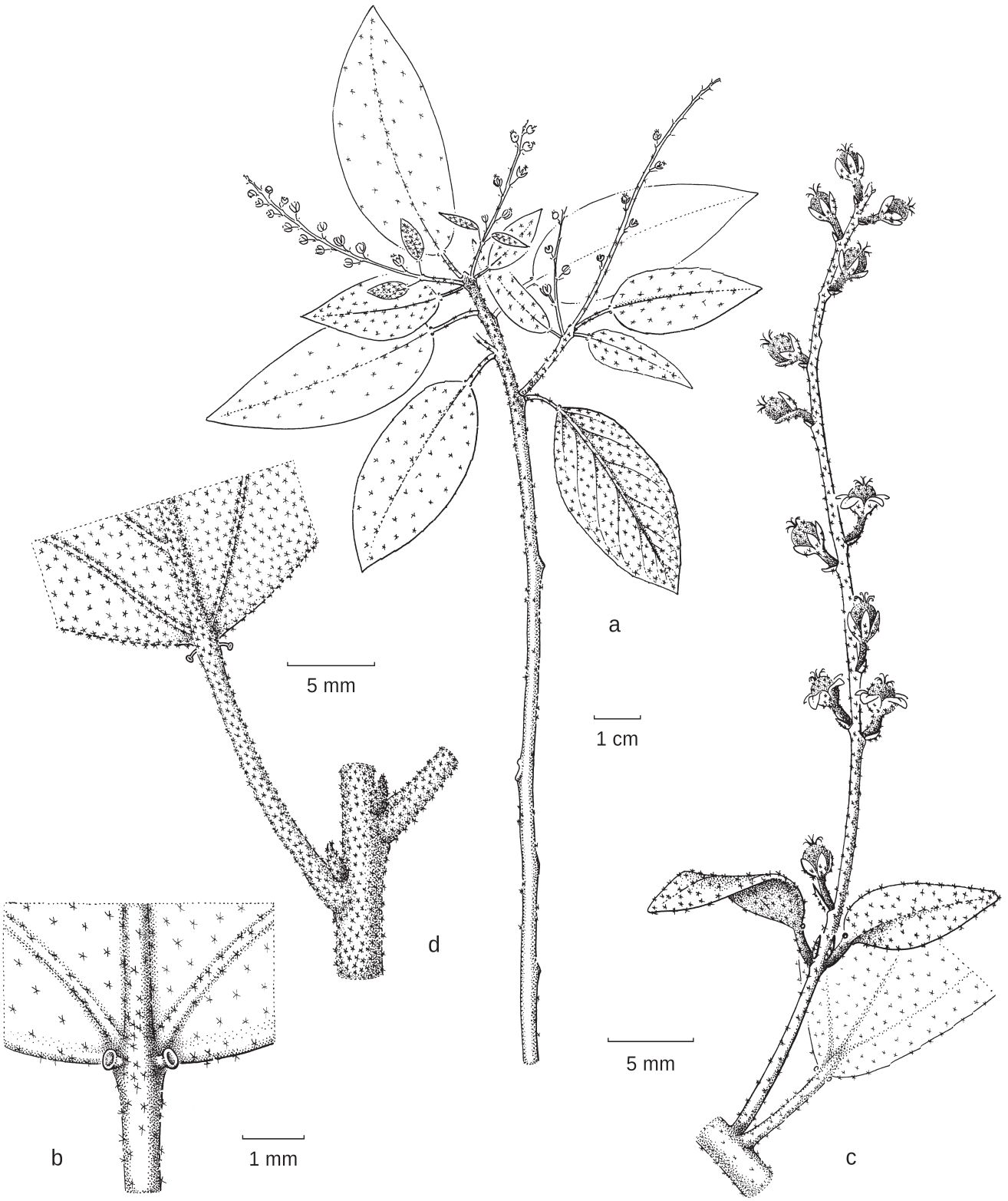

Fig. 3 *Croton pseudoverticillatus* Duijn – **a.** Habit; **b.** Abaxial stellate trichomes and extrafloral nectaries; **c.** Inflorescence, pistillate part. – *C. tomentellus* F.Muell. – **d.** Habit with stellate trichomes and stalked abaxial extrafloral nectaries (a–c: *Schmutz 844*, L.2212174; d: *Elbert 3694*, L.2212173). Illustration by Esmée Winkel.

(0.1–)0.2–0.3 mm diameter, with 20–27 radii completely or partially fused, yellowish or off-white. *Stipules* linear to linear-triangular, 3.4–6.7 by 0.5–0.7 mm, caducous, semi-pubescent (to pubescent). *Leaves* alternate to pseudo-verticillate, dark brown after drying; petiole 2–4.3 cm long, grooved above, with scattered trichomes, more dense on the pulvini, lower pulvinus 0.4–0.7 mm long, upper pulvinus c. 0.3 mm long; blade elliptic (to (ob)ovate), 5.3–13.5 by 3.2–6.3 cm, 1.7–2.4 times longer than wide, chartaceous, base obtuse, basal extrafloral nectaries stalked or sessile, laterally at the apex of the petiole, 0.4–0.6 mm diameter, when stalked then stalk 0.1–0.4 mm long, margin subentire, with colleters, apex acute to acuminate, adaxially glabrous, abaxially subglabrous with some trichomes near the base and on the venation, venation penninerved, visible up to third order and raised on both sides, secondary veins 8–13 pairs up to apex. *Inflorescences* terminal or axillary, sulcate, subglabrous; basally up to seven pistillate flowers; apically staminate flowers, apical part caducous; bracts ovate-triangular, c. 1.5 by 0.5 mm, (sub) glabrous with apically a tuft of simple trichomes, caducous. *Staminate flowers* 3–4 mm diameter; pedicel c. 2 mm long, round, glabrous; sepals 5, ovate-triangular, c. 2 by 1 mm, outside glabrous; petals 5, oblong, c. 2.2 by 0.5 mm, lanate on margin near apex, trichomes pointing inwards; stamens c. 11, filaments 2.5–3.5 mm long, anthers c. 0.5 by 0.3 mm. *Pistillate flowers* 3–4 mm diameter; bracts triangular, c. 1.5 by 0.7 mm, subglabrous, apically with simple trichomes; bracteoles triangular, (sub)glabrous, apically with simple trichomes; pedicel 2.7–4.5 mm long, subglabrous; sepals 5, ovate-triangular, c. 2 by 1.2 mm, as long as to longer than the ovary, subglabrous with simple trichomes at the apex; petals absent; disc glands absent; ovary obovoid to oblate, c. 2.5 by 1.5 mm, 3-lobed, densely pubescent, style absent, stigmas c. 2.6 mm long, divided into two to c. 0.7 mm from base. *Fruits* 3-lobed, obovoid, 3–6 by 3–6 mm, lobes conchiform, deeply sulcate, with scattered trichomes, apex depressed; pericarp c. 0.2 mm thick; columella c. 5 mm long. *Seeds* ellipsoid, 5–6 by 3.5–4.5 mm, glabrous, with a small caruncle.

Distribution — *Malesia*: Sumatra (Sumatera Utara, Riau), W Java, Borneo (Sarawak, Sabah).

Note — Descriptions of staminate flowers, fruits, and seeds from Beyer et al. (2023).

13. *Croton sumbensis* Duijn, sp. nov. — Fig. 4

Leaves small, up to 15 cm long, slender, 2.5–3 times longer than wide, extrafloral nectaries laterally on the petiole, slightly raised; inflorescence subglabrous. Different from both *C. hasskarlianus* and *C. coccymelophyllus*, with necaries laterally on the midrib or blade near the base of the leaf. The inflorescence of *C. coccymelophyllus* with scattered trichomes; *C.* hasskarlinanus with wider leaves, 3.7–4.5 times longer than wide. — Type: *C.N.A. de Voogd 2244* (holo L 2 sheets [L.2203659, L.2203660]!), Indonesia, Lesser Sunda Islands, Sumba, Prailangina. Paratypes (see also next species name): *I.D. Cowie 11097* (L [L.2211719]!), Timor Leste, north coast, c. 5 km NW of Manatuto; *E. Schmutz 622* (L [L.2203592]!], Indonesia, Lesser Sunda Islands, Flores, Warsawe; *J.A.J. Verheijen 2306* (L [L.2203588]!), Indonesia, Lesser Sunda Islands, Flores; *J.A.J. Verheijen 3483* (L [L.2203589, L. 2203590]!), Indonesia, Lesser Sunda Islands, Flores.

Croton prunifolius auct. non Airy Shaw: Airy Shaw (1978b) 56, pro paratype *Kostermans 22064* (L [L.2203593]!), Indonesia, Lesser Sunda Islands, Flores, SW part, near Mborong (also paratype of *C. sumbensis*).

Woody plants; older bark subglabrous; young twigs with scattered trichomes. *Bark* not smooth, outer layer peeling (maybe due to drying), silvery grey; young twigs sulcate, reddish brown. *Indumentum* consisting of flat stellate trichomes, 0.15–0.35 mm diameter, radii free, 8–19, off-white to hyaline; simple hairs at stipules. *Stipules* linear, c. 3 by 0.3 mm, early caducous, pubescent. *Leaves* alternate; petiole 0.6–4 cm long, grooved above, hardly pulvinate, with scattered trichomes, more densely so on the pulvini; blade elliptic, 3.1–15.1 by 1.6–5.7 cm, 2.5–3.1 times longer than wide, papery to subcoriaceous, base obtuse to cuneate, basal extrafloral nectaries flat, sessile to slightly elevated, laterally on the very apex of the petiole, 0.5–0.6 mm diameter, margin serrulate, colleters sometimes accompanied by a few simple trichomes at apices of teeth, apex acute to acuminate, apex tip emarginate with mucron at back, adaxially glabrous, abaxially subglabrous, when young with scattered trichomes, venation penninerved, adaxially visible up to third order, slightly raised, abaxially very conspicuous, much darker than leaf surface, visible up to fourth order, raised, secondary veins 9–11 pairs up to apex. *Inflorescences* terminal, sulcate, up to 13.4 cm long, (sub)glabrous; basally up to 6 pistillate flowers; apically staminate flowers; bracts triangular, 1–1.3 by 0.4–0.5 mm, (sub)glabrous, apex with simple hyaline trichomes; bracteoles linear-triangular, glabrous, apex with simple hyaline trichomes. *Staminate flowers* 3.6–4 mm diameter; pedicel 4–5.5 mm long, glabrous; sepals 5, ovate-triangular, 1.7–1.8 by 1–1.1 mm, outside subglabrous, inside glabrous, apex with small hyaline simple trichomes; petals linearly obovoid, 1.7–2 by 0.5–0.6 mm, outside glabrous, inside basally with long simple hyaline trichomes, apically with small simple hyaline trichomes; receptacle lanate; disc glands 5; stamens c. 11, filaments 1.5–2.5 mm long, glabrous, anthers 0.6–0.8 by 0.5–0.6 mm. *Pistillate flowers* 2.5–4 mm diameter; pedicel 1.5–4 mm long, with scattered trichomes; sepals 5, ovate, 1.4–1.8 by 1–1.3 mm, with a few trichomes outside, inside glabrous, apex with a tuft of hyaline simple trichomes; petals either absent or reduced to small orbital structures, once one petal developed, linear, c. 1.7 by 0.5 mm, apically tuft of simple trichomes; disc glands 5, well-developed; ovary subglobose to oblate, 1.3–1.5 by 1.5–1.9 mm, slightly 3-lobed, pubescent with whitish hyaline trichomes, style absent–0.2 mm long, stigmas c. 2.1 mm long, split into two to c. 0.8 mm from base. *Fruits* obtrigonous, lobed, lobes pointing upwards, c. 6.5 mm high by 8 mm wide, with scattered small stellate trichomes; column 3–4 mm long, very slender. *Seeds* flattened-ellipsoid, c. 5.8 by 4 by 3 mm; caruncle indistinct.

Distribution — *Malesia*: Lesser Sunda Islands (Sumba, Flores, Timor).

Habitat & Ecology — Altitude: 700 m.

Notes — At first, only a single specimen (the type) from Sumba was considered to represent this species. However, in a returned loan five specimens from Flores and Timor appeared to be conspecific, though these tend to have somewhat smaller leaf blades (3.1–9.8 by 1.6–3.7 cm versus 8.2–15.1 by 3.6–5.7 cm on Sumba). All specimens

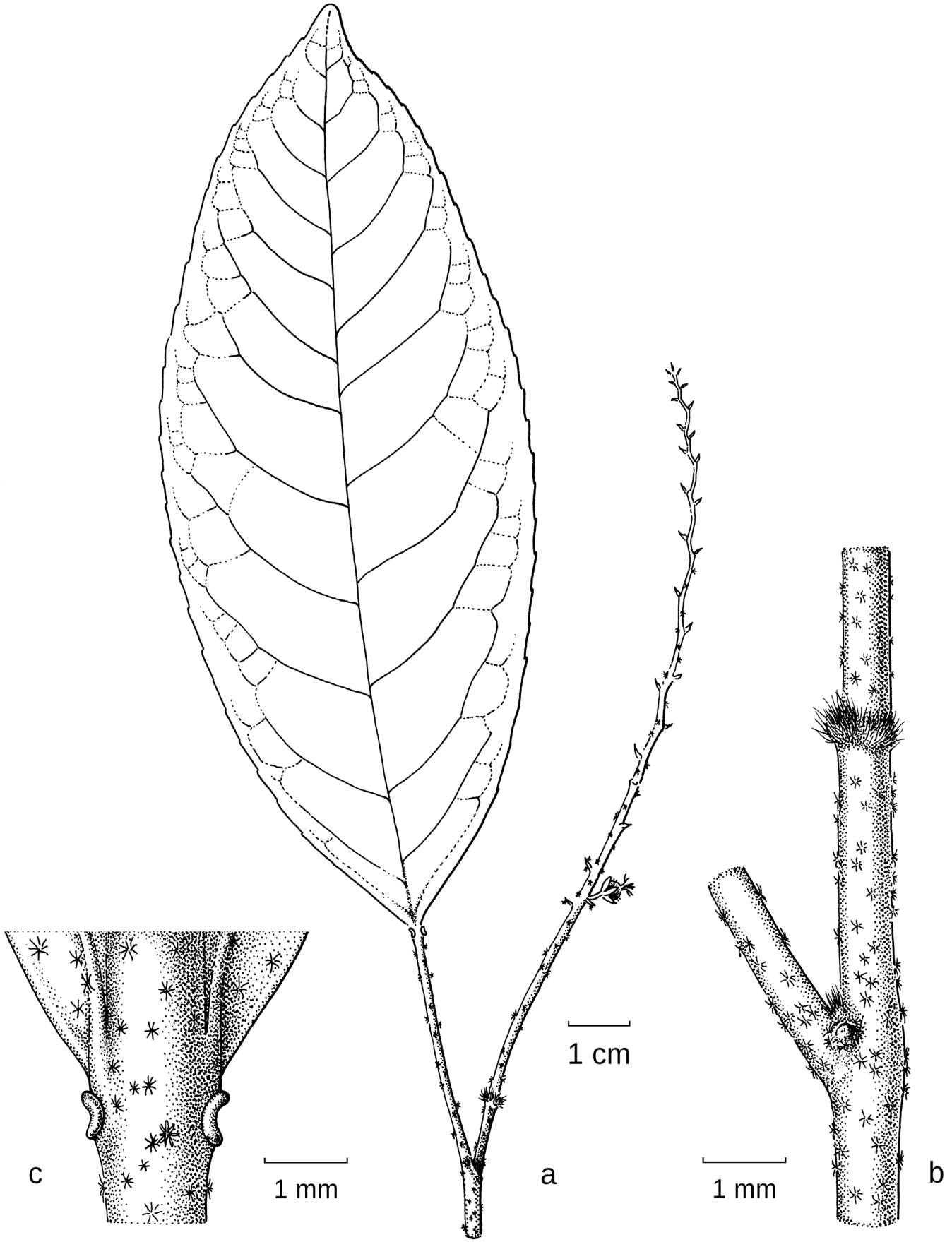

Fig. 4 *Croton sumbensis* Duijn – **a.** Habit; **b.** Branchlet; **c.** Abaxial stellate trichomes and extrafloral nectaries (*de Voogd 2244*, L.2203659). Illustration by Esmée Winkel.

were originally identified as *C. oblongus*. The material was confused with *C. coccymelophyllus*, (formerly *C. prunifolius* Airy Shaw, an invalid homonym) and even contains a paratype of *C. prunifolius*, *Kostermans 22064*. However, the Sundanese material has extrafloral nectaries on the petiole instead on the very base of the main vein, the inflorescence is (sub)glabrous instead of pubescent, petioles have trichomes instead of being glabrous. Also typical for *C. sumbensis* is the very tip of the leaves, which is narrowly emarginate with a mucron pointing upwards from the lower leaf surface.

14. *Croton tetraglandulosus* Duijn, sp. nov. — Fig. 5

Croton tetraglandulosus usually has a double set of leaf extrafloral nectaries, long and thin petioles, chartaceous blade, and a semi-pubescent indument abaxially on the leaves. It can be confused with *C. brevipetiolatus*, but the latter has short and thick petioles, and short inflorescences. *Croton tetraglandulosus* differs from *C. glabrescens* in the double set of extrafloral nectaries instead of a single set, the denser indument on the abaxial side of the leaf, and the elliptical blade with often an attenuate apex instead of an ovate blade with an acute apex. — Type: *Backer 17863* (holo L [L.2211337]!), Indonesia, Java, Res. Besoeki, Poeger. Paratype: *Zollinger 3805* (L [L.2211338]!, G-DC [G00312286]*), Indonesia, Java.

Woody plants; young twigs with scattered trichomes. *Bark* brownish grey to silver, slightly sulcate with lenticels, glabrous when older. *Indumentum* consisting of stellate trichomes, mostly flat, sometimes with a very small porrect radius, 0.25–0.43(–62) diameter, radii 8–23, cream to caramel-coloured. *Stipules* triangular, c. 0.4 by 0.35 mm, with scattered trichomes. *Leaves* alternate or pseudo-verticillate at the end of branches; petiole 2.1–4.1 cm long, c. 1 mm (or less) thick, grooved above, basally thickened for c. 2 mm, with scattered trichomes when young, soon glabrous; blade ovate to elliptic, 6.6–9.4 by 2.2–5.2 cm, 1.5–3 times longer than wide, chartaceous, base rounded, often two pairs of basal extrafloral nectaries, sessile or stalked, one on the petiole and 0.3–0.5 mm in diameter, and one on the secondary veins close to the base of the midrib and 0.5–0.6 mm in diameter, sometimes seemingly laterally on the base of the midrib, only on the secondary veins near the base of the midrib when one pair of extrafloral nectaries present, margin serrulate with colleters accompanied by one or two simple trichomes at the apices of the teeth, apex attenuate to acute, rarely acuminate, adaxially and abaxially semi-pubescent, venation penninerved, on both sides visible up to third order, adaxially slightly raised but midrib slightly sunken, abaxially raised, secondary veins 7–8 pairs up to apex. *Inflorescences* axillary or terminal, 14.9–16.2 cm long, 1–2 mm thick, with scattered trichomes, basally pistillate flowers, apically staminate flowers, up to four per node. *Staminate flowers* c. 3.3 mm diameter; bracts triangular, c. 3.2 by 0.3 mm, apex margin ciliate; bracteoles linear, apex margin ciliate; pedicel 4.5–6.3 mm long, with scattered trichomes; sepals 5, ovate, c. 1.5 by 1 mm, with scattered trichomes outside, glabrous inside, apex with simple hyaline trichomes; petals 5, obovoid, c. 1.5 by 1 mm, outside glabrous, inside with simple hyaline trichomes at the base, apex with simple hyaline trichomes; receptacle lanate; disc glands absent; stamens 11, filaments c. 1.8 mm long, anthers c. 0.6 by 0.5 mm. *Pistillate flowers* c. 3 mm diameter; bracts and bracteoles unknown; pedicel c. 2 mm long, pubescent; sepals 5, ovate, c. 1.3 by 1 mm, with scattered trichomes outside, apex with hyaline simple trichomes; petals unknown; ovary globose, c. 1.3 by 1.7 mm, pubescent with white-yellowish trichomes, style absent, stigma c. 1.7 mm long, split into two to c. 0.5 mm from the base. *Fruits* and *seeds* unknown.

Distribution — *Malesia*: Java.

Notes — 1. The two specimens representing this new species used to be identified as *C. glabrescens*, but one (*Backer 17863*) has two pairs of basal extrafloral nectaries instead of one, a serrulate margin with colleters instead of it being nearly entire or lobed, and the abaxial side of the leaf is covered with scattered trichomes instead of glabrous. The other (*Zollinger 3805*) has the same differences with *C. glabrescens*, except it has a single pair of extrafloral nectaries at the base of the leaf blades.

2. The description of the pistillate flowers is not complete, as, in total, there are only two pistillate flowers that were not dissected and had to be spared. *Fruits* and seeds are absent.

15. *Croton tiglium* L.

Croton tiglium L. (1753) 1004; Müll.Arg. (1866) 600; Hook.f. (1887) 393; J.J.Sm. (1910) 346; Merr. (1921a) 337; (1923) 427; Ridl. (1924) 262; Gagnep. (1925) 285; Merr. (1926) 382; Burkill (1935) 690; Merr. (1935) 236; Backer & Bakh.f. (1963) 477; Airy Shaw (1972a '1971') 250; Whitmore (1973) 84, in obs.; Airy Shaw (1975) 95; (1981a) 285; (1982a) 15; (1983) 20; Corner (1988) 284; Chakrab. & N.P.Balakr. (1997 '1992') 72, map 3; Philcox (1997) 94; Esser (2005) 222; P.T.Li & Esser (2008) 262; Chakrab. (2019) 3630; Beyer et al. (2023) 19. — *Croton arboreus* Shecut (1806) 470, nom. rej., nom. superfl. — *Kurkas tiglium* (L.) Raf. (1838) 62. — *Tiglium officinale* Klotzsch (1843b) 418. — *Oxydectes tiglium* (L.) Kuntze. — *Croton officinalis* (Klotzsch) Alston (1931) 264, nom. illeg., superfl. — *Croton tiglium* L. var. *tiglium*: Backer & Bakh.f. (1963) 477. — Lectotype (first step designated by Chakrabarty & Balakrishnan 1997 ('1992'); second step by Philcox 1997, left-hand specimen): Herb. Hermann 2: 6, no. 343 (lecto BM [BM000621766]*), Sri Lanka.

Croton acutus Thunb. (1784) 269 ('*acutum*'). — Type: Not indicated, likely *Thunberg s.n.* (UPS [V-138355], perhaps LD [LD1741433]), Japan.

Croton jamalgota Buch.-Ham. (1824) 258. — Syntype: *Buchanan-Hamilton 2116* (Wallich Numer. List no. 7722B p.p.) (E [E00314201]), India, Assam, Gualhara [Goalpara].

Croton pavana Buch.-Ham. (1824) 259. — Syntypes: *Buchanan-Hamilton 2116* (*Wallich Numer. List no. 7722B p.p.*) (E [E00314202], K [K000246851, p.p. Wallich 7722B]), India, Assam, Gualhara [Goalpara].

Croton camaza Perr. (1825) 112. — Type: Not indicated, Philippines.

Croton glandulosus Blanco (1837) 754 ('*glandulosum*'), nom. illeg., non L. (1759). — *Croton muricatus* Blanco (1845) 518, nom. illeg., non Vahl in Geiseler (1807); (1879) 154, t. 383. — *Oxydectes blancoana* Kuntze (1891) 610. — Neotype (designated by Beyer et al. 2023): *Merrill Species Blancoanae 308* (neo L [L.2212332]!), Philippines, Luzon, Camarines Prov. See also Merrill (1918: 220).

Croton birmanicus Müll.Arg. (1865) 112. — Syntypes: *Wallich num. list 4744* (n.v.), India, flumen Irawaddy; *Wallich num. list. 7773A* (n.v.), India, flumen Irawaddy.

Croton jatrophifolius Müll.Arg. (1866) 600 ('*jatrophaefolius*'). — *Oxydectes jatrophifolia* (Müll.Arg.) Kuntze (1891) 612. — Type: *Anonymous s.n.* (holo G-DC [G00311911]!), Indonesia, Banda (misformed).

Croton tiglium L. var. *globosus* J.J.Sm. (1910) 349. — Lectotype (designated by Beyer et al. 2023): *Koorders 14426* (lecto L

[L.2212249]!; isolecto L [L.2212250]!, U [U.1256074]!), Java, Prov. Besoeki, Pantjoer Idjen, 1000 m.

Croton tiglium L. var. *xiaopadou* Y.T.Chang & S.Z.Huang (1982) 23. — Syntypes: *L. Deng 974* (IBSC), China, Guangdong, Yangshan; X.F. Deng 174 (SCBI), China, Guangxi, Lingui.

Croton himalaicus D.G.Long (1986) 170, fig. 1Aa, Ab. — *Haines 828* (holo E). India, Darjeeling Distrixt, near Pedong.

For other synonyms see Plants of the World Online (http://www.plantsoftheworldonline.org/).

Trees; young branchlets sulcate, (sub)glabrous. *Bark* smooth, often with small, vertically oriented lenticels ordered approximately in rows, grey to yellowish brown. *Indumentum* consisting of flat, stellate trichomes, occasionally with a central porrect radius, 0.2–0.4 mm in diameter, radii 9–16, yellowish brown. *Stipules* linear, 1.2–4 by 0.3–0.4 mm, caducous, glabrous. *Leaves* alternate; petiole grooved, 2.1–4.7(–13.3) cm long, (sub)glabrous; blade ovate, rarely elliptic, 9.2–12.5 by 6.2–6.8 cm, 1.4–2.1 times longer than wide, base obtuse to rounded with the very base obtuse, basal extrafloral nectaries on margin near base, sessile to slightly stalked, 0.7–1.3 mm diameter, stalk 0.1–0.2 mm long, margin lowly serrate, sometimes biserrate, with colleters at apices of teeth, apex attenuate to acuminate, adaxial side glabrous apart from a

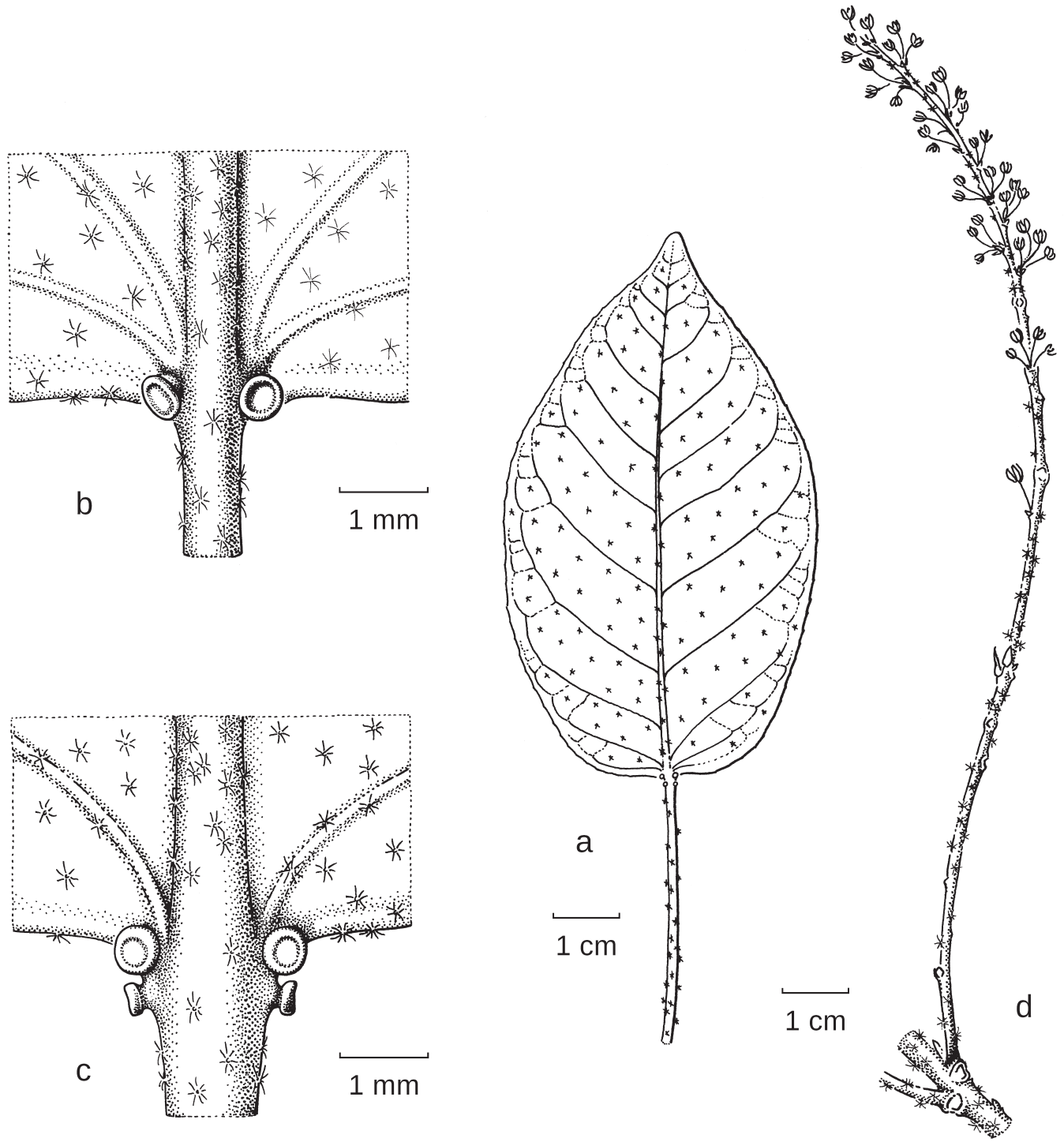

Fig. 5 *Croton tetraglandulosus* Duijn – **a.** Leaf abaxially; **b** and **c**. Variation in abaxial extrafloral nectaries; **d.** Inflorescence (*Backer 17863*, L.2211337). Illustration by Esmée Winkel.

tuft of trichomes at the base, young leaves with scattered trichomes, quickly glabrescent, abaxial side subglabrous, young leaves pubescent, glabrescent, venation distinctly triplinerved, up to third order veins slightly raised adaxially, distinctly raised abaxially, second order veins 5–7 pairs up to apex. *Inflorescences* terminal, 5.2–12.4 cm long, sulcate, with scattered trichomes to glabrous; apically staminate flowers up to 4(–5) per node; bracts triangular, 2.1–3.1 by 0.4–0.8 mm, glabrous; bracteoles linear-triangular, glabrous. *Staminate flowers* (buds) c. 2.5 mm diameter, glabrous; pedicel 2.7–3 mm long; sepals 5, ovate, 3–3.5 by 2.5–3 mm, outside subglabrous, apically a tuft of light brown simple trichomes, inside glabrous; petals 5, obovate, c. 2.8 by 1.2 mm, margin ciliate with long translucent simple trichomes, outside glabrous, inside with translucent, long, simple trichomes, brown at the sides with whitish centre, whitish centre sometimes reaching up to the apex, sometimes reaching halfway; disc not visible; stamens c. 15, filaments 1.9–2.1 mm long, anthers c. 1 by 0.8 mm. *Pistillate flowers* 6–8 mm diameter; pedicel 3–5 mm long, densely pubescent; sepals 5, triangular, 2.5–3.5 by 1–2 mm, apically spreading, slightly longer than ovary or as high, outside subglabrous, with a patch of simple trichomes on the very apex; petals absent; ovary globose to slightly ovoid, 3–4 by 2–3 mm, densely pubescent, style absent, stigmas 4–6 mm long, once divided to 3–4 mm from apex. *Fruits* globular, slightly 3-lobed, 1.5–1.9 by 1.4–1.8 cm, subglabrous, dehiscing loculicidally from the top; columella 12–14 mm long. *Seeds* ellipsoid, one side slightly flattened, 11–15 by 7–10 by 4–6 mm, glabrous; caruncle distinct.

Distribution — S and SE Asia, from India and Assam to SE China (unknown from Laos), throughout *Malesia* (absent from New Guinea), and the Caroline Islands. Introduced in Japan.

Habitat & Ecology — Heterogenous primary or secondary forest. Mostly in evergreen secondary forest. Altitude: 0–1100 m. Flowering: May–October; fruiting: May–August. (Smith 1910, Beyer et al. 2023)

Uses — Plant poisonous, causing inflammations, but often used medicinally. Oil from seeds used as purgative (strongest known, high doses can be lethal), or oil used as lamp oil, but only outside houses (smoke irritating). Plants in Malaysia grown for the oil. Plant parts also used to stupefy fish (Smith 1910). See Zhang et al. (2022) for an elaborate overview of uses worldwide, toxicology, phytochemistry and pharmacology.

Vernacular names — Java: Ki-malakian (Sundanese); Bali angin, Kletek (Madurese); Djarak bromo (Javanese), (Smith 1910).

Notes —Two individuals (*Koorders 2053, 2054*) have much bigger leaves than the other specimens. The measurements of the staminate flowers are taken from buds and the measurements are likely smaller than in mature flowers. The pistillate flowers were not seen, but the description is adapted from Beyer et al. (2023).

16. *Croton tomentellus* F.Muell. — Fig. 3d

Croton tomentellus F.Muell. (1864) 141; Benth. (1873) 126; Airy Shaw (1978b) 55; (1980b) 623; (1980c) 228; (1982a) 15; P.I.Forst. (2003) 419, fig. 28. — Lectotype (effectively designated by Forster 2003: 419): *F. von Mueller s.n.* (lecto MEL [MEL231573]*; isolecto K [K000959229, K000959230]*), Australia, (Northern Territories,) Upper Victoria River (see note).

Croton tomentellus Müll.Arg. (1865) 108, nom. superfl., non von Mueller (1864); (1866) 591. — *Oxydectes tomentella* (Müll. Arg.) Kuntze (1891) 613. — Type: *F. von Mueller s.n.* (holo G-DC [G00311954]*), Australia, Northern Territory, Arnhem's Land.

Woody plants; young branchlets densely pubescent, bark not visible; older branches pubescent to scattered trichomes; latex reddish. *Bark* smooth, brown to yellowish brown due to trichome coverage; lenticellate. *Indumentum* of sessile, stellate trichomes with 9–19 radii, adaxially 0.4–0.6 mm diameter, abaxially (0.3–)0.6–0.8 mm diameter, off-white to yellowish brown, on branches and veins 0.3–0.4 mm diameter and with 19–32 radii in all directions, more often yellowish brown than off-white. *Stipules* linear-triangular, c. 4 by 0.4 mm, densely pubescent, caducous. *Leaves* alternate; petiole 1.5–2.5 cm long, grooved above, sulcate, densely pubescent; blade elliptic, 6.9–11.5 by 4.2–5.4 cm, 1.6–2.1 times longer than wide, base obtuse to rounded with the very base obtuse, basal extrafloral nectaries stalked, laterally on the petiole, 0.6–0.7 mm diameter, stalk 0.2–0.3 mm high, margin mostly entire, sometimes serrulate with colleters accompanied by one or two trichomes, apex acute, adaxial side semi-pubescent and abaxially pubescent to densely pubescent, both sides densely pubescent when young, venation penninerved, adaxially visible up to second order, slightly sunken, abaxially visible up to third order, slightly raised, secondary veins 6–8 pairs up to apex. *Inflorescences* terminal, up to 11 cm long, sulcate, pubescent; basally c. 10 pistillate flowers, single per node or with a staminate flower; apically staminate part caducous, up to 4 flowers per node. *Staminate flowers* 2–2.5 mm long, 2–3.5 mm diameter; pedicels 1.8–4 mm long, glabrous or with scattered trichomes; sepals 5, linear-ovate, 1.6–2 by 0.9–1.2 mm, glabrous, lanate in upper half; petals 5, linear-obovate, 1.8–2 by 0.6–0.8 mm, lanate; stamens 10–11, filaments filiform, 1–2 by c. 0.1 mm, glabrous, anthers oblong, 0.4–0.6 by c. 0.3 mm. *Pistillate flowers* 3–4 mm diameter; bracts present as glands; pedicel pubescent, c. 3.3 mm long in mature fruit; sepals 5, ovoid, c. 1.6 by 0.9 mm, pubescent outside, glabrous inside; petals absent; disc glands 5; receptacle lanate; ovary 3-locular, 1.2–2 mm diameter, with thinly scattered trichomes, stigmas linear, 1.8–2.2 mm long, bifid for 0.7–1 mm, shortly connate at base, glabrous. *Fruits* globose, lobed, 4.5–7 mm long, 5–7 mm diameter, with scattered trichomes; columella c. 4 mm long. *Seeds* ovoid to obloid, 3–5 by 2.3–4 by 1.8–3.5 mm, dorsal surface rounded, ventral surface bifacial, micropylar line 2.5–3.5 mm long; caruncle present.

Distribution — *Malesia*: E Java, Lesser Sunda Islands (Sumbawa); Australia (Northern Territory, Western Australia).

Habitat & Ecology — Monsoon forest; soil: indesite breccia, not very wet. Altitude: 300–450 m.

Note — 1. Von Mueller (1864) did not indicate a holotype, therefore the specimen indicated by Forster as holotype is here regarded as lectotype. Article 9.23 of the code (Turland et al. 2025) dictates that on or after 1 January 2001 lectotypification is only effective when the term lectotype is used, therefore regarding the term holotype as an indirect lectotypification is not possible any longer.

2. Unfortunately, the same name was independently used for the same taxon by Müller Argoviensis (1865), based on a specimen in G-DC.

3. Descriptions of staminate flowers, fruits and seeds are adapted from Forster (2003); descriptions of inflorescences and pistillate flowers are supplemented by Forster (2003).

DUBIOUS SPECIES

The following *Croton* names might apply to plants of Java and the Lesser Sunda Islands, but cannot be interpreted. The names can be even synonyms of species in other genera.

Croton maculatus Vahl in Geiseler (1807) 30. — Type: Unknown (P-JU not seen), Java.

Note — Rhomboid-ovate leaves and axillary inflorescences do possibly not agree with *Croton*.

[*Croton pauciflorus* Span. (1841) 348 (‘*pauciflorum*’), nom. nud. — *Oxydectes pauciflora* (Span.) Kuntze (1891) 612, nom. nud.]

Croton peltatus Thunb. (1825) 23 (‘*peltatum*’). — Type: Not indicated, [Indonesia,] Java.

Note — The short description is too general to identify this name correctly, seemingly also no material in Uppsala (UPS). Unclear if really collected on Java.

Croton tiglioides Blume (1826) 602. — Type: not indicated, vernacular name Mamalakkian Gunung.

Note — POWO (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:343630-1) refers the name to the uninterpretable *Croton oblongus* Burm.f. (see above and below). The syntypes are probably in L, but not yet identified. The specimens in A [A00047518]* and P [P04830204]*, both containing fragments and indicated as syntypes, show fruits smaller that those of *C. tiglium*. However, the handwriting on the labels in A and P is not by Blume, thus difficult to interpret as types.

EXCLUDED SPECIES

Listed are names that were described from Java or LSI, and names that are synonyms of species known from Java. Not mentioned here are all names published under *Croton* that are cultivars of *Codiaeum variegatum* (L.) Rumph. ex A.Juss., for those see https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:85073-3

[*Croton acerrimus* Reinw. ex Blume (1823) 104 (‘*acerrimum*’), nom. nud.] = **Dalechampia bidentata** Blume.

Croton acuminatus Lam. (1786) 207 (‘*acuminatum*’) — Lectotype (effectively designated by Sierra et al. 2007: 96): *Commerson s.n.* (lecto P-JU 16580), [Papua New Guinea, New Britain,] Port Praslin. = **Mallotus tiliifolius** (Blume) Müll.Arg.

Adisca ? albicans Blume (1826) 611. — *Croton albicans* (Blume) Moritzi ex Rchb.f. & Zoll. in Zoll. (1856) 21.— Lectotype (effectively designated by van Welzen 1999: 428) *Anonymous s.n.* (lecto L [L 0023770]!), [Indonesia,] Java, Prov. Tjanjor. = **Sumbaviopsis albicans** (Blume) J.J.Sm.

[*Croton apetalus* Blume (1823) 104 (‘*apetalum*’), nom. nud.] = ***Alchornea rugosa*** (Lour.) Müll.Arg.

Croton appendiculatus Elmer (1908) 312, nom. illeg. (non Hort. Veitch. ex Rev. Hortic. (see Carrière et al.) (1877) 87). — Lectotype (designated here by van Welzen): *Elmer 9215* (lecto L [L 0435064]!; isolecto NY [NY00262990]*, US [US00109498]*, W [W1910-0010547]!, Z [Z-000053893]!), Philippines, Luzon, Province of Tayabas, Lucban. = **Mallotus paniculatus** (Lam.) Müll.Arg. var. **paniculatus**.

[*Croton baccifer* Benth. in Wall. or *C. bacciferum* Wall. (1847) no. 7826, nom. nud. — Based on *Wallich 7826A*]. = **Mallotus repandus** (Rotller) Müll.Arg.

Croton bractifer Roxb., [(1814) 104, nom. nud.], (1832) 680 (‘*bractiferum*’). — Lectotype (designated by Merrill 1917: 326): Rumph. (1743) 69 *Codiaeum silvestre*, t. 27. = **Codiaeum bractiferum** (Roxb.) Merr.

[*Croton chiamala* Wall. (1847) no. 7775, nom. nud. — Representative specimen: *Wallich 7775* (G-DC [G00325433, as s.n.]?, K-W, not seen), India, Goygalpura.] = **Alchornea tiliifolia** (Benth.) Müll.Arg.

Croton coccineus Vahl (1791) 97 (‘*coccineum*’). — Lectotype (designated by Sierra et al. 2005: 230): *König s.n.* (lecto C [C10011319]; isolecto C [C10011318], LD), Sri Lanka. = **Mallotus philippensis** (Lam.) Müll.Arg.

Croton ellipticus Geiseler (1807) 27. — Syntypes: *Burman in Herb. Vahl s.n., s.d.* (C [C10011145, C10011146]*), [Indonesia,] Java. = **Claoxylon indicum** (Reinw. ex Blume) Hassk. (identification by Esser).

Croton enantiophyllus K.Schum. in K.Schum. & Lauterb. (1905) 296. — Syntypes: *Parkinson s.n.* (B †, NSW [NSW604690, staminate specimen]), Papua New Guinea, New Britain. = **Mallotus tiliifolius** (Blume) Müll.Arg.

Croton halecum Roxb., [(1814) 104, nom. nud.] (1832) 683. — Lectotype (designated here): *Roxburgh s.n.* (lecto BR [BR0000006999841]*), India. = Likely **Claoxylum indicum** (Reinw. ex Blume) Hassk.

[*Croton incanus* Blume (1823) 104 (‘*incanum*’), nom. nud.] = **Codiaeum variegatum** (L.) Rumph. ex A.Juss.

[*Croton longifolius* Reinw ex Blume (1823) 105 (‘*longifolium*’), nom. nud.] = ? **Claoxylon longifolium** (Blume) Endl. ex Hassk.

Croton mollissimus Geiseler (1807) 73. —Type: *Herb. Vahl s.n.* (holo C [C10011316]*; photo at A*), China. = **Mallotus mollissimus** (Geiseler) Airy Shaw

Croton montanus Willd. (1805) 547. —Type: *Klein s.n.* (*Willdenow 29*) (holo B-W [B -W 17874 -01 0]*), India. = **Mallotus philippensis** (Lam.) Müll.Arg.

[*Croton multiglandulosus* Reinw. ex Blume (1823) 105, nom. nud.] — Rottlera multiglandulosa Reinw. ex Blume (1826) 609. — Lectotype (designated by van Welzen et al. 1999): *Anonymous s.n.* (L [L 0020491]!), [Indonesia,] Java. = **Melanolepis multiglandulosa** (Reinw. ex Blume) Rchb.f. & Zoll.

[*Croton muricatus* Zipp. ex Span. (1841) 348, nom. nud. — Based on *Zippelius s.n.* (L [L 0245271, L 0245278, L 0245277]!), [Indonesia, Lesser Sunda Islands, Timor]. = **Tritaxis australiensis** S.Moore.

Croton oblongus Burm. (1768) 205, t. 64.2. — Type: Not indicated.

Note — Cannot be interpreted (yet), see Results and Discussion.

[*Croton ovatus* Noronha (1790) 12 (‘*ovatum*’), nom. nud.] = **Mallotus tiliifolius** (Blume) Müll.Arg.

Croton paniculatus Lam. (1786) 207. — Lectotype (effectively designated by Forster 1999: 478): *Commerson s.n.* (lecto P-JU 16579), [Indonesia,] Java. = **Mallotus paniculatus** (Lam.) Müll.Arg. (var. paniculatus).

Croton pendulus Hassk. (1848) 266. — Neotype (designated by Esser in van Welzen et al. 2024: 190): *Junghuhn 113* (neo L [L2255820]!), [Indonesia,] Java. = **Para*croton* pendulus** (Hassk.) Miq.

Croton philippensis Lam. (1786) 206. — Type: *Sonnerat s.n.* (holo P [P00279571]), Philippines = **Mallotus philippensis** (Lam.) Müll.Arg.

[*Croton pigmentarius* Noronha (1790) 13, nom. nud.] = **Claoxylon indicum** (Reinw. ex Blume) Hassk.

Croton plicatus Vahl, Symb. Bot. 1 (1790) 78. — Syntypes: *Herbarium Vahl s.n.* (*Willdenow s.n., 1786?*) (LINN [LINN-HS1492-25-1]), *Herbarium Vahl s.n. (Rottler 195?)* (LINN [LINN-HS1492-25-2]), [India,] Tranquebar. = **Chrozophora plicata** (Vahl) A.Juss. ex Spreng.

Note — Absent from, but mentioned for Java in for instance POWO (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:60464929-2), as it was confused with *Chrozophora rottlera*, see note under *C. rottlera* in van Welzen 1999: 422; also absent from Java are the synonyms of *C. plicata* under *Croton*, see the same page in POWO).

Jatropha montana Willd. (1805) 563. — *Croton polyandrus* Roxb., [(1814) 69, nom. nud.] (1832) 682 (‘*polyandrum*’), nom. illeg., non Spreng. (1821). — *Croton roxburgii* Wall. (1840) 20 (see also Esser 2017). — Type: *Klein s.n.* (holo B [BW17927-010]!), ‘habitat in India orientali’. = **Baliospermum solanifolium** (Burm.) Suresh. (see also Chakrabarty 2019: 3630)

Croton punctatus Retz. (1788) 30 (‘*punctatum*’), nom. illeg., non Jacq. (1787). —Type: *J. König s.n.* (holo LD; iso C), Sri Lanka. = **Mallotus philippensis** (Lam.) Müll.Arg.

Croton repandus Rottler (1803) 206 (‘*repandum*’). — Lectotype (designated by Sierra et al. 2005: 234): *Rottler s.n.* = *Wall. Numer. List 7774*, fide specim. in Herb. Wall. (IDC microfiche no. 7394) (lecto LIV; isolecto K-W, L *s.n.* [L 0436491]!), India, Marmelon. = **Mallotus repandus** (Rottler) Müll.Arg.

Croton rhombifolius Willd. (1805) 555. — *Rottlera rhombifolia* (Willd.) Thwaites (1861) 272. — Type: *Roloff s.n.* (holo B-W, *Herb. Willd. 17900*, (IDC microfiche no. 1261)), Sri Lanka. = **Mallotus repandus** (Rottler) Müll.Arg.

Croton ricinoides Pers. (Sept. 1807) 586. — Lectotype (designated by Forster 1999): *Lahaye s.n.* (holo P, *Herb. A. Juss. 16578*, [IDC microfiche no. 6206]), India. = **Mallotus mollissimus** (Geiseler) Airy Shaw

Croton salicifolius Geiseler (1807) 6. — Type: *Herbarium Vahl (ex Herb. Richard) s.n., s.d.* (holo C [C10011284]) [Indonesia,] Java. = **Homonoia riparia** Lour.

Croton solanifolius Burm. (1769) 6 (‘*solanifolium*’). — Type: Rheede, Hort. Malab. 10 (1690) tab. 76. = **Baliospermum solanifolium** (Burm.) Suresh.

Croton solanifolius Geiseler (1807) 74, nom. illeg., non Burm. (1769). — *J.G.König s.n. in Herb. Vahl* (holo C [C10011196]), India = **Baliospermum solanifolium** (Burm.) Suresh. (See van Welzen 2018 for discussion).

Croton spiciflorus Thunb. (1825) 23 (‘*spiciflorum*’). — Syntypes: *Thunberg s.n.* (UPS [V-138406, V-138407]*), [Indonesia,] Java = **Claoxylon indicum** (Reinw. ex Blume) Hassk.

Note — The Thunberg specimen from Java are syntypes of *Claoxylon indicum* var. *spathulatum* Müll.Arg. Thunberg indicates that it might be *Acalypha spiciflora* Burm.f., (= *Claoxylon spiciflorum* (Burm.f.) A.Juss., but this was not correct.

Croton spinosus L. (1753) 1005 (‘*spinosum*’). — Type: Not designated, ‘Habitat in India’. = **Ricinus communis** L.

Croton tabacifolius Geiseler (1807) 26. — Type: Unknown, India orientalis. = **Claoxylon indicum** (Reinw. ex Blume) Hassk. (tentavily in synonymy in POWO: https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:341106-1).

Note — If indeed *C. indicum*, then Geiseler’s name has priority over Blume’s name.

[*Croton thebaloides* Teijsm. & Binn. (1866) 392, nom. nud. — Based on a (non-traced) specimen from the Sydney Hortus.] = Unidentified.

Croton variegatus L. (1753) 1199. — Lectotype (designated by Merrill 1917: 325): Rumphius (1743) 65, t. 25: *Codiaeum Medium Chrysosticon*. = **Codiaeum variegatum** (L.) A.Juss.

Croton volubilis Llanos (1856) 503 (‘*volubile*’). — Neotype (designated by Sierra et al. 2005: 235): *Merrill Species Blancoanae 842* (neo US [US00689404]; isoneo A [A00312842], GH [GH00312841], L, NY [NY00579097], P), Philippines, Luzon, Rizal. = **Mallotus repandus** (Rottler) Müll.Arg.

Croton rottleri Geiseler (1807) 54. — Type: *Rottler in Herb. Vahl s.n., s.d.* (holo C [C10011144]), India, Tranquebar (= Tharanambadi) = **Chrozophora rottleri** (Geiseler) Spreng.

Acknowledgements We would like to thank Roland Butôt, Stacy Dubbeldam, and Nafiesa Ibrahim for their help during the molecular part of this study, which unfortunately could not be published. Jesse Beyer and Eva Putri for their advice on species delimitation and molecular analysis. Brigitta de Wilde-Duyfjes and Ton van der Zon for their advice on species descriptions, and finally Esmée Winkel for her drawings in this paper. Two reviewers, Ben van Ee and Ricarda Riina, are thanked for their very useful remarks and improvements.

REFERENCES

Airy Shaw HK. 1963. Notes on Malaysian and other Asiatic Euphorbiaceae. Kew Bulletin 16: 341–372.
Airy Shaw HK. 1968. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 21: 353–418.
Airy Shaw HK. 1969. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 23: 1–131.
Airy Shaw HK. 1971. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 25: 473–553.
Airy Shaw HK. 1972a (‘1971’). The Euphorbiaceae of Siam. Kew Bulletin 26: 191–363.
Airy Shaw HK. 1972b. Notes on Malesian and other Asiatic Euphorbiaceae. CLVIII. New or noteworthy species of Croton L. Kew Bulletin 27: 78–85.
Airy Shaw HK. 1974a. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 29: 281–331.
Airy Shaw HK. 1974b. Noteworthy Euphorbiaceae from tropial Asia (Burma to New Guinea). Hooker’s Icones Plantarum 38: t. 3701–t. 3725.
Airy Shaw HK. 1975. The Euphorbiaceae of Borneo. Kew Bulletin, Additional Series 4: 1–245.
Airy Shaw HK. 1976. New or noteworthy Australian Euphorbiaceae. Kew Bulletin 31: 341–398.
Airy Shaw HK. 1978a. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 32: 361–418.
Airy Shaw HK. 1978b. Notes on Malesian and other Asiatic Euphorbiaceae. Kew Bulletin 33(1): 25–77.
Airy Shaw HK. 1980a. The Euphorbiaceae of New Guinea, Kew Bulletin, Additional Series 8: 1–243.
Airy Shaw HK. 1980b. The Euphorbiaceae, Platylobeae, of Australia. Kew Bulletin 35: 577–700.
Airy Shaw HK. 1980c. New or noteworthy Australian Euphorbiaceae–II. Muelleria 4: 207–245.
Airy Shaw HK. 1981a. The Euphorbiaceae of Sumatra. Kew Bulletin 36: 239–374.
Airy Shaw HK. 1981b. Notes on Asiatic, Malesian and Melanesian Euphorbiaceae. Kew Bulletin 36: 599–612.
Airy Shaw HK. 1982a. The Euphorbiaceae of Central Malesia (Celebes, Moluccas, Lesser Sunda Is.). Kew Bulletin 37: 1–40.

Airy Shaw HK. 1982b. New Euphorbiaceae from Sumatra, New Guinea, Australia and New Caledonia. Kew Bulletin 37: 377–381.
Airy Shaw HK. 1983. An alphabetical enumeration of the Euphorbiaceae of the Philippine Islands. Royal Botanic Gardens, Kew.
Alston AHG. 1931. Euphorbiaceae. In: Trimen H (ed), A handbook to the Flora of Ceylon 6, Suppl. (part IV): 255–267. Dulau & Co. Ltd., London.
Anshori ZA, Irsyam ASD, Hariri MR, et al. 2020. The occurence of Croton bonplandianus in Java and a new record of Caperonia palustris for Malesia Region. Journal of Tropical Biology and Conservation 17: 273–283.
Arévalo R, van Ee BW, Riina R, et al. 2017. Force of habit: shrubs, trees and contingent evolution of wood anatomical diversity using Croton (Euphorbiaceae) as a model system. Annals of Botany 119: 563–579. https://doi.org/10.1093/aob/mcw243
Backer CA, Bakhuizen van den Brink Jr RC. 1963. Flora of Java 1. N.V. P. Noordhoff, Groningen.
Baillon HE. 1858. Étude générale du groupe des Euphorbiacées. Librairie de Victor Masson, Paris.
Baillon HE. 1864. Species Euphorbiacearum. Euphorbiacées Américaines. Première Partie. Amérique Austro-orientale. Adansonia 4: 257–377.
Balakrishnan NP, Chakrabarty T. 1985 ('1983'). A new variety of Croton caudatus Geisel. (Euphorbiaceae) from Peninsular India. Bulletin of the Botanical Survey of India 25: 190, 191.
Bentham G. 1873. Flora Australiensis 6. L. Reeve & Co., London.
Bentham G. 1880. Euphorbiaceae. In: Bentham G, Hooker JD (eds), Genera Plantarum 3, 1: 239–340. L. Reeve & Co., Londini.
Berry PE, Hipp AL, Wurdack KJ, et al. 2005. Molecular phylogenetics of the giant genus Croton and tribe Crotoneae (Euphorbiaceae sensu stricto) using ITS and trnL-trnF DNA sequence data. American Journal of Botany 92(9): 1520–1534. https://doi.org/10.3732/ajb.92.9.1520
Berry PE, Kainulainen K, van Ee BW. 2017. A Nomenclator of Croton (Euphorbiaceae) in Madagascar, the Comoros Archipelago, and the Mascarene Islands. PhytoKeys 90: 1–87. https://doi.org/10.3897/phytokeys.90.20586.
Beyer J, Esser H-J, Eurlings MCM, et al. 2023. A revision of the genus Croton (Euphorbiaceae) in Sumatra (Indonesia). Blumea 68: 1–25. https://doi.org/10.3767/blumea.2023.68.01.01.
Blanco FM. 1837. Flora de Filipinas. Candido Lopez, Manila.
Blanco FM. 1845. Flora de Filipinas, ed. 2. Miguel Sanchez, Manila.
Blanco FM. 1879. Flora de Filipinas, ed. 3, 3. Establecimiento Tipografico de Plana & Ca., Manila.
Blume CL. 1823. Catalogus van eenige der merkwaardigste zoo in- als uit-heemsche gewassen, te vinden in 's Lands Plantentuin te Buitenzorg. Landsdrukkerij, Batavia.
Blume CL. 1826. Bijdragen tot de Flora van Nederlandsch Indië 12. Ter Lands Drukkerij, Batavia.
Buchanan-Hamilton F. 1824. A commentary on the second part of the Hortus Malabaricus. The Transactions of the Linnean Society of London 14: 171–312.
Burilli NG, Noronha Pereira AP, Caruzo MBR. 2025. Synopsis of Croton section Barhamia subsection Barhamia (Euphorbiaceae). Phytotaxa 705: 162–172. https://doi.org/10.11646/phytotaxa.705.2.3.
Burkill IH. 1914. Croton sparsiflorus, Morong, an American Invader. Agricultural Bulletin of the Federated Malay States 1: 235–237.
Burkill IH. 1935. A dictionary of the Economic Products of the Malay Peninsula 1. Governments of the Straits Settlements, etc., London.
Burman J. 1769. Flora Malabarica. Joannem Schreuderum, Amstelaedami.
Burman NL. 1768. Flora Indica. Cornelium Haek, Lugduni Batavorum, etc.
Carrière E-A, André E, Aurange, et al. 1877. Revue de quelques Plantes nouvelles. Revue Horticole (année 49): 87–90.
Caruzo MBR, Cordeiro I. 2013. Taxonomic revision of Croton section Cleodora (Euphorbiaceae). Phytotaxa 121: 1–41. https://doi.org/10.11646/phytotaxa.121.1.1
Chakrabarty T. 2019. Accepted names, relevant synonyms and typifications of Roxburgh names in Euphorbiaceae, s.l. with reference to Icones at Calcutta. Annals of Plant Sciences 8(10): 3621–3650.
Chakrabarty T, Balakrishnan NP. 1997 ('1992'). A revision of Croton L. (Euphorbiaceae) for Indian subcontinent. Bulletin of the Botanical Survey of India 34: 1–88.
Chang YT. 1982. Notes on Chinese drug "Padou" and "Xiaopadou". Wuyi Science Journal 2: 23, 24
Chang YT. 1983. Materiae ad floram Euphorbiacearum sinensium (II). Guihaia 3: 171–176.
Corner EJH. 1939. Notes on the systematics and distribution of Malayan Phanerogams III. The Gardens' Bulletin, Straits Settlements 10: 239–329.
Corner EJH. 1988. Wayside Trees of Malaya, ed. 3, 1. United Selangor Press, Kuala Lumpur.
Craib WG. 1911. LIII.–Contributions to the Flora of Siam. Bulletin of Miscellaneous Information 1911: 385–474.
Craib WG. 1912. Contributions to the Flora of Siam, Dicotyledones. Aberdeen University Studies 57: 3–210.
Croizat, L. 1940. Notes on Indian Euphorbiaceae: Croton bonplandianum (C. sparsiflorum) and Euphorbia perbacteata. Journal of the Bombay Natural History Society 41: 573–576.
Croizat L. 1942a. On certain Euphorbiaceae from the tropical Far East. Journal of the Arnold Arboretum 23: 29–54.
Croizat L. 1942b. New and critical Euphorbiaceae from the Tropical Far East. Journal of the Arnold Arboretum 23: 495–508.
Croizat L. 1948. Euphorbiaceae. In: Maguire B (ed), Plant explorations in Guiana in 1944, chiefly to the Tafelberg and the Kaieteur Plateau-IV (Continued). Bulletin of the Torrey Botanical Club 75: 400–408.
da Silva MJ, Sodré RC, Berry PE. 2015. Novelties in Croton (Euphorbiaceae) from Goiás, Brazil. Systematic Botany 40: 162–167. https://doi.org/10.1600/036364415X686468
de Jussieu A. 1824. De Euphorbiacearum generibus medicisque earumdem viribus Tentamen. Didot Junioris, Parisiis.
de Lamarck JBAPM. 1786. Encyclopédie Méthodique, Botanique 2(1). Panckoucke, Paris; Plomteux, Liège.
de Loureiro J. 1790. Flora Cochinchinensis 2. J. de Loureiro, Ulyssipone.
Elmer ADE. 1908. A century of new plants. Leaflets of Philippine Botany 1: 272–359.
Esser H-J. 2001. (1512) Proposal to reject the name Croton racemosus (Euphorbiaceae). Taxon 50: 1211–1212.
Esser H-J. 2002. Novelties in Croton (Euphorbiaceae) from Southeast Asia. Novon 12: 42–46. https://doi.org/10.2307/3393236.
Esser H-J. 2005. Croton. In: Chayamarit K, van Welzen PC (eds), Euphorbiaceae (Genera A–F). In: Santisuk T, Larsen K (eds), Flora of Thailand 8 (1): 189–226. The Forest Herbarium, Bangkok.
Esser H-J. 2010. Croton fluviatilis (Euphorbiaceae), a new species from Thailand. Thai Forest Bulletin (Botany) 38: 33–36.
Esser H-J. 2017. The correct name of Croton roxburghii N.P.Balakr., nom. illeg. (Euphorbiaceae). Thai Forest Bulletin

(Botany) 45: 25–28.
Esser H-J, Chayamarit K. 2001. Two new species and a new name in Thai Croton (Euphorbiaceae). Thai Forest Bulletin (Botany) 29: 52–57.
Esser H-J, Veldkamp JF. 2008. X. The Croton argyratus-complex (Euphorbiaceae) in the Malay Peninsula and Sumatra. Flora Malesiana Bulletin 14: 166–171.
Forster PI. 1999. A taxonomic revision of Mallotus Lour. (Euphorbiaceae) in Australia. Austrobaileya 5: 457–497.
Forster PI. 2003. A taxonomic revision of Croton L. (Euphorbiaceae) in Australia. Austrobaileya 6: 349–436.
Frodin DG. 2004. History and concepts of big plant genera. Taxon 53: 753–776. https://doi.org/10.2307/4135449.
Gaertner J. 1790. De Fructibus et Seminibus Plantarum 2(1). Guilielmi Henrici Schrammii, Tubingae.
Gagnepain F. 1922 ('1921'). Euphorbiacées nouvelles d'Indo-Chine (Croton). Bulletin de la Société Botanique de France 68: 548–562.
Gagnepain F. 1925. Croton. In: Lecomte MH (ed), Flore Générale de l'Indo-Chine 5: 256–290. Masson et Cie, Paris.
Geiseler EF. 1807. Crotonis Monographiam. F.A. Grunert, Halle.
Govaerts R, Frodin DG, Radcliffe-Smith A. 2000. World Checklist and Bibliography of Euphorbiaceae (and Pandaceae) 1-4. Royal Botanic Gardens, Kew.
Griffith W. 1848. Itinerary notes of plants collected in the Khasyah and Bootan Mountains, 1837-38, in Affghanisthan and neighbouring countries. 1839 to 1841. J.F. Bellamy, Calcutta.
Haber EA, Kainulainen K, van Ee BW, et al. 2017. Phylogenetic relationships of a major diversification of Croton (Euphorbiaceae) in the western Indian Ocean region. Botanical Journal of the Linnean Society 183(4): 532–544. https://doi.org/10.1093/botlinnean/box004
Hasskarl JK. 1848. Plantae Javanicae Rariores. A. Foerstner, Berolini.
Henderson MR. 1939. The Flora of the limestone hills of the Malay Peninsula. Journal of the Malayan Branch of the Royal Asiatic Society 17: 13–87.
Hooker JD. 1887. The Flora of British India 5. L. Reeve & Co., London.
Hooker WJ, Arnott GAW. 1838 (1830–1841). The Botany of Captain Beechey's Voyage. Henry G. Bohn, London.
Jacquin NJ. 1787. Collectanea 1. Officina Krausiana, Vindobone.
Klotzsch JF. 1841. Neue und weniger gekannte südamerikanische Euphorbiaceen-Gattungen. Archiv für Naturgeschichte 7: 174–204.
Klotzsch JF. 1843a. Euphorbiaceae. In: Bentham G (ed), XIV.–Contributions towards a Flora of South America,– Enumeration of plants collected by Mr. Schomburgk, in British Guiana. The London Journal of Botany 2: 42–52.
Klotzsch JF. 1843b. Euphorbiaceae. In: Meyen FJF (ed), Beiträge zur Botanik, gesammelt auf einer Reise um die Erde. Novorum Actorum Academiae Caesareae Leopoldinae-Carolinae Naturae Curiosorum 19, suppl. 1: 412–421.
Koorders SH. 1898. Verslag eener botanische dienstreis door de Minahasa tevens eerste overzicht der Flora van N.O. Celebes uit een wetenschappelijk en praktisch oogpunt. Mededeelingen van ´s lands Plantentuin 19: 626.
Kuntze O. 1891. Revision Generum Plantarum 2. Arthur Felix, Leipzig, etc.
Kurz S. 1877. Forest Flora of British Burma 2. Office of the Superintendent of Government Printing, Calcutta.
L'Héritier de Brutelle CL. 1784. Stirpes Novae. Typographia Philippi-Dionysii Pierres, Parisiis.
Li PT, Esser H-J. 2008. Croton. In: Wu ZY (CY), Raven PH, Hong DY (eds), Flora of China 11: 258–264. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis.
Linnaeus C. 1753. Species Plantarum 2. Laurentii Salvii, Holmiae.
Linnaeus C. 1754. Genera Plantarum, ed. 5. Laurentii Salvii, Holmiae.
Linnaeus C. 1759. Systema Naturae, ed. 10, 2. Laurentii Salvii, Holmiae.
Llanos A. 1856. Nuevo Apéndice ó suplemento a la lora de Filipinias del P. Fr. Manual Blanco. Memorias de la Real Academia de Ciencias de Madrid 4: 495–505.
Long DG. 1986. Notes relating to the Flora of Bhutan: XI. Euphorbiaceae. Notes from the Royal Botanic Garden Edinburgh 44: 163–173.
Merrill ED. 1917. An interpretation of Rumphius's Herbarium Amboinense. Bureau of Printing, Manila.
Merrill ED. 1918. Species Blancoanae: a critical revision of the Philippine species and plants described by Blanco and by Llanos. Bureau of Printing, Manila.
Merrill ED. 1921a. A bibliographic enumeration of Bornean Plants. Journal of the Straits Branch of the Royal Asiatic Society, Special Number: 327–348 (Eupborbiaceae).
Merrill ED. 1921b. A review of the new species of plants proposed by N.L. Burman in his Flora Indica. The Philippines Journal of Sceince 19: 329–388
Merrill ED. 1923. An Enumeration of Philippine flowering plants 2. Bureau of Printing, Manila.
Merrill ED. 1926. The flora of Banguey Island. The Philippines Journal of Science 29: 341–429.
Merrill ED. 1929. Plantae Elmerianae Borneenses. University of California Press, Berkeley (Univeristy of California Publications in Botany 15).
Merrill ED. 1934. A fifth supplementary list of Hainan plants. Lingnan Science Journal 13: 53–73.
Merrill ED. 1935. A commentary on Loureiro's "Flora Cochinchinensis". Transactions of the American Philosophical Society, new series 24: 1–403.
Miquel FAW. 1859. Flora van Nederlandsch Indië 1 (2). C.G. van der Post, Amsterdam, etc.
Miquel FAW. 1861. Flora van Nederlandsch Indië, Eerste bijvoegsel (2 & 3). C.G. van der Post, Amsterdam, etc.
Moore SLM. 1925. Dr Forbes's Malayan Plants. The Journal of Botany, British and Foreign 63, Supplement.
Morong T, Britton BK. 1893. II. –An Enumeration of the plants collected by Dr. Thomas Morong in Paraguay, 1888–1890. Annals of the New York Academy of Sciences 7: 45–280.
Müller Argoviensis J. 1864. Neue Euphorbiaceen des Herbarium Hooker in Kew, auszugsweise vorläufig mitgetheilt aus dem Manuscript für De Candolle's Prodomus. Flora 47: 465–487.
Müller Argoviensis J. 1865. Euphorbiaceae, vorläufige Mittheilungen aus dem für De Candolle's Prodromus bestimmten Manuscript über diese Familie. Linnaea 18: 1–224
Müller Argoviensis. 1866. Euphorbiaceae excl. Euphorbieae. In: de Candolle ALPP (ed), Prodromus Systematis Naturalis Regni Vegetabilis 15: 189–1286.
Noronha F. 1790. Relatio Plantarum Javanensium. Verhandelingen van het Bataviasch Genootschap der Kunsten en Wetenschappen 5, art. 4: 1–28.
Pax F, Hoffmann K. 1931. Euphorbiaceae. In: Engler HGA, Harms H (eds), Die natürlichen Pflanzenfamilien, ed. 2, 19C: 11–223. Wilhelm Engelmann, Leipzig.
Perrottet GGS. 1825. Catalogue Raissoné. Mémoires de la Société Linnéenne de Paris 3: 89–151.
Persoon CH. 1907. Synopsis Plantarum 2(2). Treuttel & Würtrh, Parisiis Lutetiorum; J.G. Cottam, Tuningae.
Philcox D. 1997. Euphorbiaceae. In: Dassanayake MD, Clayton WD (eds), A Revised Handbook to the Flora of

Ceylon 11: 80–283. A.A. Balkema, Rotterdam.
Pinto-Silva, N.P., Souza. K.F. de, et al. 2023. Trichomes in the megadiverse genus Croton (Euphorbiaceae): a revised classification, identification parameters and standardized terminology. Bot. J. Linn. Soc. 203: 37–49.
Radcliffe-Smith A. 1986. Euphorbiaceae. In: Nasir E, Ali SI (eds), Flora of Pakistan 172. Department of Botany, University of Karachi, Karachi.
Radcliffe-Smith A. 2001. Genera Euphorbiacearum. Royal Botanic Gardens, Kew.
Raeuschel EA. 1797. Nomenclator Botanicus. Joan Gottlob Feind, Lipsiae.
Rafinesque CS. 1838. Sylva Telluriana. Published by the author, Philadelphia.
Retzius AJ. 1788. Observationes Botanicae 5. Siegfried Lebrecht Crusium, Lipsiae.
Ridley HN. 1924. The Flora of the Malay Peninsula 3. L. Reeve & Co., Ltd., London.
Riina R, Berry PE, Secco RDS, et al. 2018. Reassessment of Croton sect. Cleodora (Euphorbiaceae) points to the Amazon Basin as its main center of diversity. Annals of the Missouri Botanical Garden 10: 330–349. https://doi.org/10.3417/2018131.
Riina R, Berry PE, van Ee BW. 2009. Molecular Phylogenetics of the Dragon's Blood Croton Section Cyclostigma (Euphorbiaceae): A Polyphyletic Assemblage Unraveled. Systematic Botany 34: 360–374. https://doi.org/10.1600/036364409788606415.
Riina R, van Ee BW, Wiedenhoeft AC, et al. 2010. Sectional rearrangement of arborescent clades of Croton (Euphorbiaceae) in South America Evolution of arillate seeds and a new species, Croton domatifer. Taxon 59(4): 1147-1160. https://doi.org/10.1002/tax.594014
Riina R., van Ee BW, Rossi Caruzo MB, et al. 2021. The Neotropical Croton sect. Geiseleria (Euphorbiaceae): Classification update, phylogenetic framework, and seven new species from South America. Annals of the Missouri Botanical Garden 106: 111166.
Rottler, J.P. 1803. Botanische Bemerkungen auf der Hin- und Rückreise von Trankenbar nach Madras. Neue Schriften, Gesellschaft Naturforschender Freunde zu Berlin 4: 180–224, pl. 3–5
Roxburgh W. 1814. Hortus Bengalensis. Mission Press, Calcutta.
Roxburgh W. 1832. Flora Indica ed. 1832, 3. W. Thacker and Co., Calcutta, etc.
Rumphius GE. 1743. Herbarium Amboinense 4. François Changuion, Jan Catuffe, Hermanus Uytwerf, Amsterdam.
Schumann K, Lauterbach K. 1905. Nachträge zur Flora der Deutschen Schutzgebiete in der Südsee. Verlag von Gebrüder Borntraeger, Leipzig.
Shecut JLEW. 1806. Flora Carolinaeensis. Published by the author, Charleston.
Sierra SEC, Aparicio M, Gebraad MJH, et al. 2007. The morphological range in Mallotus (Euphorbiaceae) and a taxonomic revision of its section Rottleropsis (including Axenfeldia) in Malesia, Thailand and Africa. Blumea 52: 21–113.
Sierra SEC, van Welzen PC, Slik JWF. 2005. A taxonomic revision of Mallotus section Philippinensis (former section Rottlera – Euphorbiaceae) in Malesia and Thailand. Blumea 50: 221–248.
Silva OLM, Riina R, Cordeiro I. 2020. Phylogeny and biogeography of Astraea with new insights into the evolutionary history of Crotoneae (Euphorbiaceae). Molecular Phylogenetics and Evolution 145. https://doi.org/10.1016/j.ympev.2020.106738.
Sinclair J. 1956. Croton hirtus an Alien new to Malaya. Gardens Bulletin Singapore 15: 1–3.
Small JK. 1913. Euphorbiaceae. In: Britton NL, Brown A (eds), An Illustrated Flora of the Northern United States, ed. 2, 2: 452–477. Charles Scriber's sons, New York.
Smith JJ. 1910. Euphorbiaceae. In: Koorders SH, Valeton T (eds), Bijdrage tot de kennis der boomsoorten op Java 12. Mededeelingen uitgaande van het Departement van Landbandbout in Nederlandsch-Indië 10: 9–637.
Spanoghe JB. 1841. Prodromus Florae Timorensis. Linnaea 15: 314–350.
Sprengel C. 1821. Neue Entdeckungen im ganzen Umfang der Pflanzenkunde 2. Fleischer, Leipzig.
Sprengel C. 1826. Systema Vegetabilium ed. 16, 3. Librariae Dieterichianae, Gottingae.
Steinmann VW. 2021. A Synopsis of Croton (Euphorbiaceae) in Michoacán, Mexico. Taxonomy 2021, 1(4): 395–424. https://doi.org/10.3390/taxonomy1040029
Teijsmann JE, Binnendijk S. 1866. Catalogus Plantarum quae Horto Botanico Bogoriensi coluntur. Ter Lands-drukkerij, Batavia.
Thaowetsuwan P, Riina R, Ronse De Craene LP. 2024. Floral morphology and development reveal extreme diversification in some species of Croton (Euphorbiaceae). Journal of Plant Research. https://doi.org/10.1007/s10265-024-01572-x
Thaowetsuwan P, Ritchie S, Riina R, et al. 2020. Divergent developmental pathways among staminate and pistillate flowers of some unusual Croton (Euphorbiaceae). Frontiers in Ecology and Evolution 8: 253. https://doi.org/10.3389/fevo.2020.00253
Thiers B. Continuously updated. Index Herbariorum. New York Botanical Garden's Virtual Herbarium. Available from: https://sweetgum.nybg.org/ih/ (last accessed: 27 June 2023).
Thin NN. 1986. The Species of the genus Croton L. (Euphorbiaceae) in the Vietnamese Flora. Journal of Biology (Vietnam) 8: 28–33.
Thunberg CP. 1784. Flora Japonica. I.G. Mülleriano, Lipsiae.
Thunberg CP. 1825. Florula Javanica. Palmblad et C., Upsaliae.
Thwaites GHK. 1861. Enumeratio Plantarum Zeylaniae 4. Dulau & Co., London.
Turland NJ, Wiersema JH, Barrie FR, et al. 2025. International Code of Nomenclature for Algae, Fungi, and Plants (Madrid Code). Regum Vegetabile 162. University of Chicago Press, Chicago. https://doi.org/10.7208/chicago/9780226839479.001.0001
Vahl MH. 1790. Symbolae Botanicae 1. Nicolaus Möller et Filius, Hauniae.
Vahl MH. 1791. Symbolae Botanicae 2. Nicolaus Möller et Filius, Hauniae.
Valduga E. 2021. Croton (Euphorbiaceae) in the Pampas grasslands. Thesis, Universidade Federal do Rio Grande do Sul, Porto Aleggre.
van Ee BW, Forster PI, Berry PE. 2015. Phylogenetic relationships and a new sectional classification of Croton (Euphorbiaceae) in Australia. Australian Systematic Botany 28(4): 219–233. https://doi.org/10.1071/SB15016
van Ee BW, Riina R, Berry PE. 2011. A revised infrageneric classification and molecular phylogeny of new world Croton (Euphorbiaceae). Taxon 60(3): 791–823. https://doi.org/10.1002/tax.603013
van Rheede tot Drakestein HA. 1690. Horti Malabarici 10. Joannis van Someren & Joannis van Dyck, Amstelodami.
van Welzen PC. 1999. Revision and phylogeny of subtribes Chrozophorinae and Doryxylinae (Euphorbiaceae) in Malesia and Thailand. Blumea 44: 411–436.
van Welzen PC. 2018. The genus Baliospermum (Euphorbiaceae) in Malesia. Blumea 63: 125–129.
van Welzen PC, Esser HJ, Middleton DJ, et al. 2024. Flora

of Singapore precursors, 45: Typifications and nomenclatural clarifications in Euphorbiaceae, Phyllanthaceae, Picrodendraceae, Rutaceae and Sapindaceae for the Flora of Singapore. The Gardens' Bulletin Singapore 76(2): 183–214.

van Welzen PC, Tyas KN, Eviyarni, et al. 1999. The Malesian species of Melanolepis (Euphorbiaceae). Blumea 44: 437–446.

Vitarelli NC, Riina, R, Caruzo MBR et al. 2015. Foliar secretory structures in Crotoneae (Euphorbiaceae): Diversity, anatomy, and evolutionary significance. American Journal of Botany 102: 833–847.

von Mueller F. 1864. Fragmenta Phytographiae Australiae 4. Joannis Ferris, Melbourne.

Wallich N. 1840. Report of Dr. Wallich on the Botanic Garden of Calcutta to G.A. Bushby. In: Plants despatched from and received into the Calcutta Botanic Garden. Bengal Public Proceedings, London (see also Esser 2017).

Wallich N. 1847. A numerical list of dried specimens in the East India Companys Museum collected under the superintendence of Dr. Wallich of the Company's botanic garden at Calcutta. Published by the author, London.

Webster GL. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

Webster GL. 1993. A provisional synopsis of the sections of the genus Croton (Euphorbiaceae). Taxon 42: 793–823. https://doi.org/10.2307/1223265

Webster GL. 1994. Synopsis of the Genera and Suprageneric Taxa of Euphorbiaceae. Annals of the Missouri Botanical Garden 81(1): 33. https://doi.org/10.2307/2399909

Webster GL. 2014. Euphorbiaceae. In: Kubitzki K (ed), The Families and Genera of Vascular Plants 11: 51–216. Springer-Verlag, Berlin, Heidelberg.

Webster GL, Burch DG. 1967. Family 97 Euphorbiaceae. In: Woodson Jr RE, Schery R (eds), Flora of Panama, part VI. Annals of the Missouri Botanical Garden 54: 211–350.

Whitmore TC. 1973. Tree Flora of Malaya 2. Longman, London.

Willdenow CL. 1805. Species Plantarum ed. 4, 4(1). G.C. Nauk, Berolini.

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. https://doi.org/10.3732/ajb.92.8.1397.

Zhang T, Liu Z, Sun X, et al. 2022. Botany, traditional uses, phytochemistry, pharmacological and toxicological effects of Croton tiglium Linn.: a comprehensive review. Journal of Pharmacy and Pharmacology 74: 1061–1084.

Zollinger H. 1856. Over de soorten van Rottlera van den botanischen tuin te Buitenzorg en in het herbarium van Zollinger en Moritzi, alsmede over eenige verwante geslachten uit de familie Euphorbiaceën. Verhandelingen der Natuurkundige Vereeniging in Nederlandsch Indië 1 (Acta Societatis Regiae Scientiarum Indo-Neêrlandicae): part 4: 1–32.

IDENTIFICATION LIST

Only material seen of Java and the Lesser Sunda Islands with collector numbers is cited.

1 = *C. adumbratus* Croizat

2 = *C. argyratus* Blume

3 = *C. bonplandianus* Baill.

4 = *C. brevipetiolatus* Duijn

5 = *C. cascarilloides* Raeusch.

6 = *C. caudatus* Geiseler

7 = *C. glabrescens* Miq.

8 = *C. hasskarlianus* Müll.Arg.

9 = *C. hirtus* L'Hér.

10 = *C. laevifolius* Blume

11 = *C. pseudoverticillatus* Duijn

12 = *C. scalaeus* J.Beyer

13 = *C. sumbensis* Duijn

14 = *C. tetraglandulosus* Duijn

15 = *C. tiglium* L.

16 = *C. tomentellus* F.Muell.

Altmann 575: 6.

Backer 1896: 2; 17863: 14; 26418: 9; 27415: 5; 28120: 5; 29364: 5; 32647: 9 – Bakhuizen van den Brink Sr. 1506: 10; 3140: 6; 3173: 2; 3523: 12; 4419: 4; 5440: 9; 6081: 2; 7070: 10 – Bakhuizen van den Brink Jr. 966: 9 – Becking 52: 2 – Beumée 1409: 6; 3808: 2; 4724: 6 – Blume 1339: 2; 1473: 10; 1499: 2; 2165a: 10 – Bogor Botanic Garden XI.B.84: 6; XV.C.17: 6; XV.K.B.XVIII.2: 9 – Boschproefstation Ja 2034: 2.

Coert 1208: 9; 1815: 9 – Cowie 11097:13; 11388: 3.

Dakkus 115: 6 – de Voogd 1765: 15; 2244: 13 – Dihm 429: 9 – Dorgelo 2226: 6 – J. Dransfield 999: 2.

Elbert 3611: 15; 3664: 15; 3694: 16; 3697: 15; 3746: 15; 4217: 15.

Franck 549: 2.

Hallier 347a: 9; 347b: 9 – Holstvoogd 130: 9.

Ja series 2034: 2; 2232: 16; 6182: 2; 6199: 2 – Junghuhn '97': 4.

Kalshoven 85: 2 – Karsten 28: 9 – Karta 308: 2 – Koorders 2031: 2; 2032: 2; 2033: 2; 2034: 2; 2036: 2; 2037: 2; 2038: 2; 2040: 2; 2041: 2; 2042: 2; 2046: 2; 2047: 2; 2048: 2; 2049: 2; 2050: 2; 2053: 15; 2054: 15; 2055: 15; 2056: 15; 2057: 15; 2058: 15; 2060: 2; 2063: 15; 2609: 15; 11456: 2; 11742: 2; 11743: 2; 11744: 2; 11962: 10; 12380: 2; 12826: 2; 13099: 2; 14426: 15; 15371: 10; 15685: 2; 15783: 15; 20059: 2; 20572: 6; 20574: 15; 20607: 15; 20772: 15; 22024: 2; 23327: 15; 23873: 2; 24570: 2; 24617: 7; 24817: 2; 25559: 4; 25616: 10; 26287: 4; 26884: 2; 26893: 2; 27149: 2; 27364: 2; 27379: 2; 28932: 2; 29784: 2; 30560: 2; 31115: 2; 32845: 4; 33002: 2; 34229: 2; 38455: 15; 38643: 15; 38788: 15; 39443: 6; 39520: 4 – Kooy 315: 15 – Kostermans 19311: 2; 22057: 5; 22064: 13 – Kostermans, Kuswata, Soegeng & Soepadmo KK+SS 287: 2.

Lam 2290: 2 – Landbouwcons. I: 15.

McDonald & Afriastini 3388: 4 – Meijer 110644: 7 – Metzner 158: 10 – Mousset 1052: 6.

Nedi & Idjan 8: 9.

Powell 436: 6; 444: 6. – Powell & Chey 453: 6.

Sarip 72: 2; 137: 2 – Sauveur 128: 15 – Schiffner 2143: 9 – Schmutz 184: 15; 212: 15; 586: 15; 622: 13; 844: 11; 1130: 1; 1656: 5; 1889: 11; 1911: 1; 2768: 1; 3584: 1; 4215: 5; 3161: 5.

Thorenaar 226: 7.

van Borssum Waalkes 562: 2; 595: 4 – van Ooststroom 12573: 9 – van Steenis 17478: 6; 18013: 15; 18021: 15 – Verheijen 151: 15; 1078: 5; 1079: 5; 1080: 5; 1183: 15; 1184: 15; 1185: 15; 2104: 5; 2306: 13; 2611: 5; 3331: 5; 3442: 1; 3444: 10; 3483: 13; 4484: 10.

Walsh 33: 15 – Wasjijat Ja 6182: 2; Ja 6199: 2 – Widjaja 1204: 7 – Winckel 1789: 10; 1842: 10 – Wirawan 396: 2 – Wiriadinata 1057: 2 – Woerjantoro 72: 6; 73: 6.

Zollinger 642: 6; 852: 2; 963-Z: 2; 1779: 8; 2702: 7; 3212: 2; 3805: 14; 3809: 2.