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RESEARCH ARTICLE

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A revision of the genus *Croton* (*Euphorbiaceae*) in Sumatra (Indonesia)

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Key words

Croton
Crotonoideae
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ITS
Malesia
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Sumatra
taxonomic revision

Abstract *Croton* (*Euphorbiaceae*) is a very large genus of over 1 200 species of herbs, shrubs and trees occurring mainly in the (sub)tropics. The major diversity of *Croton* is within the Neotropics; and there are comparatively few species in South-East Asia. This contribution provides a revision of *Croton* from the Sumatran region in Indonesia, including descriptions and a determination key. In total sixteen species are recognized for Sumatra, including four species new to science, *C. beccarii*, *C. scalaeus*, *C. simalurensis*, and *C. viridifolius*. Two new synonyms and lectotypification of numerous names are also included. Besides a taxonomic treatment, a molecular analysis, using the nuclear ribosomal internal transcribed spacer (ITS), based on former data extended with Sumatran species, was performed to create a phylogeny that places the Sumatran species in a phylogenetic context. In total 13 new sequences were created, which were combined with 56 sequences obtained from GenBank. The results from the phylogenetic analysis, based on Bayesian inference, are in line with the phylogeny as published for mainly the Australian species of *Croton* by Van Ee et al. (2015).

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INTRODUCTION

Croton L. is one of the 'giant genera' of angiosperms (Frodin 2004), with an estimated total number of species between 1 200 and 1 300 (Govaerts et al. 2000). The genus comprises herbs, shrubs, trees and occasionally lianas and occurs worldwide in the subtropics and tropics as an ecologically prominent part of the secondary vegetation (Webster 1993). Although being a pantropical genus, *Croton* has the highest diversity in the Neotropics and in Madagascar, with around two thirds of the species occurring in the New World (Radcliffe-Smith 2001, Van Ee et al. 2011). Here, the genus description in Radcliffe-Smith (2001) is mainly used to characterize *Croton*. However, all descriptions are based on Sumatran material unless stated differently. Typical for *Croton* is the presence of variously coloured stellate or lepidote trichomes, clear to coloured latex, stipules linear to triangular, leaves alternate to crowded, sometimes pseudo-verticillate, with two basal extrafloral nectaries, inflorescences terminal or subterminal, two sexes of flowers in the same terminal spicate or racemose thyrsoid inflorescence, with the staminate flowers often fasciculate per node in the upper part of the axis and the pistillate flowers usually single per node at the basal part, flowers actinomorphic, sepals 5, ovate-elliptic, usually fused at base, mostly 5 petals per flower, free, staminate flowers with stamens inflexed in bud, pistillate flowers pubescent at least in parts, petals much smaller than the sepals or more often absent, 3-locular small to large capsules, 1 seed per locule. However, worldwide many exceptions exist, e.g., species lacking the extrafloral leaf nectaries, dioecy, bisexual cymules, completely free to almost completely fused sepals, pistillate flowers with 6–8 sepals, ovaries with more locules.

Within *Euphorbiaceae*, *Croton* belongs to the subfamily *Crotonoideae* (Webster 1994, 2014, Radcliffe-Smith 2001, Wurdack et al. 2005). The subfamily is characterized by the exine pattern of the pollen, which comprises triangular supratectal elements (Nowicke 1994) and the presence of articulate or inarticulate lacticifers with reddish or yellowish latex (Webster 1994). The subfamily has been divided into as many as 12 tribes (Webster 1994, 2014, Radcliffe-Smith 2001), but molecular research shows that the subfamily and some of its tribes are not monophyletic (Wurdack et al. 2005). The tribe *Crotoneae* Dumort., however, seems to consist of a well-supported clade (Berry et al. 2005) when small changes are made to the traditional classification of Webster (1994). Taking these changes into account, then tribe *Crotoneae* consists of seven genera: *Acidocroton* Griseb., *Astraea* Klotzsch, *Brasiliocroton* P.E.Berry & Cordeiro, *Croton*, *Ophellantha* Standl., *Sagotia* Baill., and *Sandwithia* Lanj., whereby most of the diversity within the tribe is present in the 30 species covered by the small genera beside *Croton* (Van Ee et al. 2011, Silva et al. 2020). *Sagotia* and *Sandwithia* together form a sister clade with the rest of the tribe (Berry et al. 2005).

Most research on *Croton* since the last sectional overview by Webster (1993), including species concepts, phylogeny or revisions, concerned the Neotropical species of the genus (Van Ee et al. 2011), whereby the molecular phylogeny of the New World *Croton* by Van Ee et al. (2011) is the most comprehensive. Other research either revises sections of *Croton*, like *Cleodora* (Klotzsch) Baill. (Caruzo & Cordeiro 2013, Riina et al. 2018), *Geiseleria* (A.Gray) Baill. (Riina et al. 2021), *Heptallon* (Raf.) Müll.Arg. (Van Ee & Berry 2010a) and *Cyclostigma* Griseb.

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(Riina et al. 2009, Feio et al. 2018), or revises *Croton* for regions such as the Cerrado in Brazil (Da Silva et al. 2015) and Cuba (Van Ee et al. 2008). Although *Croton* studies from outside the New World are rare, there are some extensive studies from Madagascar (Berry et al. 2017, Haber et al. 2017, Kainulainen et al. 2017), Australia (Airy Shaw 1980a, Forster 2003, Van Ee et al. 2015) and South East Asia, Thailand (Esser 2002b, 2005), Malay Peninsula (Whitmore 1973), and the various island groups: Sumatra (Airy Shaw 1981a), Java (Backer & Bakhuizen van den Brink 1963), Borneo (Airy Shaw 1975), New Guinea (Airy Shaw 1980b), a checklist for central Malesia (Airy Shaw 1982a) and a checklist for the Philippines (Airy Shaw 1983).

In this study, the *Croton* species of Sumatra are revised. During the last complete revision of *Euphorbiaceae* for this island, nine species were recognized (Airy Shaw 1981a): *C. argyratus* Blume, *C. cascarilloides* Raeusch., *C. caudatus* Geiseler, *C. erythrostachys* Hook.f., *C. glandulosus* var. *hirtus* (L'Her.) Müll.Arg. (here considered as *Croton hirtus* L'Her. based on Webster & Burch 1967 and Sinclair 1956), *C. heterocarpus* Müll.Arg., *C. hookeri* Croizat, *C. oblongus* Burm.f. and *C. tiglium* L. Of these nine species, *C. hirtus* is an invasive or introduced taxon in Sumatra, originally only occurring in the Neotropics, with less than a handful of records in Asia (Airy Shaw 1981a). From the eight certain *Croton* species in Sumatra, *C. oblongus* and *C. tiglium* are both placed in *Croton* section *Tiglium* (Klotzsch) Baill., *C. caudatus* in section *Cascarilla* Griseb. and *C. heterocarpus* in section *Furcaria* Boivin ex Baill. (Webster 1993). *Croton cascarilloides* is yet unplaced, Webster (1993) suggested section *Anisophyllum* Baill. and section *Monguia* Baill. *Croton argyratus* was placed in the later created *Croton* section *Argyrati* B.W.van Ee, P.I.Forst. & P.E.Berry (Van Ee et al. 2015), and Van Ee et al. reassigned *C. caudatus* to the monotypic section *Caudati* B.W.van Ee, P.I.Forst. & P.E.Berry. Van Ee & Berry (2010b) show that as *C. tiglium* is the lectotype for the genus, it should be placed in *C.* section *Croton* (autonym rule) and not *C.* section *Tiglium*, which means that *C. oblongus* should also be reassigned to section *Croton* (but see Discussion for this species). Besides the nine species listed by Airy Shaw (1981a), *C. adumbrates* Croizat (likely section *Argyrati*) also occurs on Sumatra, as it appears to be a distinct species and not a synonym of *C. argyratus* (Esser & Veldkamp 2008), bringing the total to ten known species.

Besides the taxonomic revision, the position of the species in the phylogeny of Van Ee et al. (2011, 2015) will be checked by sequencing the ITS and *trn*L-F markers.

MATERIAL AND METHODS

Taxonomic treatment

This study was performed at Naturalis Biodiversity Center. The collections of L (Leiden herbarium) and U (former Utrecht herbarium), both stored at Naturalis, formed the backbone material of this study. Type specimens, if sufficiently detailed, were examined from high resolution pictures via the Global Plants facility of JSTOR (https://plants.jstor.org/). Other specimens named in the nomenclature were looked at and located in the local online database of the concerned herbarium. All scanned images of herbarium specimens seen are marked with an * in the nomenclature sections, actual specimens seen are indicated with an !. Barcodes are used as unique identifiers when a herbarium houses several duplicates of a type collection.

The species concept was based on morphological characters, and specimens from neighbouring areas were checked (see notes under species) to confirm the species delimitation. The main morphological characters used for the species delimitations were: habit and growth form, indumentum, leaf size and shape, location and form of the basal extrafloral leaf glands, presence of marginal leaf glands, shape of the leaf base, margin, apex and venation of the leaf, inflorescence form, form and size of pistillate flowers and capsules. Although leaf shape and indumentum density can vary within a species, they were useful for delimitation between species. For each species, the nomenclature was checked. The identification key for the Sumatran species is based only on vegetative characters, as these are always present. For a list of all studied specimens and their identification see the Identification List at the end (includes material checked from outside Sumatra).

Molecular marker selection

Based on earlier performed molecular studies of *Croton* and other *Euphorbiaceae* (Berry et al. 2005, Wurdack et al. 2005, Van Ee et al. 2011, 2015, Van Welzen et al. 2021) the nuclear ribosomal internal transcribed spacer (ITS1 and ITS2) and the plasmid *trn*L-F markers were chosen for inferring the phylogeny. In earlier studies these markers proved to be phylogenetically informative at the species and sectional level. All DNA samples newly sequenced in the present study were extracted from (old) herbarium specimens, for which PCR amplification of DNA is more difficult than for material obtained from silica-dried samples or fresh material. For *Croton*, ITS is the marker most easily sequenced from herbarium specimens, and *trn*L-F, although less successful than ITS, is the chloroplast marker most readily sequenced from the same specimens (Van Ee et al. 2015).

Taxonomic sampling

Because this study is about Sumatran *Croton*, a sample set of mainly Old World species was selected. All earlier published sequences (Berry et al. 2005, Van Ee et al. 2008, 2011, 2015, Pang et al. 2010, Rinthong et al. 2011) were combined in the matrix created by Van Ee et al. (2015), which was focused on Australian *Croton*, and, therefore, contained nearly all current Old World sequences of this genus. These sequences were obtained from GenBank (https://www.ncbi.nlm.nih.gov/genbank/). *Astraea lobata* (L.) Klotzsch and *Brasiliocroton mamoninha* P.E.Berry & Cordeiro were selected as outgroups for *Croton* based on the findings of Berry et al. (2005) and Wurdack et al. (2005). Five New World *Croton* taxa were selected as additional outgroup taxa for the Old World *Croton*. Of these five species one, *C. hirtus*, occurs in Sumatra as an invasive species. The rest of the matrix obtained from GenBank, previously included in Van Ee et al. (2015), contains twelve species of Africa and Madagascar, seven from mainland Asia, twelve from Australia and eight species from Malesia. Additionally, 13 specimens distributed over eight species were newly sequenced for this work and added to the matrix, which comprised 13 of the 16 species present on Sumatra. Species names, vouchers and accession numbers are given in the Appendix for all analysed sequences.

DNA extraction, amplification and sequencing

Most of the herbarium specimens of *Croton* from Sumatra are of very old age, from the late 19th century until 1980, and in a degraded state due to outdated collection and drying methods. Therefore, the extraction method and primers used were chosen for the highest chance of yield instead of the best quality. Initial DNA extraction of the Sumatran material was done using small (c. 1 cm^2) pieces of leaves from herbarium specimens, using the CTAB DNA extraction method (Doyle & Doyle 1987). Due to the age and state of the material, ITS was sequenced in two parts. First ITS1 with primers M13F-17SE and M13R-5.8I1 and secondly ITS2 with primers M13F-5.8I2 and M13R-26SE (Sun et al. 1994). Amplifications for ITS were conducted in a total volume of 25 µL containing 1 µL template 20× diluted DNA, 13.4 µL mQ water (Ultrapure, Uithoorn, The Netherlands), 5 µL

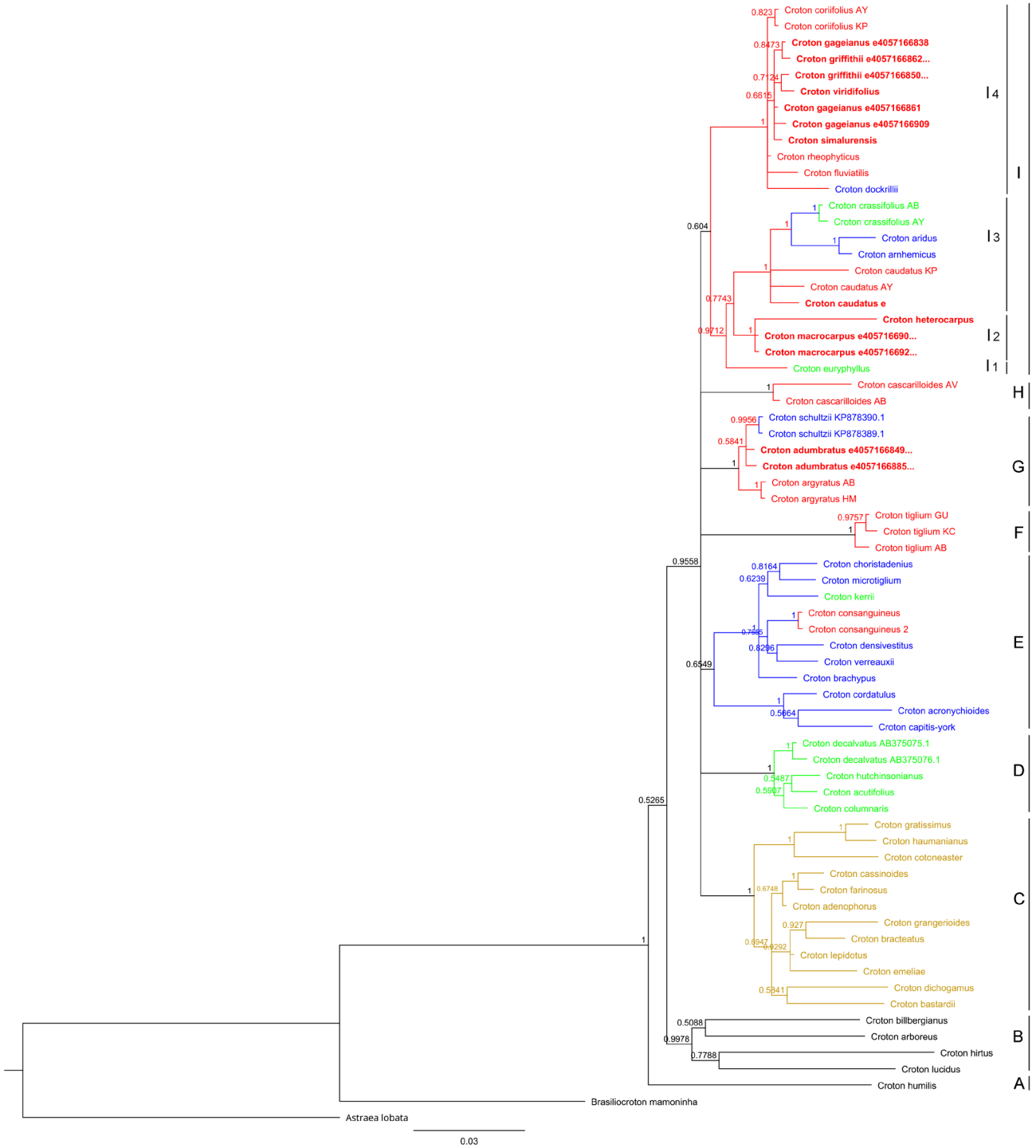

Fig. 1 Bayesian phylogram based on ITS sequences excluding the 5.8S region. The values at nodes represent the Bayesian-inference posterior-probability support values. *Astraea* and *Brasiliocroton* are outgroups. Black names: New World, yellowish brown: Africa–Madagascar, green: mainland Asia, blue: Australia–West Pacific, red: Malesia. Accessions with **bold** names correspond to the newly sequenced taxa, all ocurring in Sumatra. Bar: nucleotide substitutions.

5× PCR buffer (Thermo Fisher Scientific, Waltham, USA), 1 µL 25mM $MgCL_2$ (Qaigen, Valencia, USA), 1 µL 10 mg/ml BSA (Promega, Madison, USA), 1.3 µL of each primer with a concentration of 10 pMol/uL, 0.5 µL 2.5 mM dNTP and 0.5 µL Phire Green Hot Start II DNA Polymerase (Thermo Fisher Scientific, Waltham USA). Amplification conditions included an initial denaturation of 60 s at 98 °C, followed by 40 cycles of 10 s denaturation at 98 °C, 10 s annealing at 52 °C, and 20 s extension at 72 °C, followed by a final 5 min extension at 72 °C. A disadvantage of this method is that the 5.8S region between the two ITS regions is not sequenced. For the *trn*L-F region, the primers used were M13F-*trn*L-g and M13R-*trn*L-h (Taberlet et al. 2007) which are renowned for amplifying old and degraded material due to the small size of the target fragment (~100 bp). These proved to be too small and did not contain any phylogenetic information at the species level and are thus ignored in the Bayesian analysis. High throughput Sequencing took place at Baseclear (Leiden, the Netherlands).

Alignment and phylogenetic analyses

The multiple chromatograms obtained for each marker of each accession were edited, and contiguous sequences assembled using Geneious v. 2019 2.3 (http://www.geneious.com; Kearse et al. 2012). Sequences were aligned with the MAFFT plugin (Katoh & Standley 2013) within Geneious and afterwards manually checked and edited. Because ITS was sequenced in two parts, it was necessary to scaffold the two non-overlapping pairs of chromatograms by using the existing full *Croton* sequences

obtained from GenBank. The gap, which included the whole 5.8S region, was filled with placeholder 'any' bases (N). The data were analysed with Bayesian inference using MrBayes (Ronquist & Huelsenbeck 2003), as plugins within Geneious and separate with MrBayes v. 3.2.7a (Ronquist & Huelsenbeck 2003). The Bayesian inference tree (Fig. 1) was created by using 4 heated chains, heating parameter = 0.2, 10 000 000 generations, starting from random trees, default priors, sampling every 1 000 generations, and discarding the first 25 % of the sampled trees. The convergence of the chains was checked with Tracer v. 1.7.2 (Rambaut et al. 2018). Bayesian Posterior Probabilities (PP) of 0.95 or more are considered to be strong indicators of node support.

RESULTS

Taxonomic treatment

Our study increased the total number of species of *Croton* occurring on Sumatra from nine (Airy Shaw 1981a) to 16 species. In comparison with the species named by Airy Shaw (1981a), *C. coriifolius* Airy Shaw, *C. gageianus* P.T.Li, *C. griffithii* Hook.f., and *C. macrocarpus* Ridl. were new for Sumatra. As mentioned in the introduction, *C. adumbratus* was separated from *C. argyratus* by Esser & Veldkamp (2008). Two species included by Airy Shaw (1981a) do actually not occur in Sumatra, namely *C. erythrostachys* and *C. hookeri*. *Croton erytrostachys* was only known from one collection located in L, but this specimen (*de Wilde & de Wilde-Duyfjes 18103*) was wrongly identified and appears to be *C. gageianus*. The two *C. hookeri* collections (*Brooks 7606* and *Yates 2491*) from Sumatra were already indicated by Airy Shaw as doubtful and could not be found during this study. Specimens identified as *C. oblongus*, a name that gave much confusion in its interpretation because of the very bad original drawing (Burman 1768), appeared to be *C. laevifolius* Blume (Blume 1826). Of the 16 species accepted here to occur on Sumatra, four are new to science. The name *C. viridifolius* J.Beyer, sp. nov., refers to the light green colour of the leaves after drying, a character unique for Malesian *Croton*. Other distinct characters within Sumatra are the low number of lateral veins (only 4–6), the small leaves and flowers, the short inflorescences and the narrow leaf shape. *Croton simalurensis* J.Beyer, sp. nov., is mainly known from the island of Simalur or Simeulue, 150 km west of Sumatra. All specimens of this species were previously placed within *C. laevifolius*, but clearly differ in multiple important aspects. The most prominent and easiest difference is in the location of the leaf glands. In *C. laevifolius* these are always present on the very apex of the petiole, while in *C. simalurensis* they are basilaminar (away from the petiole, as shown in Fig. 2c). Other character differences are the very different fruit sizes and indumentum abundance and density. *Croton beccarii* J.Beyer, sp. nov., is named after Odoardo Beccari, an Italian collector in the 19th century, who collected and described species based on material that he collected in Sumatra, Borneo, and New Guinea. This species was also previously placed within *C. laevifolius*, and the main distinctive characters are the densely pubescent sepals of the pistillate flowers and the densely pubescent capsules. The name *C. scalaeus* J.Beyer, sp. nov., indicates that it differs in the indumentum, lepidote trichomes instead of the stellate trichomes, from all other Sumatran *Croton* species except the very different *C. adumbratus* and *C. cascariolloides*. Morphologically it most closely resembles *C. coriifolius*, which is present on both Sumatra and Borneo, but differs in indumentum and leaf glands.

Molecular analysis

In total, 13 ITS sequences distributed over 8 species, from Sumatra, were successfully generated for the study, whereas

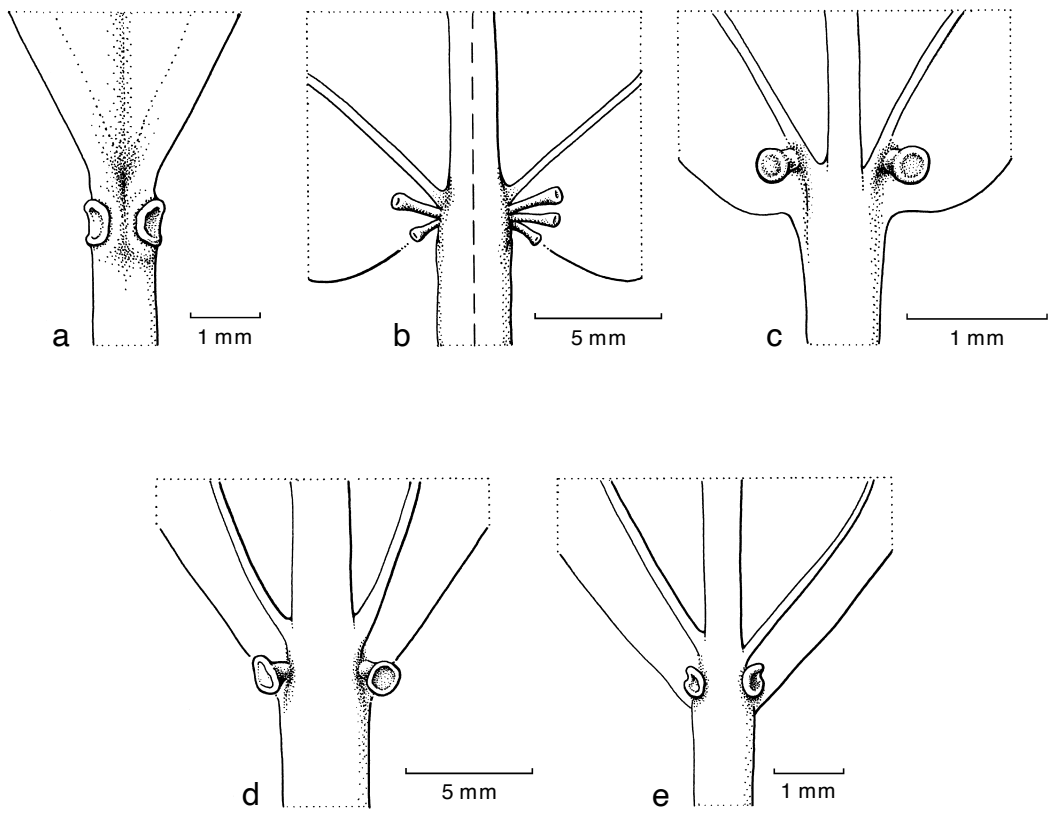

Fig. 2 Different types of leaf glands. a. *Croton heterocarpus*, glands sessile and placed more adaxially on the apex of the petiole; b. *C. caudatus*, glands 1–3 pairs, distinctly stalked and abaxially on the midrib base; c. *C. viridifolius*, glands slightly stalked and located either on the leaf blade base or as in drawing on the side veins; d. *C. macrocarpus*: glands with a thick stalk located on the midrib base; e. *C. adumbratus*: glands sessile on the midrib base (a: *Lörzing 13830*; b: *Forbes 2989*; c: *Kleinhoonte 460*; d: *de Wilde & de Wilde-Duyfjes 20590*; e: *de Wilde & de Wilde-Duyfjes 19604*; all L). — Illustration by Esmée Winkel, 2021.

56 sequences distributed over 45 species were obtained from GenBank (Appendix). The Sumatran species for which molecular data were not successfully sequenced were *C. beccarii*, *C. laevifolius*, and *C. scalaeus*. Tracer (Rambaut et al. 2018) showed that all variables had Effective Sample Sizes (ESS values) far above 200, showing good convergence of the chains.

Most data used to create the phylogeny are from Van Ee et al. (2015), therefore, the results will be compared with those of Van Ee et al. (2015). In accordance with Van Ee et al. (2015) the Bayesian phylogram (Fig. 1: group A) shows the New World *C. humilus* L. to split off first, just like the New World basal clade (Fig. 1: group B). In Fig. 1 all other clades form a polytomy; here Van Ee et al.'s f. 1 (2015) shows more resolution as there is a major split between African/Arabian/Madagascar taxa and the mainly Asian/Australian/Pacific taxa (including a few African ones). The African/Madagascar clade (posterior probability, pp, 1) in Fig. 1 (group C) deviates slightly from Van Ee et al. (2005: f. 1), Madagascan *C. cotoneaster* Müll.Arg. groups with the two African taxa (*C. gratissimus* Burch. and *C. haumanianus* J.Léonard), all other clades in this group correspond with Van Ee et al. (2015). The Asian clade of *C. acutifolius* Esser, *C. columnaris* Airy Shaw, *C. decalvatus* Esser, and *C. hutchinsonianus* Hosseus (pp 1; Fig. 1: Group D) also forms a clade in Van Ee et al. (2015). The Australian clade has low support (pp 0.6459 in Fig. 1: Group E) and consists of a polytomy in Van Ee et al. (2015); it comprises two clades in Fig. 1, both with high support (pp 1), the clade of Australian *C. acronychioides* F.Muell., *C. capitis-york* Airy Shaw, and *C. cordatulus* Airy Shaw corresponds with the top clade in Van Ee et al.'s f. 1 (2015), the other clade represents species spread over a polytomy in Van Ee et al. (2015). *Croton tiglium* (Fig. 1: group F) and *C. cascarilloides* (Fig. 1: Group H) form separate clades (both pp 1) in a polytomy in our and Van Ee et al.'s study (2015). The clade of Australian *C. schultzii* Benth. and Asian *C. argyratus* (pp 1; Fig. 1: group G) is extended with *C. adumbratus*. The top clade has low support (pp 0.604 in Fig. 1: group I) and splits into a clade (pp 0.9712; Fig. 1: group I_1) with *C. euryphyllus* W.W.Sm. (in polytomy in Van Ee et al. 2015) basally to a clade of *C. heterocarpus* and *C. macrocarpus* (new, not in van Ee et al. 2015; pp 1, Fig. 1: group I_2) and a clade (pp 1; Fig. 1: group I_3) with basally in a polytomy *C. caudatus* and two branches, one with Asian *C. crassifolius* Geiseler and one with Australian *C. arnhemicus* Müll.Arg. and *C. aridus* P.I.Forst. (corresponding with Van Ee et al. 2015). The top clade (pp 1; Fig. 1: group I_4) has basally in a polytomy Australian *C. dockrillii* Airy Shaw, *C. fluviatilis* Esser (Riau pocket) and a clade containing the other Riau pocket species *C. rheophyticus* Airy Shaw with now newly added most Sumatran species. Within this clade the groupings are not well supported.

DISCUSSION

In this revision, a total of 16 species of *Croton* are recognised for Sumatra, including the Bangka – Belitung and Riau islands east of the main island, as well as smaller islands like Simalur, Nias, and Siberut west of it. Of these 16 species, five are new species records for Sumatra but already known from Malesia, two changed names and four are new to science.

Part of the herbarium material available for this study was not suitable due to its state and age. Not all specimens yielded useable DNA. The six samples (two samples each of *C. beccarii*, *C. laevifolius*, and *C. scalaeus*) not included failed during the extraction and amplification phase, despite multiple attempts with different PCR reaction mixes and markers. This was expected, because they were the oldest and worst in preservation quality. Different DNA techniques, e.g., HybSeq, or younger material may yield sequences for *C. beccarii*, *C. laevifolius*, and *C. scalaeus.* Another disadvantage of the used primers is that the 5.8S region of ITS is missing, which might have increased the resolution of the phylogeny.

The phylogeny (Fig. 1) has a similar structure to that of Van Ee et al. (2015), with an unresolved back bone (polytomy) for the Old World taxa. The main differences of our phylogenetic pattern with the previous one (Van Ee et al. 2015) are the slightly higher clade supports at some of the deep nodes, which is expected with the inclusion of a plastid marker in Van Ee et al. (2015). Our phylogenetic results do not provide enough resolution at the species level within any of the four clades where Sumatran species were recovered.

The ITS phylogenetic analysis places the Sumatran *Croton* species in four well-supported clades, similar to Van Ee et al. (2015), the latter with an emphasis on Australian species but including species from Africa, Asia, and the New World. The most interesting group is formed by the species in the 'Riau pocket' group (Fig. 1: group I_4), a term coined by Corner (1960). This group is extended and now comprises the whole of Sumatra, not only the Riau Province. Formerly, only rheophytic species from Riau were included in the phylogeny of Van Ee et al. (2015), but with the extension also non-rheophytic species are present. The group, now incorporating several Sumatran species (and perhaps also the *C. laevifolius* species group), may, with improved phylogenies, deserve recognition at sectional level. They all have very small caruncles, lack colleters (secretory glands at the tips of the lamina serrations) and show similarities in trichomes and leaf shape. This group is sister to *C.* section *Dockrilliorum* B.W.van Ee, P.I.Forst. & P.E.Berry, which contains the rheophytic *C. dockrillii* (Fig. 1: clade I_3). Biogeographically, a distribution linking Sumatra with Australia is strange, but future inclusion of the other Malesian species, especially those of New Guinea, will likely result in a phylogeny that shows dispersal/vicariance along various stepping stones through Malesia.

The *C. caudatus* specimen that was added (Fig. 1, **bold** in group I_3) groups with the other *C. caudatus* specimen, but the polytomy, already shown in Van Ee et al. (2015), is not resolved. *Croton caudatus*, the only Asian *Croton* climber/scrambler species, is widespread in S.E. Asia and Malesia and biogeographically it can connect Asian and Australian groups. *Croton heterocarpus* and *C. macrocarpus* (Fig. 1: group I_2) form a sister clade to group I_3 (Fig. 1). Based on the presence of colleters they may in the future be recognized as a section if all Asian *Croton* are sequenced and phylogenetically analysed.

The Asian *C. adumbratus* nicely groups with the Asian *C. argyratus* and the Australian *C. schultzii*. *Croton adumbratus* and *C. schultzii* were often considered to be synonyms of *C. argyratus* (Esser & Veldkamp 2008, Van Ee et al. 2015, respectively). *Croton adumbratus* can be classified in *C.* section *Argyrati* (together with *C. argyratus* and *C. schultzii*).

The new taxa here described used to be placed (misidentified) under the very diverse 'dumpster' species *C. oblongus*. This species was described based on material from India, but the original publication lacked sensible information (Burman 1768), as the description and the attached figure were so limited that most *Croton* in the Old World would fit the description and figure (Corner 1939). Therefore, the decision to regard *C. laevifolius* as a synonym of *C. oblongus* (Merrill 1921b) is strange, especially because of the very good description of *C. laevifolius* provided by Smith (1910). *Croton laevifolius* was described by Blume (1826) from material from Java, and the lectotype selected and other Javanese specimens compare with the Sumatran material, which is therefore regarded as *C. laevifolius*. Even with this species taken out, the remaining specimens identified as *C. oblongus* were still highly diverse, and appeared

to cover six well-delimited species (*C. beccarii*, *C. coriifolius*, *C. griffithii, C. laevifolius, C. scalaeus*, and *C. simalurensis*) based on characters like the location and shape of the basal leaf glands and structure of fruit and indumentum. The remaining material identified as *C. oblongus* in the Naturalis Herbaria should be critically re-examined, and likely most specimens can be identified with the key provided here to their proper name, though possibly other species, not occurring on Sumatra, are likely part of this confusion. In summary, *C. oblongus* should be regarded as a dubious name, which cannot be interpreted.

The species in the Riau pocket group (group I_4 in Fig. 1) comprise rheophytic species. Riina et al. (2010) mentioned that rheophytic species in the neotropics have seeds with arils and are likely dispersed by fish eating the arils. However, the Sumatran species lack arils and the seeds have very small caruncles and are likely not dispersed by fish.

TAXONOMIC TREATMENT

Morphologically important characters in the Sumatran species of Croton

Habit

All native Sumatran species are woody, either as strangling climbers (*C. caudatus*), shrubs, or trees up to 30 m tall and with a diameter to 90 cm. In contrast with all native species, the introduced *C. hirtus* is an annual herb.

Indumentum

The indumentum of *Croton* consists of stellate trichomes with free radii in all directions, lepidote trichomes with partly to completely fused radii in one plane, and some simple trichomes in the floral parts. The amount of indumentum can differ from complete and densely pubescent (no epidermis visible) to totally glabrous. Young branchlets are usually densely pubescent and differ in the length of time in becoming glabrous.

Leaf morphology

Leaves are alternate to pseudo-verticillate. The size of the blades differs from 2.5 by 0.7 cm for *C. viridifolius* to 35 by 10 cm in *C. macrocarpus*. The leaves always have a distinct petiole of variable length, often grooved above. The petioles are pubescent to glabrous depending on the species. The blade can be chartaceous, membranous or rarely subcoriaceous (*C. coriifolius*, *C. macrocarpus*, and *C. scalaeus*). The leaf blades are simple and vary in shape, base, and apex. The blade margins are entire to serrate, with teeth occasionally topped with a marginal leaf gland (*C. caudatus* and *C. macrocarpus*) or a patch of simple trichomes (*C. heterocarpus*). The venation is pinnate and sometimes palmate (triplinerved), usually distinct and visible on both sides of the leaf. The secondary veins are always looped and closed near the margin in the Sumatran species, while higher order nerves are reticulate.

Glands

Croton species have various secretory structures in the leaves (e.g., Vitarelli et al. 2015). Externally the most obvious are the petiolar/basilaminar extrafloral nectaries. The shape, size and location of these nectaries (Fig. 2) is one of the most important characters in species delimitation on Sumatra and in *Croton* in general. The glands come in one, two, or rarely three (*C. caudatus*) pairs that are either sessile, stalked or less commonly sessile but elevated without a distinct stalk. For species with more than one pair of glands, the number of pairs is variable per individual. Lastly, the location of the glands is fixed for the individual species, varying between abaxial on the base of the midrib, abaxial on the base of the leaf blade close but not on the midrib, abaxial on the very apex of the petiole, or adaxial on the very apex of the petiole.

Besides the extrafloral nectaries on the leaves or petiole, also the tips of the lamina serrations generally end in a secretory gland called a colleter.

Inflorescence and flowers

Staminate and pistillate flowers can be found in bisexual terminal or subterminal unbranched elongated thyrsoid inflorescences. The basal part is pistillate with one pistillate flower per node, whereas the apical part is staminate with a single to usually multiple flowers per cymule. Flowers are grouped in condensed cymules, the pistillate flowers solitary or sometimes together with lateral staminate flowers in the same cymule. The staminate part is usually caducous during fruit set. Like many other *Euphorbiaceae*, dichogamy is common, i.e., pistillate flowers flower before the staminate ones (protogynous), thus promoting outcrossing. Species or specimens with completely staminate or pistillate inflorescences are rarely found. The flowers consist of five sepals, which are fused at the base, and five free petals (mostly absent in the pistillate flowers). Differences between the species on Sumatra are generally found in the shape of the sepals and petals, and the hairiness of the sepals. Also, the number of stamens can differ between species, but is mostly between ten and twelve. The style is here defined as the joined part on top of the ovary, which splits (generally) into 3 arms, which are termed the stigma, which are only once divided except for *C. cascarilloides*, where they are divided twice. Outside Sumatra the diversity in number of stamens and stigma forms is larger.

Fruits and seeds

Croton has 3-locular small (diam up to 2.5 mm) to large (diam up to 28 mm) capsular fruits. The capsules are usually globose or obovoid and can vary between deeply sulcate and not sulcate at all. When fruits are present, most species on Sumatra can easily be determined due to the differences in shapes and indumentum between the species. In Sumatra all but *C. caudatus* have glabrous seeds, either with a small and indistinct to distinct apical caruncle (fleshy part).

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; P.T.Li & Esser (2008) 258; G.L.Webster (2014) 169, f. 39. — Lectotype (designated by Small 1913: 454): *Croton tiglium* L.

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

(Description based on the Sumatran species). Trees, shrubs or herbs, sometimes climbing, monoecious; branching usually pseudo-verticillate; latex colourless or red. *Indumentum* consisting of stellate to lepidote, variously coloured trichomes; simple trichomes in inflorescences. *Stipules* linear to triangular, eglandular, caducous to quite persistent. *Leaves* alternate to crowded, sometimes pseudo-verticillate; petiole distinct, eglandular except sometimes the apex; blade simple, symmetric, variable in shape and margin, pubescent to a various degree, always with a pair of glands on the lower (seldom upper) base of the blade or midrib or on the petiole apex, sometimes with additional marginal glands; venation usually visible on both surfaces, pinnate or triplinerved, secondary veins arching and hardly to distinctly looped and closed near the margin (but always distinctly looped at the apex), tertiary veinlets reticulate. *Inflorescences* terminal or subterminal, unbranched, thyrsoid, bisexual, basal part pistillate with usually 1 flower per cymule

(or additionally with a few staminate flowers), the apical part staminate with 1–3(–5) flowers per cymule, caducous at fruit set, more rarely completely pistillate or staminate; pubescent at least in parts; bracts usually triangular-ovate, eglandular or rarely glandular, persistent or caducous. *Flowers* actinomorphic, pedicellate; sepals 5, ovate-elliptic to triangular, fused at base; petals if present 5, free. *Staminate flowers*: sepals usually ending with a patch of simple trichomes on apex; petals similar to sepals but less pubescent and with a ciliate-lanate margin; disc lobed, receptacle pilose (the flowers therefore filled with whitish simple trichomes c. 1 mm long); stamens (8–)10–20(–30), inflexed in bud, free, filaments longer than the anthers, anthers 2-thecate, basifixed, opening latrorse with lengthwise slits; pistillode absent. *Pistillate flowers* pubescent at least in parts; petals usually absent otherwise much smaller than the sepals; staminodes absent; disc annular; ovary 3-locular, smooth or muriculate, always pubescent, with 1 ovule per carpel; style short or absent, stigmas 3, apically bifid to various degree, sometimes even quadrifid. *Fruits* capsular, 3-locular, small to large, usually sulcate, smooth or shallowly muriculate, usually densely pubescent. *Seeds* 3 per fruit, dry, ellipsoid, brown, glabrous or rarely with scattered trichomes, smooth, with a caruncle.

Between 1200 and 1300 species (Govaerts et al. 2000) occurring pantropically, but mainly found in the Neotropics (2/3 of species) and Madagascar. Sixteen species on Sumatra.

KEY TO CROTON SPECIES OF SUMATRA

1. Annual herbs, up to 0.4 m high . . . . . .10. *C. hirtus*
1. Climbers, shrubs or trees, with distinctly woody stem, higher than 0.4 m 2
2. Young and mature leaves completely and densely pubescent abaxially, appearing silvery-whitish to golden or brownish, epidermis not visible (not even with a hand lens) 3
2. Mature leaves with dense to scattered trichomes abaxially or glabrous, not completely silvery-whitish or golden-brown, epidermis visible 5
3. Indumentum consisting of only lepidote trichomes, with 60–80 fused radii. Higher order leaf nerves very indistinct. Capsules distinctly 3-lobed, obovoid, deeply sulcate . . . . . 4. *C. cascarilloides*
3. Indumentum consisting of stellate to lepidote trichomes, with less than 40 fused radii or radii free. Higher order leaf nerves distinct. Capsules globose, not to hardly sulcate . 4
4. Leaves (2–)2.4–3.5 times longer than wide, the very base rounded to subcordate. Basal leaf glands (0.1–)0.5–0.9 mm diam. Staminate flowers 4–5 mm diam. Pistillate flowers 4.5–6 mm diam. Capsules 5–7 mm high 1. *C. adumbratus*
4. Leaves 1.5–2.3(–2.9) times longer than wide, the very base distinctly cordate and slightly peltate. Basal leaf glands 1–1.5 mm diam. Staminate flowers 5–6.5 mm diam. Pistillate flowers 8–9 mm diam. Capsules (10–)13–19 mm high . . . . . 2. *C. argyratus*
5. Leaves basally slightly to distinctly triplinerved, secondary veins 3–7 pairs 6
5. Leaves basally not or very indistinctly triplinerved, secondary veins (4–)6–17 pairs 8
6. Leaf blade narrowly elliptic, 2.5–7.2 by 0.7–2.2 cm. Inflorescences to 2.5 cm long . . . . . 16. *C. viridifolius*
6. Leaf blade elliptic, more than 2.5 cm wide. Inflorescences longer than 2.5 cm 7
7. Plant a straggling shrub, woody climber or liana, distinctly pubescent. Leaf blade with marginal glands. Capsules with thick woody pericarp . . . . . 5. *C. caudatus*
7. Plant a non-climbing shrub or tree, soon glabrescent. Leaf blade without marginal leaf glands. Capsules with thin fragile pericarp . . . . . 15. *C. tiglium*
8. Leaf margin (sub)serrate to crenate, never entire, teeth either topped with a patch of simple trichomes or distinct marginal glands (colleters) present 9
8. Leaf margin entire to shallowly serrate (rarely distinctly serrate), teeth never topped with a patch of simple trichomes; marginal glands (colleters) absent 10
9. Leaf blade obovate (to elliptic), 2.5–10(–12) by 1.2–4.1 cm. Capsules c. 5 mm high, c. 5 mm diam . . . . . 9. *C. heterocarpus*
9. Leaf blade elliptic, 15–30(–35) by 5–10 cm. Capsules c. 28 mm high, c. 22 mm diam . . . . 12. *C. macrocarpus*
10. Leaf glands abaxially on midrib base or leaf base. Abaxial leaf side with scattered but distinct trichomes to densely pubescent 11
10. Leaf glands abaxially on the very apex of the petiole. Abaxial leaf side (sub)glabrous 14
11. Leaf glands lateral on the abaxial base of the midrib . 12
11. Leaf glands abaxially at the very base of the leaf, close to but not on the midrib 13
12. Stellate trichomes on leaves 0.4–0.9 mm diam, with (11–)15–25(–30) free radii. Leaf blade narrowly elliptic, (3.1–)3.4–5.2 times longer than wide, abaxial side slightly to densely pubescent. Inflorescences shorter than 5.5 cm. Capsules globose, slightly sulcate . . . . . 7. *C. gageianus*
12. Stellate trichomes on leaves 0.1–0.4(–0.6) mm diam, with 11–17 free radii. Leaf blade elliptic, (1.9–)2.3–3.3(–3.8) times longer than wide, abaxial side with scattered trichomes to densely pubescent. Inflorescences longer than 6 cm. Capsules distinctly 3-lobed, obovoid, extremely sulcate . . . . . 8. *C. griffithii*
13. Leaf glands slightly to distinctly stalked discs, (0.4–)0.6–1 mm diam, stalk 0.1–0.3 mm long. Leaf blade elliptic to obovate, 5.5–18 by 2.7–7.5 cm, 1.7–2.8 times longer than wide; secondary veins 8–10 pairs. Inflorescences (7–)10–20 cm long. — Simalur/Simeulue Island . . . . . 14. *C. simalurensis*
13. Leaf glands slightly stalked discs, 0.2–0.4 mm diam, stalk 0.1–0.2 mm long. Leaf blade narrowly elliptic, 2.5–7.2 by 0.7–2.2 cm, 2.4–4.2 times longer than wide; secondary veins 4–6 pairs. Inflorescences 0.5–2.5 cm long. — Sumatera Barat (West Sumatra) Province 16. *C. viridifolius*
14. Indumentum on leaves consisting of only lepidote trichomes, flat, with 20–40 completely fused radii . . 13. *C. scalaeus*
14. Indumentum on leaves consisting of only stellate trichomes, flat to slightly porrect, often with a central short porrect radius, with 8–20(–30) free to basally slightly fused trichomes 15
15. Leaf glands sessile (Fig. 2a or 2e), flat, 0.8–1.5 mm diam . . . . . 6. *C. coriifolius*
15. Leaf glands stalked or sessile but elevated (Fig. 2c or 2d), 0.1–0.6(–1) mm diam, stalk 0.1–0.5(–1) mm high . . . 16
16. Stipules filiform to subulate, 0.3–0.5 mm wide. Inflorescences 2–7 cm long. Sepals (both pistillate and staminate) with scattered trichomes to densely pubescent on outside. Capsules globose, 4–5 by 4–5 mm, rough, hardly sulcate, very densely pubescent . . . . . 3. *C. beccarii*
16. Stipules subulate, 0.5–1 mm wide. Inflorescences 5–23 cm long. Sepals (both pistillate and staminate) glabrous to subglabrous on outside. Capsules distinctly 3-lobed, obovoid, 5–8(–13) by 4–7 mm, smooth, sulcate, with scattered trichomes . . . . . 11. *C. laevifolius*

1. *Croton adumbratus* Croizat — Fig. 2e, 3a–c

Croton adumbratus Croizat (1942b) 495; Esser & Veldkamp (2008) 167, f. 1a–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.

Trees or shrubs, up to 15 m tall, dbh up to 60 cm; young branchlets densely pubescent, hardly glabrescent. *Outer bark* smooth, whitish grey to pale dark green; inner bark pinkish to red. *Indumentum* consisting of lepidote trichomes on leaves to stellate-lepidote trichomes on stems, diam 0.2–0.3 mm on leaves, 0.3–0.5 mm on stems, flat, with 25–40 fused radii (c. 20 free to fused radii on young branchlets), with small brownish centre (then appearing silvery-hyaline) or brown throughout. *Stipules* filiform to subulate, (2–)4–10 by 0.2–1 mm, densely pubescent on both sides, caducous. *Leaves* alternate; petiole 1.5–5(–7) cm long, slightly grooved above, densely pubescent, sulcate; glands abaxial as flat discs lateral on the very base of the midrib, (0.1–)0.5–0.9 diam, sessile but distinct (Fig. 2e); blade elliptic to slightly ovate, 6–21 by (2–)3.5–8.5 cm, (2–)2.4–3.5 times longer than wide, membranous to chartaceous, base cuneate with the very base rounded to subcordate, margin entire, apex acuminate, adaxial side glabrous (rarely with scattered trichomes on young leaves), abaxial side very densely and completely silvery to brownish pubescent with the surface not visible; venation distinct, sunken above, basally not to slightly triplinerved, lateral veins 6–10 pairs, higher order nerves distinct. *Inflorescences* racemose, 1(–3) per node, (5–)8–12(–15) cm long, erect, bisexual (occasionally one sex only), white to greenish, densely pubescent all over, basally 3–8 pistillate flowers, apically 20 or more staminate flowers; bracts triangular-ovate, 1–1.5 by 0.5–1 mm, densely pubescent outside, inside subglabrous. *Staminate flowers* 4–5 mm diam; pedicel 2–3 mm long, round, densely pubescent; sepals ovate, 2–2.5 by 1–2 mm, densely pubescent outside, lanate on margin; petals triangular-ovate, 2–2.5 by 0.8–1.5 mm, outside subglabrous; stamens 9–11, free, filaments 2–3 mm long, anthers c. 1 by 0.4 mm. *Pistillate flowers* 4.5–6 diam; pedicel 1–5 mm long, sulcate, densely pubescent; sepals ovate to almost oblong, 2.5–4 by 1.3–2 mm, fused at base, longer than ovary, outside densely pubescent, inside with scattered trichomes; petals ensiform, c. 2 by 0.5 mm, usually absent; ovary subglobose, 1.5–2.5 by 1.5–2 mm, densely yellowish brown pubescent; style 0.2–0.5 mm long, densely pubescent; stigmas 3–5 mm long, once divided to 2.5–4 mm from apex, pubescent near base. *Capsules* globose, 5–7 mm high by 6–7 mm diam, hardly 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 carunculate.

Distribution — Malay Peninsula, Sumatra (Aceh, Sumatera Utara, Sumatera Barat, Jambi, Sumatera Selatan, Bangka-Belitung), Borneo (Kalimantan Barat) and Sulawesi.

Habitat & Ecology — Primary and secondary lowland forests. Altitude: sea level to 750 m, often on sandstone but also on limestone hills. Flowering: March–April, July–August, October–November; fruiting: March, July, October.

Affinities — Based on the phylogenetic analysis and similar morphology to be classified in *Croton* section *Argyrati* (Van Ee et al. 2015).

Vernacular names — Bali anghiri (Simalungen), Kayu bulan (Sumatera Selatan), Kayu semangkil (Bangka).

Note — Several plants were collected with galls (*Krukoff 4022*, *4281*; *De Wilde & de Wilde-Duyfjes 20147*). These leafy galls, looking like Brussels sprouts, seem to be very characteristic for *C. adumbratus* and are not seen in any other *Croton* from Western Malesia (Esser & Veldkamp 2008); other collections with galls (not seen, from other areas): *Alvins 264*, *KEP (Abdullah) 33070*.

2. *Croton argyratus* Blume — Fig. 3d–f

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. (1925) 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-f. 81; Chakrab. & N.P.Balakr. (1997 '1992') 22, f. 1, map 1; Esser (2005) 193, f. 45, plate X: 2; Esser & Veldkamp (2008) 169, f. 1d–f; Chakrab. (2019) 629. — *Croton argyratus* Blume var. *genuinus* Müll. Arg. (1866) 526, nom. inval. — *Oxydectes argyrata* (Blume) Kuntze (1891) 611. — Lectotype (designated by Esser & Veldkamp 2008): *Blume s.n.* (lecto L [L0233566]!; possible isolecto A [00106971]!, 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 (1826), 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: 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 here): *Zollinger 963-Z* (lecto U [U 007936]!, as Unknown s.n.; isolecto A [0010017]!), Indonesia, Java.

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

Croton argyratus Blume var. *brevipes* Müll.Arg. (1866) 527. — Lectotype (designated by Esser & Veldkamp 2008): *Zollinger 3212* (lecto G-DC [G00311485]!; isolecto A [00047510]!, G [G00434384]!, [G00434386]!), Indonesia, Java.

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

Croton avellaneus Croizat (1942b) 498. — Type: *BS (Ramos & Edaño) 43977* (holo A [00047539]!; iso BM!, G!, W [1930-0001714]!), Philippines, Sulu Archipelago, Tawitawi.

Trees, to 30 m tall, dbh to 40 cm; young branchlets densely pubescent, slightly glabrescent. *Outer bark* smooth, dark grey; inner bark white to pink. *Indumentum* consisting of stellate to stellate-lepidote, hyaline trichomes with a small brownish centre on leaves and sepals, creamish brown trichomes on leaf veins and capsules, 0.2–0.4 mm diam, flat, often with a central porrect radius, with 15–25 free to slightly fused radii. *Stipules* filiform to subulate, (3–)8–20(–25) by 0.3–2 mm, densely pubescent on both sides, caducous. *Leaves* alternate; petiole (2–)4–12(–15) cm long, sulcate, slightly grooved above, densely pubescent; glands as flat discs lateral on the very base of the midrib, 1–1.5 mm diam, sessile, often hard to spot; blade elliptic to slightly ovate, 9–22 by 5.5–10 cm, 1.5–2.3(–2.9) times longer than wide, chartaceous, base obtuse to rounded with very base distinctly cordate and slightly peltate, margin entire to subserrate, apex acuminate, adaxial side glabrous, abaxial side completely and densely silvery-pubescent without visible surface and not glabrescent, brownish trichomes only on the largest veins and on immature leaves; venation distinct, sunken above, raised below, very indistinct to distinct with 3 or 5 prominent basal veins, secondary veins 8–10 pairs, higher order nerves distinct. *Inflorescences* 1(–3) per node, 10–22(–30) cm long, bisexual (occasionally one sex only), densely pubescent all over, basally 7–17(–26) pistillate flowers, rarely 1–2 staminate flowers in the same cymule of a pistillate flower, apically 1–3 staminate flowers per node; bracts

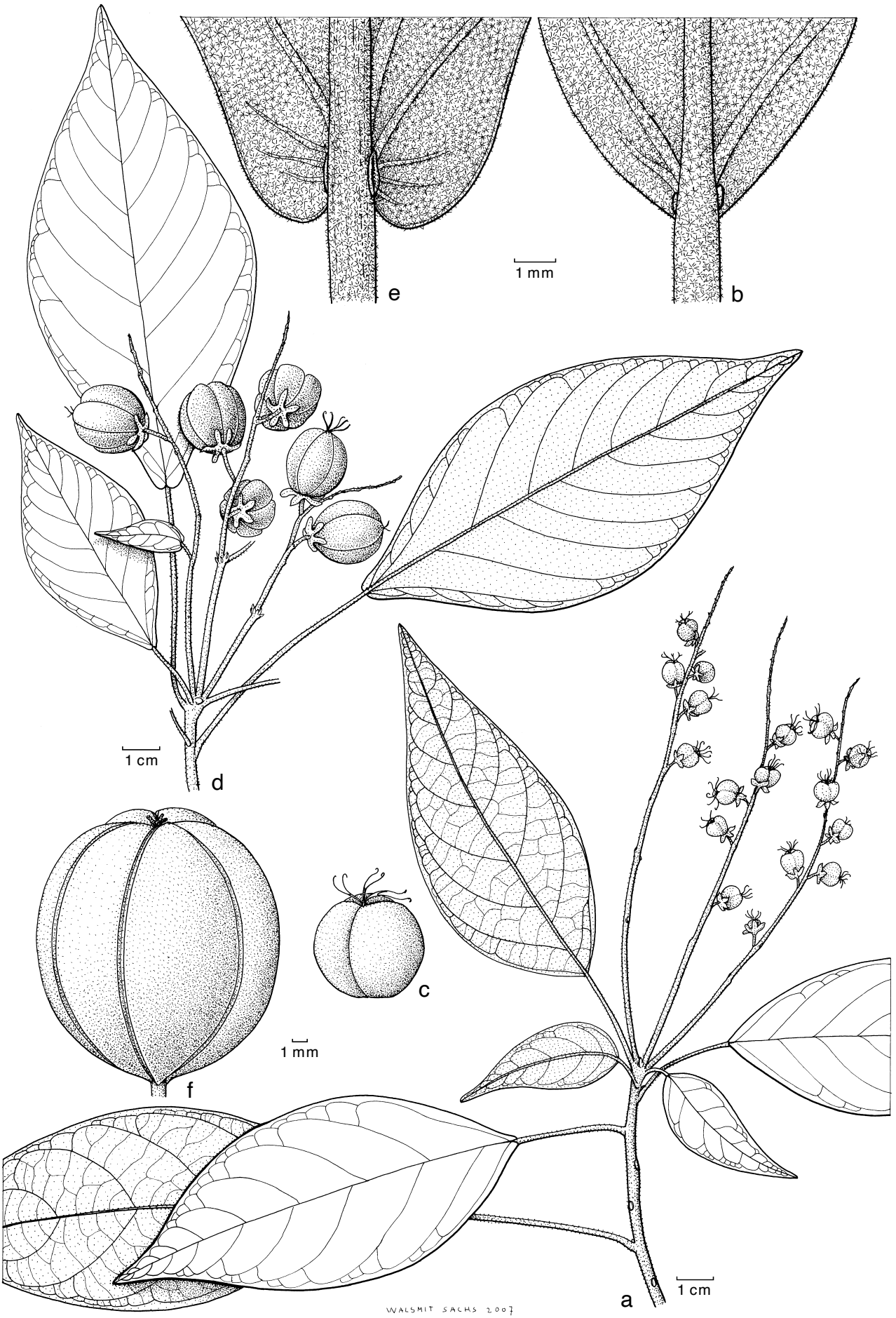

Fig. 3 a–c. *Croton adumbratus* Croizat. a. Habit; b. detail of cuneate leaf base, abaxial view; c. fruit. — d–f. *Croton argyratus* Blume: d. Habit; e. detail of narrowly emarginate leaf base, abaxial view; f. fruit (a–c: *de Wilde & de Wilde-Duyfjes 19604*; d–f: *Chellia KEP 104397*; all L). — Illustration by Anita Walsmit Sachs, 2007.

ensiform to triangular-ovate, 1.3–2 by 0.5–0.8 mm, densely pubescent outside, inside subglabrous, caducous. *Staminate flowers* 5–6.5 mm diam; pedicel 4–6 mm long, round, densely pubescent; sepals triangular-ovate, c. 2.5 by 0.5 mm, outside densely pubescent; petals oblong, c. 2.8 by 1 mm, outside glabrous to slightly lanate; stamens 11–15, filaments 3–4 mm long, anthers 1–1.5 by 0.2–0.5 mm. *Pistillate flowers* 8–9 mm diam; pedicel 4–6 mm long (up to 12 mm in fruit), sulcate, densely pubescent; sepals elliptic, 4–6 by 2–3 mm, apex obtuse (to acute), outside densely pubescent, inside slightly lanate, much longer than ovary; petals elliptic, c. 3 by 1.5 mm, apex acute, outside densely pubescent, inside with scattered trichomes, margin lanate, usually absent; ovary globose, 2–3 by 2–3 mm, densely yellowish brown pubescent; style less than 0.4 mm long, densely pubescent; stigmas 6–8 mm long, once divided to 5–7.5 mm from apex, pubescent near base. *Capsules* globose (sometimes near obovoid), (10–)13–19 mm high by (10–)12–18 mm diam, not sulcate, densely pubescent; pericarp very thick (1–2 mm) and woody; columella 12–15 mm long. *Seeds* ellipsoid, flattened, 11–14 by 8–11 mm, glabrous, with a very small caruncle.

Distribution — Thailand, *Malesia*: Peninsular Malaysia, Sumatra (Aceh, Sumatera Utara, Sumatera Barat, Riau, Jambi, Sumatera Selatan, Lampung), Java, Borneo, Philippines, Sulawesi, Lesser Sunda Islands, Moluccas.

Habitat & Ecology — Open areas, hill slopes and partly disturbed places in evergreen primary forest, secondary forest or mountain forest, at rocky streams and roadsides. Altitude: sea level to 1200 m. Flowering: April – June, September, December; fruiting: August – November, January.

Affinities — *Croton* section *Argyrati* (Van Ee et al. 2015).

Vernacular names — Kayu bulan (Burkill 1935), Kayu Poskas (Sumatera Utara), Kayu si marattimang (Sumatera Utara), Dada kedih (Aceh), Giyak putih (Lampung), Setima (Burkill 1935).

Uses — Wood seemingly of little value, but in some areas of the Malay Peninsula used for building, or to keep fires going (Andaman Islands) as it smoulders for a long time. Decoctions of leaves and stem are used to cure diarrhoea, also given after childbirth (Burkill 1935).

3. *Croton beccarii* J.Beyer, *sp. nov.*

Resembling *C. laevifolius* vegetatively but differing in stipule shape and width (filiform, 0.3–0.5 mm wide in *C. beccarii* vs subulate, 0.5–1 mm wide in *C. laevifolius*), leaf indument (abaxially scattered trichomes in *C. beccarii* vs (sub)glabrous in *C. laevifolius*); also *C. beccarii* has shorter inflorescences (2–7 cm long vs 5–23 cm long), densely pubescent sepals and pedicels in pistillate flowers, and densely pubescent small, globose, hardly sulcate capsules (4–5 mm diam), while *C. laevifolius* has overall more glabrous inflorescences and larger distinctly 3-lobed obovoid capsules (5–8(–13) mm high by 4–7 mm diam) with scattered trichomes. — Type: *Beccari PS 973* (holo L [L.2203857]!, iso FI-B!), Indonesia, Sumatera Barat, Sungei Bulu, Sept. 1878.

Trees or shrubs, young branchlets densely pubescent, soon glabrescent. *Indumentum* consisting of creamy to amber stellate trichomes with a darker centre, 0.1–0.3 mm diam, flat to slightly erect, often with a short central porrect radius and 10–20 free radii. *Stipules* filiform to subulate, 2–6(–8) by 0.3–0.5 mm, densely pubescent on both sides, caducous. *Leaves* pseudoverticillate; petiole 0.5–3.5 cm long, grooved above, with scattered trichomes to slightly pubescent (denser at very base and very apex); glands elevated to slightly stalked discs, lateral on the very apex of the petiole, 0.3–0.5 mm diam, elevation/stalk 0.1–0.4 mm high; blade elliptic, 7–15 by 3–7 cm, 1.6–2.6(–3) times longer than wide, chartaceous, base obtuse to acute, margin slightly serrulate to subentire, teeth 4–6 mm apart, without apical trichomes nor marginal glands, apex acuminate, adaxial side glabrous, abaxial side with scattered trichomes (denser near base and large veins), epidermis visible; venation distinct, sunken above, not triplinerved, secondary veins 7–11 pairs, higher order nerves slightly indistinct. *Inflorescences* 1–2(–5) per apical whorl, 2–7 cm long, erect, basally 1–18 pistillate flowers, rarely 1 or 2 staminate flowers at the same node as a pistillate flower, apically 1–2 staminate flowers per node; bracts triangular-ovate, c. 0.5 by 0.2 mm, slightly pubescent on both sides, with a patch of simple trichomes on apex, caducous. *Staminate flowers* 3.5–4 mm diam; pedicel 1–2 mm long, round to slightly flattened, slightly pubescent; sepals triangular-ovate, 1.5–2 by 1–1.5 mm, outside with scattered trichomes to slightly pubescent; petals oblong, c. 1.7 by 0.5 mm, outside glabrous; stamens c. 11, filaments 1–2 mm long, anthers c. 0.4 by 0.4. *Pistillate flowers* 3.5–4 mm diam; pedicel 0.5–1.5 mm long, densely pubescent; sepals triangular-ovate, 2–2.5 by 0.8–1.5 mm, slightly longer than ovary, outside densely pubescent, glabrescent near apex and margin, with a patch of very short simple trichomes on apex; petals absent; ovary 3-lobed, globose, c. 2 by 2 mm long, sulcate, very densely yellowish pubescent to almost hispid; style nearly absent to 0.2 mm long, densely pubescent; stigmas c. 2.3 mm long, fused at base, once divided to c. 2 mm from apex. *Capsules* globose, 4–5 mm diam, rough, hardly sulcate, very densely yellowish pubescent; pericarp very thin (c. 0.1 mm). *Seeds* probably obovoid, c. 3.5 by 2 mm, glabrous, likely carunculate.

Distribution — Endemic to Sumatra (Sumatera Barat).

Habitat & Ecology — Flowering: September.

Affinities — Unknown, as molecular data are lacking, but morphologically highly similar to *C. laevifolius* (which is also not included in the phylogeny) and other species within the 'Riau pocket' clade (Fig. 1: group I_4), based on the lack of colleters and similarities in trichomes and leaf shape.

Note — The description of seeds and capsules is based on very limited material, only three capsules were present and one seed, all very distorted.

4. *Croton cascarilloides* Raeusch.

Croton cascarilloides Raeusch. (1797) 280; Merr. (1934) 60, non Geiseler (1807); (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; B.T.Li & Esser (2008) 260. — *Croton punctatus* Lour. (1790) 581 ('*punctatum*'), nom. illeg., non Jacq. (1786); Müll.Arg. (1866) 565; Gagnep. (1925) 290. — Lectotype (first step, appointing herbarium: Merrill 1935: 34; second step, appointing sheet, designated here): *Loureiro s.n.* (lecto BM [BM000926610]!; isolecto BM [BM000926609]!), Cochinchine (= southern Vietnam).

Croton polystachyus Hook. & Arn. (1838) 270, nom. illeg., non *C. polystachyus* 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 here): *Cuming 1384* (lecto G [G00434383]!; isolecto A [00099662] packet!, BM [BM000926594]!, E!, GDC [G00311739]!, GOET [GOET003339]!, [GOET003340]!, [GOET003341]!, K [K000959761]!, [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 here): *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 here): *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). Remaining syntypes: *Harmand 631* (P!), Vietnam, Nui-cam; *Thorel s.n.* (A!, P!), Laos, La-khon.

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

Shrubs or small trees, to 5 m tall, dbh to 12 cm; young branch-lets densely pubescent, hardly glabrescent. *Outer bark* thin, smooth, dark grey. *Indumentum* consisting of lepidote, hyaline trichomes with a yellow brownish centre to completely brown, scattered (on leaves) to dense (floral parts and stems), 0.3–0.6 diam, flat, circular, with c. 60–80 fused radii (less on adaxial side of leaf). *Stipules* ensiform, 3–6 by 0.5–1.2 mm long, densely pubescent on both sides, caducous. *Leaves* alternate in lower parts, pseudo-verticillate apically with 2–4(–6) leaves per 'whorl'; petiole (0.5–)1–5 cm long, sulcate, grooved above, densely pubescent; glands as flat discs lateral on the base of abaxial midrib, 0.4–1 mm diam, sessile; blade elliptic, (6–)8–22 by 2.5–8 cm, (2–)2.6–3.4 times longer than wide, chartaceous, base rounded to subcordate, margin entire, apex acuminate (occasionally acute to obtuse), adaxial side pubescent in young leaves to (sub)glabrous in old leaves, abaxial side completely and densely silvery-pubescent without visible surface, not glabrescent, scattered darker trichomes visible as distinct dots; venation with a very distinct main vein, sunken above, not triplinerved, secondary veins 9–15 pairs, higher order nerves very indistinct. *Inflorescences* 1(–2) per node, 0.5–2 cm long, densely brownish pubescent throughout, not glabrescent, with very few flowers, erect, basally 1–3 pistillate flowers, apically 2–6 staminate flowers, the medium part sometimes with scars only (flowers caducous), staminate flowers never at the same node as a pistillate flower; bracts triangular, 1.5–3 by 1–1.5 mm, densely pubescent on both sides, eglandular, soon caducous. *Staminate flowers* c. 4 mm diam; pedicel 0.5–1.5 mm long, round, densely pubescent; sepals triangular-ovate, c. 2 by 1.5 mm, silverly brown to dark brown, completely pubescent; 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 diam; pedicel 1.5–3 mm long, round, densely pubescent; sepals elliptic, 2–3 by 1–2 mm, densely pubescent, 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, fused at the very base, divided twice to 1–2 mm from apex. *Capsules* obovoid, clearly 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 — Japan (Ryukyu Islands), Taiwan, S China, Thailand, Laos, Vietnam, *Malesia*: Malay Peninsula, Sumatra (Aceh, Sumatera Barat), Java, Borneo, Philippines, Sulawesi, Lesser Sunda Islands, Moluccas.

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; collected on limestone, sandstone, clayey substrate. Altitude: sea level to 600 m. Flowering and fruiting the whole year through.

Affinities — The specimens present in our analysis and in that of Van Ee et al. (2015) showed a monophyletic species clade (Fig. 1: group H), part of a large polytomy with African, Asian, Australian and Pacific taxa. This species is not yet classified in any section, though Webster (1993) suggested either *C.* sect. *Anisophyllum* or *C.* sect. *Monguia*.

Uses — Bark and roots are used as an antipyretic (Esser 2005).

Notes — 1. Only one specimen from Sumatra was with fruit, therefore Thai specimens were used for describing the capsules and seeds.

2. An isotype of *C. vidalii* Airy Shaw (*Vidal y Soler 555* in A [00100144]!) is *C. cascarilloides*, but the holotype (K [K000959255]*) and another isotype (L [L.2212494]!) are most certainly not *C. cascarilloides* and indeed *C. vidalii*.

5. *Croton caudatus* Geiseler — Fig. 2b, 4

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; Esser (2005) 198; P.T.Li & Esser (2008) 262; Chakrab. (2019) 3629. — *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): *Rottler s.n.* (lecto C [C10011161]!), India orientalis.

Croton racemosus Burm.f. (1768) 206 ('306'), nom. rej. — Lectotype (designated by Esser 2001): *Anonymous (Herb. Houttuyn) s.n.* (lecto G!), Sri Lanka.

Croton aromaticus Gaertn. (1791) 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 here): *Unknown s.n.* (lecto L [L.2210974]!), (Java,) Nussa Kambang.

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

Croton malvifolius Griff. (1848) 200. — Lectotype (designated here): *Griffith 2518* (lecto BM [BM000951453]*), Boutan (= Bhutan). Other syntype: *Griffith 1166* (GH [00099667]!), Bootan (= Bhutan).

Croton sumatranus Miq. (1859) 381. — *Oxydectes sumatrana* (Miq.) Kuntze (1891) 613. — Lectotype (designated here): *Anonymous* (*likely 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 here): *Hooker & Thomson s.n., s.d.* (holo GDC [G00311925]*), Assam.

Croton caudatus Geiseler var. *oblongifolius* Müll.Arg. (1866) 600. — Lectotype (designated here): *Zollinger 642* (lecto GDC [G00311913]*; isolecto A [00047516]*, [00106972]!, GDC [G00311912]!, [G00311921]!, G [G00434381]!, [G00434382]!, L [L 0234052]!), 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 here): *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 here): *Griffith s.n.* (lecto K [K000246826]*), India, Assam; other syntype: *Wallich num. list no. 8938* (BM!, CAL [CAL0000023625]*, K!, K-W!), India, Silhet.

Croton caudatus Geiseler var. *malaccanus* Hook.f. (1887) 389 ('*malaccana*'); Ridl. (1924) 259. — Lectotype (designated here): *Griffth KD 4775* (lecto CAL [CAL0000023572]*; isolecto: K [K000246829]* without number, [K000246830]* without number, [K000959168]* without number, [K000959169]* without number, [K000959170]*, M [M-0241964]!, GDC [G00311922]!, GH [00099677]! without number, [00100129]! 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 here): *Couderc s.n.* (P [P00610256]*), Cambodia, Vat-Preah. Other syntypes: *Harmand s.n.* (A [00047489]!, K [K000959152]*), Cochinchine, delta du Mè-Không; *Pierre s.n.* (P n.v.) Cochinchine, Prov. de Bien-hoa.

Croton caudatus Geiseler var. *obovoideus* N.P.Balakr. & Chakrab. (1985 '1983') 190, f. 1. — Type: *Sebastine 25343A* (holo MH, n.v.; isotypes MH [MH 00001136*, MH 00001133*, MH00001135*, MH00001134*), India, Kerala, Kottayam Dist., Velara.

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

Straggling shrubs, woody climbers or lianas, to 12(–25) m long; young branchlets densely pubescent, slowly glabrescent.

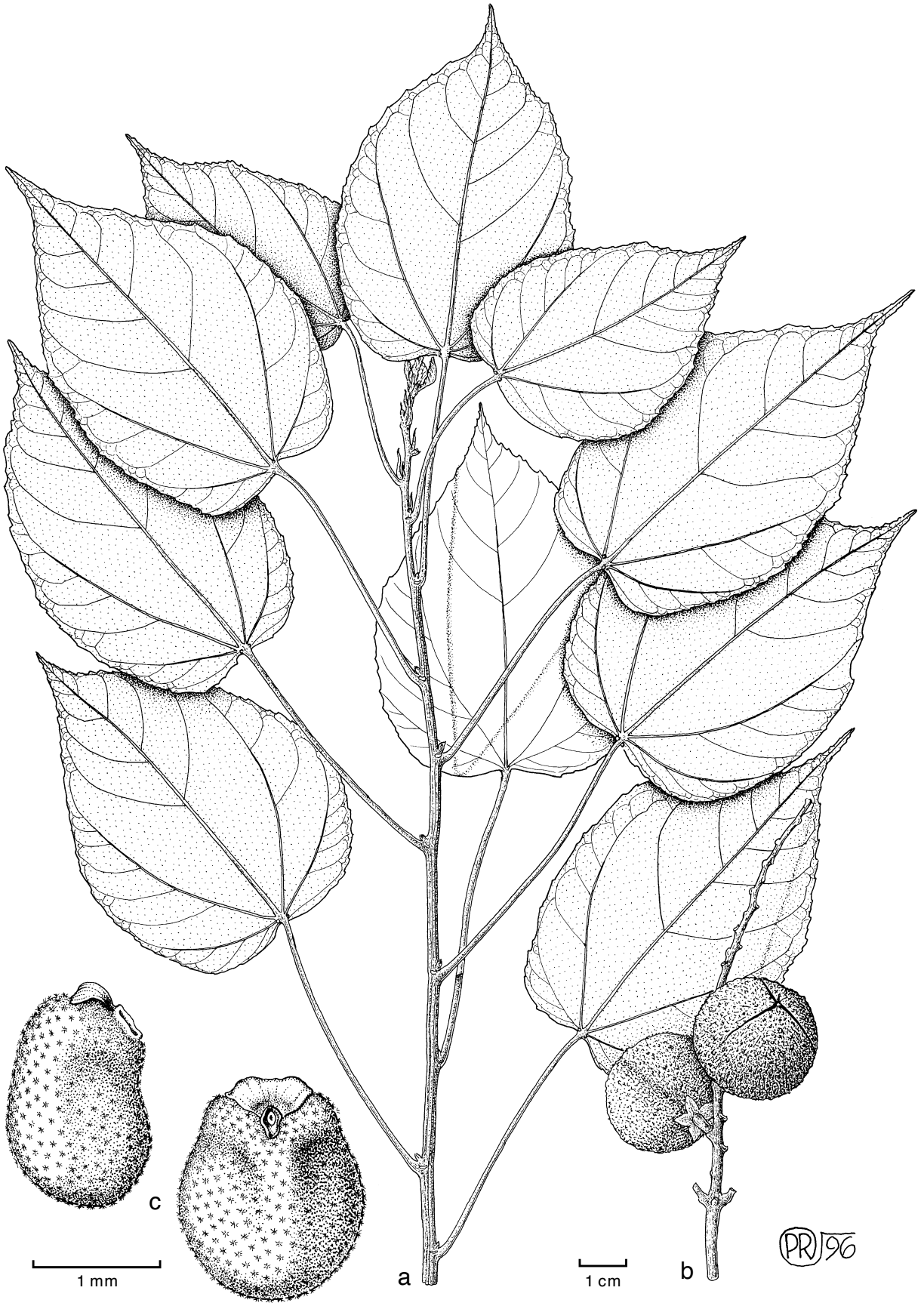

Fig. 4 Habit of *Croton caudatus* Geiseler. a. Habit; b. fruits; c. seed with lepidote hairs (a, b: source unknown; c: *Maxwell 82-286*, L). — Illustrations: a, b by Priyono, 1996; c by Esmée Winkel 2022.

Indumentum consisting of yellowish brown stellate-dendritic trichomes, with often a long central porrect radius, (0.1–)0.3–1.2 mm diam, with 6–13 free radii. *Stipules* filiform, 4–9 by 0.1–0.5 mm, sightly to densely pubescent on both sides, caducous. *Leaves* alternate; petiole 1–3.5(–5) cm long, round to slightly grooved above, densely to slightly pubescent; glands 1–2 (rarely 3–4) pairs of distinctly stalked discs, lateral on the very base of the abaxial midrib, 0.3–0.8(–1) mm diam, stalk 0.6–1(–2) mm long, additional smaller marginal glands common, 0.2–0.5 mm diam, stalk 0.1–0.6(–1) mm long (Fig. 2b); blade ovate to elliptic, 4–11 by 2.2–6.6 cm, 1.1–2.1(–2.5) times longer than wide, membranous to chartaceous, base cordate, sometimes nearly rounded, margin (double-)serrate to subentire, apex acute to acuminate, distinctly brownish pubescent on both sides (very variable in density), on veins more dense than in between, adaxial side less densely pubescent than abaxial side, leaf surface always visible; venation very distinct, sunken above, actinodromous with 3 or 5 prominent basal veins, secondary veins 4–7 pairs, higher order nerves reticulate. *Inflorescences* thyrsoid, 1–3 per node, 6–18 cm long, bisexual (occasionally only staminate flowers), densely pubescent all over, basally 6–21 pistillate flowers, apically 1–2(–3) staminate flowers per node; bracts filiform, 2–3 by 0.1–0.2 mm, eglandular (very rarely with a small but distinct stalked gland), outside pubescent, inside subglabrous, soon caducous. *Staminate flowers* 4–5.5(–7) mm diam; pedicel 3–8 mm long, round, densely pubescent; sepals triangular-ovate, 2–3 by 1.2–2 mm, outside densely pubescent, lanate on margin and apex, inside glabrous; petals oblong to slightly obovate, 2.5–3 by 0.7–1(–1.5) mm, outside glabrous to slightly lanate, inside glabrous to slightly lanate; stamens 18–30, filaments 2–4 long, anthers 0.5–1 by 0.3–0.5, free. *Pistillate flowers* 6–8 mm diam; pedicel 1–2 mm long (up to 4 mm in fruit), densely pubescent; sepals triangular-ovate, 3–4 by 1.5–3.5 mm, outside slightly pubescent, inside (sub)glabrous, with a patch of simple trichomes on apex, sometimes margin with small glandular bumps, slightly longer than ovary; petals absent; ovary globose, c. 3 by 3 mm, densely yellowish hispid; style absent; stigmas 4–6 mm long, once divided to 3.9–5.9 mm from apex, slightly pubescent near base. *Capsules* globose, 12–20 mm high by 12–22(–25) mm diam, not sulcate, rough to slightly muriculate, densely brownish pubescent; pericarp woody, 0.5–1.3(–2) mm thick; columella 10–13 mm long. *Seeds* globose, partly flattened, 8–10 by 8–11 mm, with scattered trichomes to slightly pubescent, carunculate.

Distribution — Pakistan, India, Sri Lanka, Bangladesh, Nepal, Bhutan, China (Yunnan), Myanmar, Thailand, Laos, Vietnam, Cambodia, *Malesia*: Malay Peninsula, Sumatra (Aceh, Sumatera Utara, Sumatera Barat, Sumatera Selatan, Banka-Belitung), Java, Borneo, Philippines, Sulawesi, Lesser Sunda Islands; Australia.

Habitat & Ecology — In peat swamp forest, deciduous and evergreen forest, secondary forests and thickets, along rivers and streams. Altitude: sea level to 700 m. Flowering and fruiting the whole year through.

Affinities — The sole member of *Croton* section *Caudati* (Van Ee et al. 2015).

Uses — Mainly medicinal, a root decoction is used for purging the intestines, also used when the person has a cold or is feverish, in combination with *Plumbago* the decoction can act as abortifacient. The leaves can also be used as poultice with fevers. Twigs are used in basketry (all Burkill 1935). In Indonesia, dried bark is used to relieve stomach disorders (Esser 2005).

Notes — 1. Highly diverse in density of indumentum and size and amount of muricae on the capsules. Only one Sumatran collection with a pistillate flower, therefore material from the Malay Peninsula was also used. Only specimen *Elbert s.n.* (L.2211126) has a small gland on two floral bracts.

2. The type sheets of *Croton caudatus* var. *obovoideus*, *Sebastine 25343* at MH, were later numbered B–D by Chakrabarty, but these are not part of the original collection numbers, all sheets are clearly duplicates of the same gathering.

6. *Croton* cf. *coriifolius* Airy Shaw

Croton cf. *coriifolius* Airy Shaw (1974a) 311. — Type: *Haviland 'c.l.r.h.'* (holo K [K000959189]*, iso SING!), Borneo, Sarawak, First Division, Matang.

Woody, probably tree or shrub, size unknown; young branchlets densely pubescent, soon glabrescent. *Indumentum* consisting of only stellate trichomes, yellowish to brown in the centre with whitish to yellowish radii, 0.1–0.4 mm diam (up to 0.6 mm on pistillate flowers), flat, often with a short central porrect radius, with 8–20(–30) free to rarely slightly fused radii. *Stipules* subulate to narrowly triangular, 2–4(–6) by 0.4–0.8 mm, subglabrous to slightly pubescent on both sides. *Leaves* pseudoverticillate (occasionally almost alternate in lower parts); petiole 0.5–3.5 cm long, grooved above, sulcate, densely pubescent when young, soon glabrescent, (sub)glabrous when old; glands lateral on the very apex of the petiole, sessile, hardly elevated, 0.8–1.5 mm diam; blade narrowly elliptic to slightly obovate, 5.5–20 by 1.5–5 cm, (2.2–)2.7–4 times longer than wide, chartaceous to subcoriaceous (rarely membranous), base attenuate to cuneate (sometimes almost obtuse at very base), margin (sub)serrate, teeth 3–6 mm apart, often slightly revolute, without apical trichomes or glands, apex attenuate to acuminate, adaxial side glabrous, abaxial side slightly lighter when dried, with scattered trichomes when young (especially on midrib), later (sub)glabrous, epidermis well visible; venation distinct, not triplinerved, midrib sunken above, secondary veins 9–13 pairs, higher order nerves visible to distinct. *Inflorescences* terminal, 1–3(–5) per whorl, 6–19 cm long, (sub)glabrous, basally 8–20(–30) pistillate flowers, never staminate flowers at the same node as pistillate flowers, apically 1–3 staminate flowers per node; bracts triangular, 1–2.2 by 0.3–0.8 mm, (sub)glabrous except for patch of simple trichomes on apex. *Staminate flowers* 2.5–3 mm diam; pedicel 2–3 mm long, round to slightly flattened, glabrous; sepals ovate, c. 1.5 by 1 mm, fused at base, outside glabrous; petals oblong, c. 1.6 by 0.3 mm, glabrous outside; stamens 8–11, free, filaments 1.7–2.2(–3.3) long, anthers c. 0.3 by 0.2 mm. *Pistillate flowers* 3.5–4.5 mm diam; pedicel 1–2 mm long (up to 3 mm in fruit), with scattered trichomes; sepals ovate, 1.8–3 by 1–1.5 mm, longer than ovary, outside with scattered trichomes, patch of simple trichomes on apex; petals absent; ovary obovoid to round, 1.1–2 by 1.2–1.6 mm, slightly sulcate, very densely whitish pubescent; style c. 0.3 (–0.5) mm long; stigmas 2.5–3.5 mm long, once divided, to 2–3 mm from apex. *Capsules* obovoid, 3–4 mm high, 3–5 mm diam, sulcate, apex slightly depressed, with scattered but distinct trichomes. *Seeds* unknown (on Borneo, type specimen: c. 4 mm wide), likely with a small caruncle.

Distribution — *Malesia*: Sumatra (Sumatera Utara, Riau, Jambi, Sumatera Seletan), Borneo (Sarawak).

Habitat & Ecology — Altitude c. sea-level to 50 m. Flowering: March, April, October; fruiting: February.

Affinities — Part of the 'Riau pocket' clade (Fig. 1: group I_4).

Vernacular name — Tjongheul (Jambi).

Note — Very limited material from Sumatra was found and none of the specimens had both staminate and pistillate flowers. *Croton coriifolius* is described from Borneo, where it only occurs in kerangas (heath) forests (low and species-poor forest on poor sandy soil; the last author has been there and has seen it). It is unclear where the Sumatran material was collected, and kerangas forest is not known from Sumatra (with the exception of Banka and Biliton Islands), thus the identification of the Sumatran material has to be treated with caution (hence the cf.

with the name). Many taxa have thicker leaves under the acid kerangas conditions, therefore Airy Shaw (1974a) indicates that this species might be a sclerophyllous ecotype of *C. oblongus*, which is a very doubtful species (see Discussion).

7. *Croton gageianus* P.T.Li

Croton gageianus P.T.Li (1994) 131. — *Croton lucidus* Gage (1922) 236, nom. illeg., non L. (1759, '*lucidum*'). — Lectotype (indirectly designated by Li 1994 as holotype, here the second lectotypification of the sheet): *Ridley 12176* (lecto K [K000959158]*; isolecto SING!), Malaysia, Johor, Gunong Pulai. Other syntype: *Ridley 12194* (SING!), Malaysia, Johor, Gunong Pulai.

Shrubs or treelets, to 5 m tall, young branchlets densely pubescent, soon glabrescent. *Indumentum* consisting of only whitish hyaline stellate trichomes, with a yellowish centre, 0.4–0.9 mm diam on leaves, 0.2–0.7 mm diam on stems and inflorescences, flat, with a short central porrect radius, with (11–)15–25(–30) free radii. *Stipules* triangular-ovate, c. 1.1 by 0.4 mm long, densely pubescent on both sides, caducous and usually absent. *Leaves* pseudo-verticillate; petiole 0.5–2(–3.5) cm long, deeply grooved above, subglabrous to densely pubescent; glands as slightly stalked discs lateral on the midrib base, diam 0.3–0.7 mm, stalk 0.1–0.3 mm long; blade narrowly elliptic, 7–25 by 2–5.5 cm, (3.1–)3.4–5.2 times longer than wide, membranous, base attenuate with very base often obtuse to rounded, margin (sub)entire, apex acute to acuminate, adaxial side glabrous, abaxial side slightly to densely pubescent but with surface always visible between the trichomes; venation distinct, sunken above, not to indistinctly triplinerved, secondary veins 6–8 pairs, higher order nerves often hard to see especially on abaxial side. *Inflorescences* 1(–3) per node, 3–5.5 cm long, erect, slightly pubescent all over, basally 1–3 pistillate flowers, apically 1–2 staminate flowers; bracts triangular-ovate c. 0.5 by 0.5 mm, slightly pubescent on both sides, soon caducous. *Staminate flowers* c. 3 mm diam; pedicel 1–2 mm long, round, densely pubescent; sepals elliptic, c. 1.8 by 0.8 mm, outside densely pubescent, inside glabrous; petals elliptic, c. 1.4 by 0.4 mm, outside glabrous, inside lanate; stamens c. 11, immature. *Pistillate flowers* c. 3 mm diam; pedicel c. 2 mm long, sulcate, densely pubescent; sepals triangular-ovate, c. 2 by 1 mm, longer than ovary, outside densely pubescent, inside glabrous; petals absent; ovary globose, c. 1.3 by 1.3 mm long, slightly sulcate, densely yellowish hispid; style absent; stigmas c. 3 mm long, once divided to c. 2.5 mm from apex, glabrous. *Capsules* globose, c. 5 by 6 mm, slightly sulcate, with scattered trichomes; pericarp c. 0.5 mm thick; columella 4–5 mm long. *Seeds* globose to slightly obovoid, c. 5 by 4 mm, glabrous, with a small caruncle.

Distribution — *Malesia*: Malay Peninsula, Sumatra (Atjeh, Sumatera Barat, Bengkulu).

Habitat & Ecology — In primary lowland (Dipterocarp) rainforest, found on ridges and alluvial soil. Altitude: 100–700 m. Flowering: June; fruiting: February.

Affinities — Riau pocket group (Van Ee et al. 2015), part of a polytomy (Fig. 1: group I_4), thus close affinities are unknown.

Notes — 1. Gage (1922) made a later homonym for a Linnean name (Linnaeus 1759) and mentioned two syntypes, *Ridley 12176* and *Ridley 12194* (SING). Li (1994) restored the error by using a new name. He regarded *Ridley 12176* as the holotype, thus indirectly creating a lectotype.

2. Only six specimens (of which one as uncertain) were seen, of them only one specimen had a pistillate flower, one with a fruit, one with seed and one with an almost matured staminate flower, which was too fragile to measure the stamens.

3. Outside L only known from three collections, of which two collections are named by Gage (1922) and Li (1994), *Ridley 12176 & 12194*, both from the Malay Peninsula, Johor, Gunong Pulai. Besides these two Ridley collections there are also *Sinclair 7277* (E [E00201750]*, US [01246063]*) and *Sinclair SFN 39510* (SING*), Malay Peninsula, Gunong Pulai (summit). The specimen at US is incorrectly placed under *Croton lucidus* L. (in error for *C. lucidus* Gage).

8. *Croton griffithii* Hook.f.

Croton griffithii Hook.f. (1887) 392; Ridl. (1924) 261; Burkill (1935) 689; Airy Shaw (1972a '1971') 246; Esser (2002b) 42; (2005) 205. — *Oxydectes griffithii* (Hook.f.) Kuntze (1891) 614. — Lectotype (designated by Esser 2002b: 42): *Griffth KD 4781* (lecto K, 2 sheets [K000959159]!, K000959160]!), Malaysia, Malacca. Both K sheets are the same collection (labeled sheet 1 and 2) and together can be regarded as the lectotype. Other syntypes: *Griffith KD 4778* (K [K000959159!], K000959160!]), Malaysia, 'Malacca'; *King's Collector 1115* (G!, K!, L!), Malaysia, Perak; *King's Collector 4484* (CAL [CAL0000023613]*, K!), Malaysia, Perak; *King's Collector 4629* (CAL [CAL0000023608]*), Malaysia, Perak; *King's Collector 4820* (CAL [CAL0000023605*]), Malaysia, Perak, Goping; *King's Collector 6157* (K!, WU!), Malaysia, Perak; *Maingay 1406* (CAL [CAL0000023612*], K!), Malacca; *Scortechini s.n.* (CAL [CAL0000023611*], K!, SING!), Malaysia, Perak; *Scortechini 1423* (CAL [CAL0000023610*], Malaysia, Perak; *Wallich numer. list 7754* (K-W!), Singapore; *Wallich numer. list 7967* (K-W, n.v.), Singapore.

Croton confusus Gage (1922) 237 ('*confusum*'). — Syntypes: *Curtis 1585* (A [00106965]!, K!, SING!), Malaysia, Penang, Moniots Road; *Hullet s.n.* (SING, n.v.), Singapore, Sungei Bei; *King's collector 5452* (n.v.), Malaysia, Perak, Larut; *Ridley 3170* (CAL [CAL0000023570*], SING, n.v.), Malacca, Mount Ophir and Gunong Ledaung; *Ridley 3446* (SING, n.v.), Singapore, Changi; *Ridley 7642* (SING, n.v.), Malaysia, Selangor, Guning Bua; *Ridley 10404* (SING, n.v.), Singapore, Bukit Timah; *Ridley 10860* (SING, n.v.), Singapore, Bukit Timah; *Ridley 12561* (SING, n.v.), Singapore, Woodlands; *Ridley s.n.* (n.v.) Singapore, Botanic Garden. (When the species is revised in its full distribution, then a lectotype should be designated).

Croton laevifolius auct. non Blume: Whitmore (1973) 85, p.p. excl. *C. laevifolius*; Corner (1988) 284, p.p. excl. *C. laevifolius*.

Shrubs or trees, to 18 m tall (up to 26 m in Borneo), diam to 90 cm; young branchlets densely pubescent, glabrescent (later than most other *Croton* species). *Outer bark* smooth but brittle and patchy, light greyish brown. *Indumentum* consisting of only whitish hyaline stellate trichomes with a yellowish centre, 0.1–0.4 mm diam (up to 0.6 mm on developing ovaries), flat but often with a very short central porrect radius, with 11–17 free radii. *Stipules* subulate to ensiform, (1.5–)2.5–5 by 0.4–1 mm, densely pubescent on both sides, caducous to quite persistent. *Leaves* alternate to apically crowded or almost whorled, 2–6 per pseudo-whorl; petiole (0.5–)2–11 cm long, grooved above, very thick (up to 4 mm diam), with scattered trichomes to slightly pubescent; glands abaxially as flat discs lateral on the very base of the midrib, (0.3–)0.7–1.5 mm diam, sessile, not to distinctly elevated; blade elliptic, (8.5–)10–26 by (3–)5–12 cm, (1.7–)2–3(–3.8) times longer than wide, chartaceous, base rounded to obtuse (rarely subcordate or attenuate), margin subentire (to shallowly serrate especially in young leaves, teeth without trichomes or glands apically), apex acute to acuminate, adaxial side glabrous, abaxial side of old leaves densely whitish pubescent (with epidermis visible) to subglabrous, epidermis visible, in young leaves completely whitish pubescent with surface hardly visible, sometimes more densely pubescent at the very base of the midrib; venation distinct, sunken above, basally not triplinerved, secondary veins (6–)11–15. *Inflorescences* both terminal and axillary, 8–30 cm long, with scattered trichomes, basally 6–15 pistillate flowers, often 1–3 staminate flowers on the same node of a pistillate flower, apically 1–3 staminate flowers per node; bracts triangular-ovate, c. 1 by 0.5 mm, both sides subglabrous, with a patch of simple trichomes at the apex, eglandular, quite persistent. *Staminate flowers* c. 4 mm diam; pedicel 1.5–4(–6) mm long, round to flattened, subglabrous (to slightly pubescent); sepals triangular-ovate, 1.5–2 by 1–1.5 mm, fused at base, dark around base, hyaline-

whitish near apex, outside with scattered trichomes to subglabrous; petals oblong, 1.5–2 by 0.3–0.5 mm, outside glabrous; stamens 8–12, filaments 2–3 mm long, anthers c. 0.6 by 0.4 mm. *Pistillate flowers* 3–4 mm diam; pedicel 1–3 mm long, not sulcate, slightly to densely pubescent; sepals triangular, 1.5–2 by 1–1.5 mm, outside densely to slightly pubescent, denser near base, with a patch of simple trichomes at the apex, as long as ovary; petals absent; ovary globose to obovoid, 1.5–2 by 1.5–2 mm, deeply sulcate, densely pubescent; style absent; stigmas 3–4.5 mm long, once divided to 1.5–3 mm from apex. *Capsules* 3-lobed, obovoid, 5–8 mm high, diam 7–14 mm, extremely sulcate when dry, with scattered trichomes; pericarp strong and thick (c. 0.8 mm); columella c. 8 mm long. *Seeds* ovoid but flattened on inner side, 7–9 by 5–6 mm, glabrous, with a small caruncle.

Distribution — Thailand, *Malesia*: Malay Peninsula (Perak, Selangor, Pahang, Terengganu, Johor), Sumatra (Sumatera Barat (Siberut), Kepulauan Riau (Singkep)), Borneo.

Habitat & Ecology — In evergreen forest and along streams, on granite bedrock. Altitude: 40–850 m. Flowering: February–April; fruiting: July, August.

Affinities — Riau pocket group (Van Ee et al. 2015; clade I_4 in Fig. 1).

Uses — A decoction of the leaves is used in Malaysia as bath after childbirth (Esser 2005).

Notes — 1. The leaves usually dry into a typical yellowish brown colour. The species is not known from the main island of Sumatra; one specimen is known from Pulau Singkep (one of the Riau islands) and the other from Pulau Siberut (Mentawai islands, west of Sumatra). Other specimens examined are from Sarawak and Malay Peninsula.

2. Three specimens were wrongly determined as *C. erythrostachys*. The main differences between these two species are that *C. erythrostachys* has marginal leaf glands on a long stalk and large trichomes (0.6–07 mm diam) with 9–10 radii spreading in all directions. The flowers and capsules of *C. griffithii* are smaller and less hairy.

9. *Croton heterocarpus* Müll.Arg. — Fig. 2a

Croton heterocarpus Müll.Arg. (1866) 621; Hallier f. (1911) 7; Merr. (1921a) 337; (1923) 425; Ridl. (1924) 262 (‘*heteropetalum*’); Merr. (1926) 382; Whitmore (1973) 85; Airy Shaw (1975) 93; (1981a) 285; (1983) 18; Corner (1988) 284. — *Oxydectes heterocarpa* (Hook.f.) Kuntze (1891) 612. — Lectotype (designated here): *Zollinger 3982* (lecto L [L 0234540]!, Herb. Hasskarl; isolecto G-DC [G00312279]!, W [W 1889-0024627]!, [W 1889-0024628]!), Sumatra, Prov. Lampong, River Toelang Bawang.

Croton ardisioides Hook.f. (1887) 393; Merr. (1909) 278. — *Oxydectes ardisiodes* (Hook.f.) Kuntze (1891) 614. — Lectotype (designated here): *Griffith KD 4783* (lecto K [K000959156]*; isolecto CAL [CAL0000023600]*, GH [00100136]!, P [P00623696]!), Malacca. Other syntype *Griffith s.n.* (CAL [CAL0000023620]*, K [K000959157]*, P [P00623695]!), Malacca. (Hooker (1887) indicates as collecting locality Borneo, but all specimens show Malacca).

Trees, to 12 m tall, diam to 35 cm; young branchlets densely pubescent, soon glabrescent, scar tissue very common on branches and between whorls of leaves. *Outer bark* smooth, brownish. *Indumentum* consisting of yellowish brown stellate trichomes, 0.2–0.4 mm diam, flat, with c. 10–25 free radii, and patches of erect simple trichomes, c. 0.5 mm long. *Stipules* ensiform to triangular, 2–4 by 0.5–1 mm, densely pubescent on both sides. *Leaves* alternate in lower parts, pseudo-whorled apically, with every branch ending with a whorl of leaves and inflorescences; petiole 0.5–2 cm long, round at base, upwards soon flattened to apically with an adaxial sharp groove, trichomes scattered; glands adaxially on the very apex of the petiole, sessile but slightly elevated (less than 0.5 mm high), 0.3–0.6 mm diam (Fig. 2a); blade obovate (to elliptic), 2.5–10(–12) by 1.2–4.1 cm, 1.9–3 times longer than wide, membranous to chartaceous, base attenuate to cuneate, margin serrate to slightly crenate, teeth 2–5(–7) mm apart, patches of erect trichomes on apex of teeth, apex acute to nearly rounded, adaxial side glabrous, abaxial side subglabrous with very few scattered trichomes, glabrescent, epidermis well visible; venation distinct, sunken above, basally not triplinerved, secondary veins 6–10 pairs, higher order veins visible. *Inflorescences* 2–4 per node, 5–20 cm long, erect, greenish white, basally 6–14 pistillate flowers, staminate flowers never on same node as pistillate flowers; bracts triangular-ovate, c. 1 by 1 mm, eglandular, glabrous except for patch of simple trichomes on apex, quite persistent. *Staminate flowers* c. 3 mm diam; pedicel c. 1 mm long, round to slightly flattened, sulcate, glabrous; sepals ovate, c. 1.5 by 1 mm, subglabrous outside; petals oblong, c. 1.2 by 0.4 mm, outside glabrous, inside and margin lanate; stamens 8–12, free, filaments c. 2 mm long, anthers c. 0.5 by 0.4 mm. *Pistillate flowers* c. 3 mm diam; pedicel 0.5–1 mm long, subglabrous; sepals oblong to ovate, 1.5–2 by c. 1 mm (up to 2.5 by 1.5 mm in fruit), fused at the very base, subglabrous but on the very apex a patch of simple trichomes, slightly longer than ovary; petals absent; ovary globose, 1–1.5 by 1–1.5 mm, very densely yellowish pubescent; style less than 0.1 mm long; stigmas 2–2.5 mm long, free and thickened at base, once divided to 1.5–2 mm from top. *Capsules* obovoid, c. 5 mm high, c. 5 mm diam, slightly sulcate, surface rough, with scattered trichomes, green (immature); pericarp c. 0.5 mm thick; columella c. 5 mm long. *Seeds* obovoid, flattened on inner side, c. 3 by 3 mm, glabrous, carunculate.

Distribution — *Malesia*: Malay Peninsula, Sumatra (Sumatera Utara, Lampung), Borneo, Philippines, Moluccas.

Habitat & Ecology — In primary forest, mangroves, swamp forests and on riverbanks, always near water. Altitude: sea level to 90 m. Flowering: unknown for Sumatra; fruiting: August.

Affinities — *Croton* section *Furcaria* (Webster 1993). *Croton heterocarpus* groups together with *C. macrocarpus* (Fig. 1: group I_1), which might also be classified in this section, though the sections of Webster (1993) are not always recognized after phylogenetic analyses.

Vernacular names — Borneo: Djingah berkosah.

Uses — Roots are used as medicine in Sabah (N Borneo, *Neil 7064*).

10. *Croton hirtus* L’Hér.

Croton hirtus L’Hér. (1784) 17, t. 9; J.Sinclair (1956) 1, f. 1; G.L.Webster & D.G.Burch (1967) 262; Whitmore (1973) 84; Philcox (1997) 88; Esser (2005) 206. — *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.

[For other synonyms see Plants of the World Online (http://www.plantsoftheworldonline.org/) except for *Podostachys hirta* (L’Hér.) Klotzsch (see note).]

Erect, annual herbs, to 40 cm high; whole plant with hispid, irritating trichomes. *Indumentum* consisting of stellate-porrect, whitish to pale brownish trichomes, 0.6–1.5 mm diam on leaves, up to 3 mm diam on stems, flat but usually with distinctly longer central porrect radius, with 6–12 (on adaxial side often only 2–6) free radii. *Stipules* filiform, 4–7 by 0.2–0.5 mm, with scattered trichomes, quite persistent. *Leaves* alternate below, but crowded to pseudo-verticillate on apical branches; petiole 0.5–2(–4) cm long, flattened, slightly sulcate, hispid; glands as stalked discs lateral-abaxial on the petiole/blade junction, stalk 0.5–1.5 mm long, 0.2–0.4 mm diam; blade ovate, 1.9–5.4 by 1.1–4.1 cm, 1.1–2.1 times longer than wide, chartaceous,

base rounded to obtuse, margin double serrate, apex acute, adaxial side with scattered trichomes to slightly hispid, abaxial side densely hispid; venation distinctly triplinerved, indistinct and sunken on adaxial side, distinct on abaxial side; secondary veins 3–5 pairs, not looped and closed near margin. *Inflorescensces* thyrsoid, 2–5 cm long, erect, basal 2–7(–12) nodes with a pistillate flower, never staminate flowers in the same cymule of a pistillate flower; bracts filiform, 1.5–4 by 0.1–0.3 mm, scarcely hispid, with 1–3 pairs of filiform, gland-tipped, free or partly fused lobes at base. *Staminate flowers* c. 2 mm diam; pedicel c. 1 mm long, slightly flattened, hispid; sepals ovate, c. 1 by 0.5 mm, hyaline, outside pubescent, with a patch of simple trichomes on apex; petals oblong, c. 1 by 0.3 mm, hyaline, outside glabrous, inside slightly lanate; stamens 10 or 11, filaments 0.5–1 mm long, slightly fused at base, subglabrous, anthers c. 0.4 by 0.4 mm. *Pistillate flowers* c. 2 mm diam but soon to 5–7 mm diam; pedicel c. 0.3 mm long (up to 2 mm in fruit), hispid; sepals obovate, c. 1.5 by 0.5 mm, soon elongating to 3.5–4 by 1–1.5 mm (up to 7 by 2 mm in capsules), fused at the base, spreading at the apex, hispid outside, glabrous inside, longer than ovary; petals absent; ovary globose, c. 2 by 2 mm, hispid; stigmas c. 1.5 mm long, once divided to c. 1.4 mm from apex. *Capsules* subglobose, 3–4.5 by 2.5–4 mm, smooth, slightly sulcate, sparsely pubescent; pericarp very thin (c. 0.1 mm); columella 2.5–3 mm long. *Seeds* globose, slightly flattened, c. 3 by 2 mm, variously mottled, shiny but minutely reticulate-foveolate, carunculate.

Distribution — Native to C and S America; introduced and naturalizing in W and E Africa, Sri Lanka, Thailand, throughout *Malesia* including Sumatra (Sumatera Selatan).

Habitat & Ecology — Weed on waste places, old plantations, roadsides. Altitude: sea level to 100 m. Flowering and fruiting: February, March, June.

Affinities — *Croton* section *Geiseleria* subsection *Geiseleria* (Riina et al. 2021).

Note — *Podostachys hirta* (L'Hér.) Klotzsch (1841: 194) is mentioned by Plants of the World Online (http://www.plantsoftheworldonline.org/) as a synonym, but Klotzsch indicates it as his own species (a nomen nudum) and there is no reference to L'Héritier de Brutelle, therefore, the name is not considered here to be a synonym.

11. *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. — Lectotype (designated here): *Blume 1473* (lecto L [L.2203878]!; isolecto L [L. 2203879]!), Indonesia, Java.

Croton diadenus Miq. (1861) 451, 180 ('*diadenum*'), p. 451 contains description and type, p. 180 vernacular name. — 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 here): *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.

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. See note.

Treelets, 3–8 m tall, diam c. 6 cm, young branchlets slightly pubescent, soon glabrescent. *Indumentum* consisting of stellate trichomes only, yellowish brown in the centre with whitish radii, 0.1–0.4 mm diam, often with a central porrect radius, with 11–20 free to basally slightly fused radii. *Stipules* subulate, 2–5(–7) by 0.5–1 mm, outside slightly pubescent (occasionally subglabrous), inside densely pubescent (occasionally subglabrous), quite persistent to caducous. *Leaves* alternate to pseudo-verticillate; petiole 1–5 cm long, deeply grooved above, subglabrous; glands abaxially (sometimes almost adaxially) on the very apex of the petiole, sessile but elevated to slightly stalked, 0.3–0.6(–1) mm diam, stalk 0.1–0.5(–1) mm high; blade obovate to elliptic (rarely ovate), 5–17 by 3–7 cm, 1.7–3(–3.5) times longer than wide, chartaceous, base cuneate to obtuse, margin slightly serrate (teeth without trichomes or glands) to almost entire, apex acuminate, adaxial side glabrous, abaxial side lighter when dried, subglabrous to glabrous, epidermis visible; venation distinct, sunken above, basally not triplinerved, secondary veins 7–10 pairs, higher order veins reticulate. *Inflorescences* terminal to axillary (always near apex), (1–)2–6 per apical node, 5–23 cm long, erect, basally (2–)5–20(–26) pistillate flowers, sometimes completely staminate, rarely 1–3 staminate flowers at same node as a pistillate flower, apically 1–3(–5) staminate flowers per node; bracts triangular-ovate, 0.8–2 by 0.4–1 mm, glabrous to slightly pubescent, often with a small patch of simple trichomes on apex, quite persistent (especially with staminate flowers). *Staminate flowers* 3–3.5 mm diam; pedicel 0.8–3 mm long, round, glabrous to subglabrous; sepals ovate, 1.2–2 by 0.9–1.2 mm, fused at base, glabrous to subglabrous; petals oblong, 1.7–2.1 by 0.3–0.5(–1) mm, always slightly longer than sepals, glabrous except for small patch of simple trichomes on apex; stamens 10 or 11, free, filaments 1.5–2 mm long, anthers c. 0.5 by 0.4 mm. *Pistillate flowers* 3–4.5 mm diam; pedicel 1–3 mm long (up to 4 mm in fruit), glabrous to slightly pubescent; sepals triangular-ovate, 1.8–2 by 1–1.5 mm, fused at very base, longer than ovary, with scattered trichomes (denser near base) to glabrous except for a small patch of simple trichomes at the apex; petals oblong, c. 1.2 by 0.3 mm, usually absent; ovary obovoid, c. 1.5 by 1.5 mm, deeply sulcate, very densely yellowish pubescent, style 0.2–0.4 mm long; stigmas 2–3 mm long, thickened at base, once divided to 1.5–2 mm from apex. *Capsules* distinctly 3-lobed, obovoid, 5–8(–13) mm high by 4–7 mm diam, sulcate, apex slightly depressed, with scattered but distinct trichomes; pericarp 0.3–0.5(–1) mm thick; columella 4–6 mm long. *Seeds* obovoid to almost prolate, 5–6(–8) by 3–4(–6.5) mm, glabrous, with a small caruncle.

Distribution — *Malesia*: Sumatra (Sumatera Barat, Riau, Sumatera Selatan, Banka-Belitung), Java, Borneo, Sulawesi, Lesser Sunda Islands.

Habitat & Ecology — In rather open primary or secundary forest. On clayey, sandy soil or granitic sand. Altitude: 0–1000 m. Flowering: August–January, April; fruiting: May.

Affinities — No sequence data are available, but morphologically highly similar to species in the 'Riau pocket' clade (Fig. 1: group I_4), based on the lack of colleters and similarities in trichomes and leaf shape.

Vernacular names — Kelangin (Banka-Belingtung).

Note —*Croton laevifolius* is considered to be a synonym of *C. oblongus* (see Discussion; e.g., Airy Shaw1982a). *Croton oblongus* forms a species complex from which various species could be split off for Sumatra. This complex needs further study in the remaining distribution area.

12. *Croton macrocarpus* Ridl. — Fig. 2d

Croton macrocarpus Ridl. (1925) 332 (non Rchb. ex Müll.Arg. (1866) 698, nom. nud.). — *Croton grandifructus* Radcl.-Sm. & Govaerts (1997) 187, nom. superfl., see note 2. — Lectotype (designated here): *I.H. Burkill 6519* (lecto K [K000959163]*; isolecto A [00105623]*), Malaysia, Selangor, Telok Forest Reserve, Klang.

Treelets, c. 6 m tall, dbh c. 10 cm; young branchlets densely pubescent, hardly glabrescent. *Indumentum* consisting of creamy to

amber stellate trichomes with a darker brown centre, 0.3–0.6 mm diam (up to 1.2 mm on ovary), often slightly porrect, with one short central radius and 6–12 free radii. *Stipules* ensiform to subulate, 5–8 by 0.5–0.8 mm, densely pubescent on both sides, soon caducous. *Leaves* alternate; petiole (3–)6–13 cm long, round, slightly sulcate, at most slightly grooved above, densely to slightly pubescent; glands 1 or 2 pairs of distinctly stalked discs, lateral abaxially on the very apex of the petiole, 0.5–1 mm diam, stalk 0.3–1 mm long (Fig. 2d), additional smaller marginal glands common, 0.3–0.6 mm diam, stalk 0.2–0.5 mm long; blade elliptic, 15–30(–35) by 5–10 cm, 2.8–3.6 times longer than wide, chartaceous to subcoriaceous, base subcordate, margin (sub)serrate, teeth 2–6 mm apart, apex acuminate, adaxial side glabrous, but midrib pubescent, abaxial side slightly to densely pubescent, surface always visible except in very young leaves; venation distinct, raised on both sides, basally not to indistinctly triplinerved, secondary veins 13–17 pairs, higher order veins distinct on both sides. *Inflorescences* 1–4 per node, 11–35 cm long, erect, densely pubescent all over, basally 20–30 pistillate flowers, rarely 1–2 staminate flowers in the cymule of a pistillate flower, apically 1–4 staminate flowers per node; bracts narrowly triangular, 2–3.5 by 0.5–1.5 mm, outside with scattered trichomes, with a patch of simple trichomes on apex, inside glabrous, soon caducous. *Staminate flowers* 5–6 mm diam; pedicel 3–9(–11) mm long, round, densely pubescent; sepals triangular-ovate, c. 2.5–3 by 1.5–2 mm, outside pubescent near base to glabrous near apex, inside glabrous; petals oblong, 2–2.3 by 0.7–1 mm, outside glabrous; stamens c. 15, free, filaments 3–4 mm long, anthers c. 1 by 0.5 mm. *Pistillate flowers* 10–13 mm diam; pedicel c. 4 mm long (to 10 mm in fruit), sulcate, densely pubescent; sepals triangular-ovate to narrowly triangular, 4.5–6 by 2–3 mm, outside densely to slightly pubescent, with a patch of short simple trichomes on apex, much longer than ovary; petals triangular-ovate to ensiform, 2–2.5 by 0.4–0.7 mm, outside densely pubescent, hispid on margin and apex, not caducous; ovary globose, 3.5–5 by 3–4 mm, densely yellowish hispid, style absent, stigmas c. 7 mm long, once divided to c. 5.5 mm from apex, slightly pubescent near base. *Capsules* cylindrical globose, slightly trilobate, c. 28 mm high, c. 22 mm diam, sulcate, densely pubescent; pericarp very thick (c. 1.5 mm) and woody; columella c. 23 mm long. *Seeds* obovoid, heavily flattened, c. 19 by 13 mm, with a groove on the inside, glabrous, carunculate.

Distribution — *Malesia*: Malay Peninsula, Sumatra (Aceh).

Habitat & Ecology — Partly logged-over forest, dry land forest on rolling hills, yellow-red loamy soil. Altitude: c. 30–40 m. Flowering: August; fruiting: August.

Affinities — Related to *C. heterocarpus* (Fig. 1: group I_2) and should be classified in *C.* section *Furcaria* (Webster 1993), though that section still has to be corroborated phylogenetically.

Notes — 1. Only one collection from Sumatra (*de Wilde & de Wilde-Duyfjes 20590*, L) and one from the Malay Peninsula (*Burkill 6519*, A, K).

2. Radcliffe-Smith & Govaerts (1997) assumed that Müller's name (1866) was correct and regarded Ridley's name (Ridley 1925) as a later incorrect homonym. However, Müller only noted the name without a description, which makes it an invalid name. Therefore, Ridley's name is correct and Radcliffe-Smith & Govaerts created a superfluous name (see Esser 2002a: 21).

3. Two sequences, duplicates of the same collection, were used in the phylogenetic analysis. These showed up as a trichotomy in the cladogram (Fig. 1) with one specimen of *C. heterocarpus*. However, the branches leading to the two entries of *C. macrocarpus* are very short, which proves that they belong to the same specimen indeed.

13. *Croton scalaeus* J.Beyer, *sp. nov.* — Fig. 5

Lepidote trichomes present instead of stellate trichomes on the leaves and stems, differing from other species with lepidote trichomes (*C. adumbratus*, *C. argyratus* and *C. cascarilloides*) in the not completely covered abaxial leaf side (still epidermis visible in *C. scaleus*). Differs from *C.* cf. *coriifolius* based on larger and differently shaped stipules and small stalked leaf glands, whereas *C.* cf. *coriifolius* has larger and sessile leaf glands. Differs from *C. laevifolius* in the stellate trhichomes of up to 20 free radii, whereas the lepidote trichomes of *C. scalaeus* have more, 2–40, completely fused radii. The number of secondary veins in leaves of *C. scalaeus* is much higher than in the other species. — Type: *Haviland & Hose 1846* (holo L [L.2212508]!; iso L [L.2212509]!), Malaysia, Sarawak, 1st division, Kuching, 22 Feb. 1952.

Paratypes: *Buwalda 6681* (L [L.2203308]!), Indonesia, Sumatra, Riau, road from Sungei Berapit to Pekan Heran; *George et al. S 58358* (L [L.2210922!]), Malaysia, Borneo, Sarawak, Sri Aman Div., Selepong Lop, Rumah Ungin; *Pereira et al. 835* (L [L.2210921]!), Malaysia, Borneo, Sabah, Keningau, Nabawan, near Mukim Labau; *Yates 2227* (L [L.2203859]!), Indonesia, Sumatra, Sumatera Utara, Asahan, Kwala Masihi.

Woody, shrubs or trees; young branchlets slightly pubescent, soon glabrescent. *Indumentum* consisting of lepidote trichomes on stems and leaves, 0.1–0.3 mm diam, flat, with 20–40 (very hard to count) fused radii, and stellate to stellate-lepidote trichomes on inflorescences, 0.2–0.3 mm diam, flat, with 8–15 free to slightly fused radii. *Stipules* linear, 3–8 by 0.5–1 mm, with scattered trichomes to slightly pubescent, caducous. *Leaves* pseudo-verticillate; petiole 1–4 cm long, deeply grooved above, with scattered trichomes; glands lateral on the very apex of the petiole, slightly stalked to sessile but elevated, 0.4–0.8 mm diam, stalk 0.1–0.5 mm long; blade elliptic to slightly obovate, 7.5–13.5 by 3–6 cm, 2–2.6 times longer than

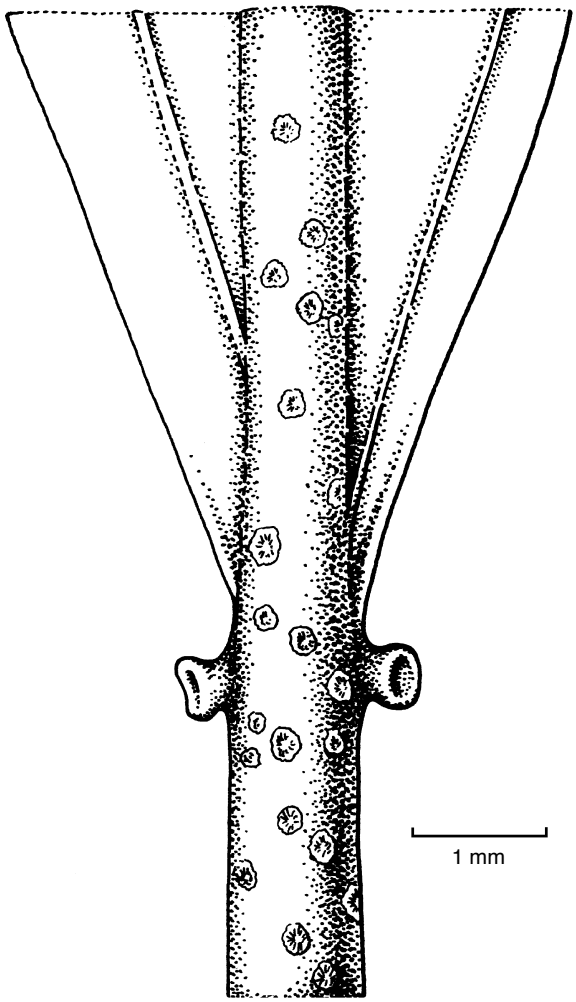

Fig. 5 Abaxial leaf surface of *Croton scalaeus* J.Beyer showing the extrafloral nectaries and the lepidote trichomes. — Illustration by Esmée Winkel, 2021.

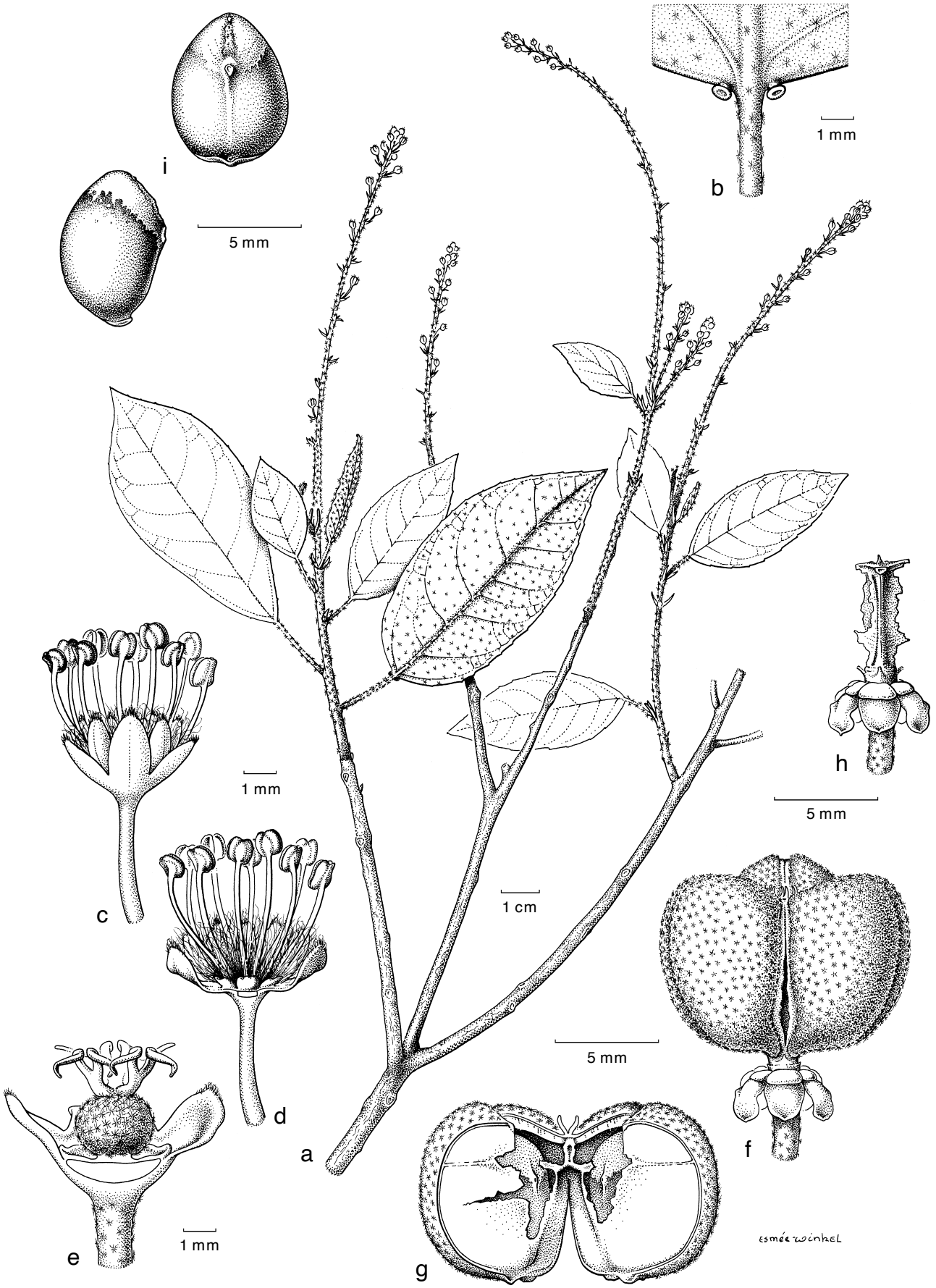

Fig. 6 *Coton simalurensis* J.Beyer. a. Habit; b. basal leaf glands, slightly elevated; c. staminate flower; d. staminate flower with part of sepals and petals removed; e. pistillate flower with part of sepals removed; f. fruit; g. part of fruit wall of septicidally dehisced fruit; h. columella; i. seeds in lateral and front view, with lighter colour (no caruncle) (a–d: *Achmad 299*; e: *Rahmat Si Boeea 9519*; f–i: *Achmad 298*; all L). — Illustration by Esmée Winkel, 2022.

wide, chartaceous to subcoriaceous, symmetric, base attenuate to obtuse but with very base attenuate, margin subentire, with hair patches or glands, apex acuminate, adaxial side glabrous, abaxial side with scattered trichomes near base, apically subglabrous, epidermis visible; venation distinct, sunken above, basally not triplinerved, secondary veins 9–13 pairs, higher order veins distinct below. *Inflorescences* 1–4 per node, 6–22 cm long, erect, basally up to 20 pistillate flowers, apically 1–5 staminate flowers per node; axis sulcate, subglabrous; bracts triangular-ovate, c. 1.5 by 0.5 mm, (sub)glabrous except for patch of simple trichomes on apex, caducous. *Staminate flowers* 3–4 mm diam; pedicel c. 2 mm long, round, glabrous; sepals triangular-ovate, c. 2 by 1 mm, outside; petals oblong, c. 2.2 by 0.5 mm, lanate on margin near apex, trichomes pointing inwards; stamens c. 11, free, filaments 2.5–3.5 mm long, anthers c. 0.5 by 0.3 mm. *Pistillate flowers* 3–3.5 mm diam; pedicel 2–3 mm long, with scattered trichomes; sepals triangular-ovate, 1.5–1.8 by 1–1.5 mm, longer than ovary, (sub)-glabrous except for a small patch of simple trichomes on apex; petals absent; ovary obovoid, c. 2 by 2 mm, deeply sulcate, slightly to densely pubescent; style absent; stigmas c. 1.5 mm long, apically once divided to c. 1 mm from apex, glabrous. *Capsules* 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. *Seeds* ellipsoid, 5–6 by 3.5–4.5 mm, glabrous, with a small caruncle.

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

Habitat & Ecology — Primary and secondary forest, kerangas. Altitude: close to sea level. Flowering: September, February, April; fruiting: September.

Affinities — Unknown, as the sequence data are lacking, but morphologically highly similar to the species in the 'Riau pocket' clade (Fig. 1: group I_4), based on the lack of colleters and similarities in trichomes and leaf shape.

Vernacular name — Ambin bua (Riau).

Note — The description is only based on two specimens from Sumatra, both with sparse inflorescences, and four specimens from Borneo. Distinctly different from other species in the *C. oblongus* complex by the presence of lepidote trichomes with a high number of fused radii instead of stellate trichomes with free radii.

14. *Croton simalurensis* J.Beyer, *sp. nov.* — Fig. 6

Characteristic for *C. simalurensis* are stalked leaf glands placed abaxially at the very base of the leaf, close to but not on the midrib; scattered but distinct trichomes on abaxial leaf side; large densely pubescent 3-lobed oblate capsules. *Croton simalurensis* was confused with *C. laevifolius* but can easily be distinguished by the location of leaf glands, as *C. laevifolius* has them on the apex of the petiole instead of the leaf blade. — Type: *Achmad 298* (holo L [L.2203305]!; iso U [U.1256144]!), Indonesia, Sumatra, Aceh, Simaloer (Simeulue).

Paratypes: *Achmad 99* (U [U.1256142]!); *Achmad 286* (L [L.2203303]!, U [U.1256145]!); *Achmad 299* (L [L.2203304]!, U [U.1256143]!); *Achmad 482* (L [L.2203861]!); *Achmad 870* (L [L.2203858]!); *Achmad 1100* (U [U.1256146]!); *Achmad 1780* (L [L.2203850]!), all *Achmad* collections from: Indonesia, Sumatra, Simaloer; *Rahmat Si Boeea 9364* (L [L.2203848]!), Indonesia, Sumatra East Coast, Asahan, Aek Moente; *Rahmat Si Boeea 9519* (L [L.2203849]!), Indonesia, Sumatra East Coast, Asahan, Tor Matoetoeng; *Rahmat Si Boeea 10029* (L [L.2203846]!), Indonesia, Sumatra East Coast, Asahan, Tomoean Dolok.

Woody, probably shrubs or trees; young branchlets densely pubescent, only partially glabrescent. *Indumentum* consisting of stellate trichomes, yellowish brown in the centre with whitish radii, 0.3–0.6 mm diam (0.1–0.6 mm diam on stems and capsules), flat (sometimes not flat on stems), with a central porrect radius, with (8–)15–25 free (or fused) radii. *Stipules* ensiform to subulate (occasionally narrowly triangular), 3–7(–9) by (0.4–)0.8–1.5 mm, densely pubescent on both sides. *Leaves* alternate; petiole (0.5–)1–5 cm long, slightly grooved above, with scattered but distinct trichomes to puberulous; glands abaxially at the very base of the leaf, close to but not on the midrib, slightly to distinctly stalked discs, (0.4–)0.6–1 mm diam, stalk 0.1–0.3 mm long; blade elliptic to obovate, 5.5–18 by 2.7–7.5 cm, 1.7–2.8 times longer than wide, chartaceous, base cuneate to obtuse, sometimes nearly rounded, margin in young leaves subserrate, soon almost entire, never with trichomes or glands at teeth, apex acuminate (rarely obtuse to rounded), adaxial side glabrous, abaxial side lighter than adaxial side when dried, trichomes scattered but distinctly pubescent (with surface always visible), more densely pubescent on the midrib and near the base, hardly glabrescent; venation distinct, sunken above, basally not triplinerved, secondary veins 8–10 pairs, higher order veins distinct below. *Inflorescences* 1(–4) per apical node, (7–)10–20 cm long, erect, basally 3–9 pistillate flowers, often 1 or 2 staminate flowers on same node as a pistillate flower, apically 1–4 staminate flowers per node; bracts triangular-ovate, 1.5–2.5 by 0.8–1.2 mm, subglabrous except for patch of simple trichomes on apex, quite persistent. *Staminate flowers* 3–4 mm diam; pedicel 1.5–4 mm long, round, with scattered trichomes to glabrous; sepals ovate, c. 2 by 1.5 mm, fused at base, subglabrous outside; petals oblong, c. 2 by 0.5 mm, outside glabrous; stamens 10–12, free, filaments 2.5–3.5 mm long, anthers c. 0.7 by 0.4 mm. *Pistillate flowers* 5–6 mm diam; pedicel 3–6 mm long with scattered but distinct trichomes to puberulous; sepals ovate to elliptic, c. 3 by 2 mm, fused at very base, apex acute, outside puberulous near base to glabrous near apex, with patch of simple trichomes on apex, inside glabrous, longer than ovary; petals filiform, c. 2 by 0.1 mm, usually absent; ovary globose, c. 2 by 2 mm, very densely yellowish pubescent, style less than 0.1 mm long; stigmas 2.5–4 mm long, thickened at base, once divided to 1.5–3 mm from apex. *Capsules* distinctly 3-lobed, oblate, 7–9 mm high by 10–12 diam, lobes conchiform, heavily sulcate, surface rough, densely pubescent, apex slightly depressed; pericarp 0.4–0.6 mm thick; columella 6–7 mm long. *Seeds* ovoid, c. 6 by 5 mm, glabrous, carunculate.

Distribution — *Malesia*: Endemic to Sumatra (Aceh (Simalur Isl.), Sumatera Utara).

Habitat & Ecology — Altitude: to 1000 m. Flowering: January, March, June–August; fruiting: March, June, November.

Affinities — Riau pocket group (Van Ee et al. 2015).

Vernacular names — Dulu Dulu, Lasa-Lasa (Simalur); Kajoe depdep batoe (*Rahmat Si Boeea 9364*); Kayu Polir Aek (Sumatera Utara).

Notes — 1. No ecological information is known from the collections of Sumatra, where it was mainly collected on Simalur island.

2. The capsules can be affected by insects and become galled, being larger and seemingly more than 3-locular. Affected capsules are also less pubescent than regular ones and they are more oblate in shape. Highly affected capsules often have 1 to 3 holes in their pericarp possibly made by the insects.

15. *Croton tiglium* L.

Croton tiglium L. (1753) 1004; Müll.Arg. (1866) 600; Hook.f. (1887) 393; 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. — *Tiglium officinale* Klotzsch (1843b) 418. — *Oxydectes tiglium* (L.) Kuntze (1891) 614. — *Croton officinalis* (Klotzsch) Alston (1931) 264, nom. illeg.,

superfl. — Lectotype (first step designated by Chakrabarty & Balakrishnan 1997; second step by Philcox 1997): *Herb. Hermann 2: 6, no. 343* (lecto BM [BM000621766]*), Sri Lanka. Other original material: BM [BM000621766]* (*Herb. Hermann 2: 76, no.343*), [BM000621811]* (*Herb. Hermann 3: 6, no. 343*), [BM000628053]* (*Herb. Hermann 4: 10 no. 343*]), Sri Lanka.

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

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

Croton tiglium L. var. *globosus* J.J.Sm. (1910) 349. — Lectotype (designated here): *Koorders 14426* (lecto L [L.2212249]!; isolecto L [L.2212250]!, U [U.1256074]!), Java, Prov. Besoeki, Pantjoer Idjen, 1000 m. **Syn. nov.**

For other synonyms see World Flora Online (http://www.plantsoftheworldonline.org/); more will be incorporated when other regions of Malesia are treated.

Shrubs or trees, to 6 m tall, diam to 15 cm; young branchlets with scattered trichomes, soon glabrescent. *Indumentum* consisting only of yellowish stellate trichomes, 0.2–0.9 mm diam on leaves, up to 0.5 mm on stems, flat, often with a short central porrect radius, with 9–15 free radii. *Stipules* filiform to ensiform, (0.5–)1.5–3(–4) mm long, densely pubescent on both sides to subglabrous, caducous. *Leaves* alternate; petiole 3–8(–10) cm long, hardly to shallowly grooved above, with scattered trichomes to subglabrous; glands always lateral on the basal leaf margin close to but not on the midrib, 0.5–1 mm diam, sessile to slightly stalked (always less than 0.5 mm long), marginal teeth often topped by colleters; blade ovate (to elliptic), 6–18.5 by 4–9 cm, (1.7–)1.9–2.3 times longer than wide, membranous, base obtuse with very base attenuate, margin slightly serrate to subentire, teeth 3–6 mm apart, without glands, apex mostly acuminate, sometimes acute, abaxial side slightly lighter then adaxial side when dry, with scattered trichomes to subglabrous on both surfaces, sometimes more densely pubescent at the very base of the bigger veins, epidermis visible; venation very distinctly triplinerved, actinodromous, with 3(–5) prominent basal veins, secondary veins 4–6 pairs. *Inflorescences* thyrsoid, 1–3 per whorl, (4–)7–13 cm long, erect, basally 4–10 pistillate flowers, sometimes 1 or 2 staminate flowers at the same node as a pistillate flower, apically 1–3 staminate flowers per node; axis with scattered trichomes to subglabrous; bracts triangular-ovate, 2–4 by 0.5–1 mm (staminate ones smaller than pistillate ones), quite glabrous, eglandular, caducous to persistent. *Staminate flowers* 4–4.5 mm diam; pedicel 3–5 mm long, subglabrous; sepals triangular-ovate, c. 2.5 by (1.5–)2 mm, subglabrous outside; petals oblong, c. 2 by 1 mm, glabrous outside; stamens 15–20, free, filaments 1–3.5 mm long, anthers c. 0.6 by 0.5 mm. *Pistillate flowers* 6–8 mm diam; pedicel 3–5 mm long, densely pubescent; sepals triangular, 2.5–3.5 by 1–2 mm, fused at base, apically spreading, slightly longer than ovary or as high, outside subglabrous, with a patch of simple trichomes on the very apex; petals absent; ovary distinctly 3-locular, globose to slightly ovoid, 3–4 by 2–3 mm, densely pubescent; stigmas 4–6 mm long, once divided to 3–4 mm from apex. *Capsules* 3-lobed, prolate, 18–25 by c. 15 mm, sulcate, surface with scattered trichomes to subglabrous; pericarp fragile and thin (less than 1 mm thick); columella c. 17 mm long. *Seeds* prolate, one side slightly flattened, c. 13 by 8 mm, glabrous, with small caruncle.

Distribution — Naturally occurring in Sri Lanka, India, through SE Asia to China, and in *Malesia* from the Malay Peninsula to the Philippines and the Moluccas, though it is often not possible to ascertain if a specimen was collected in the wild (check https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:343631-1; last visited on 5 August 2022). Cultivated and introduced in North America and Africa. On Sumatra in Sumatera Utara, Sumatera Barat, Jambi.

Habitat & Ecology — Mostly in evergreen secondary forest. Altitude: sea level to 1100 m. Flowering: May–October; fruiting: May–August.

Affinities — *Croton* section *Croton* (Van Ee & Berry 2010b).

Vernacular names — Simalakian (Burkill 1935); Croton oil plant (English).

Uses — Burkill (1935): Seeds or oil of seeds is used in very low doses (at most 1 seed or 1 drop) as purgatives, but very poisonous (blistering mouth and intestines if too much, blistering and inflamating skin); therefore also used for poisoning humans, and in hunting to stupefy fish or to make poison arrows (bark and leaves also suitable for that purpose). The seed oil can also be used for illumination, but only outdoors as the fumes are poisonous, same if the wood is used as firewood. Still, in former times planted for the seed oil, which was exported to Europe; today the market is limited to some medical treatments, especially for skin peeling.

16. *Croton viridifolius* J.Beyer, *sp. nov.* — Fig. 2c, 7

Unique on Sumatra are the small and narrow leaves (2.5–7.2 by 0.7–2.2 cm), the few (4–6) secondary veins, the light green colour after drying, the short inflorescences (only 0.5–2.5 cm long) and very narrow pistillate sepals. — Type: *Kleinhoonte 460* (holo L [L.2212218]!), Indonesia, Sumatera Barat, Sarasah Bunta.

Shrubs or trees; young branchlets densely pubescent, soon glabrescent. *Indumentum* consisting of whitish to yellowish brown stellate trichomes, 0.2–0.4 mm diam, flat, often with a short central porrect radius, with 15–25 free to slightly fused radii (occasionally completely fused on stems). *Stipules* triangular-ovate to ensiform, 0.6–2 by 0.2–0.8 mm, densely pubescent on both sides, caducous. *Leaves* alternate to apically crowded; petiole 0.3–1(–1.5) cm long, deeply grooved above, with scattered trichomes to slightly pubescent; glands as slightly stalked discs abaxially at the very base of the leaf (Fig. 2c), close to but almost never on the midrib base, diam 0.2–0.4 mm, stalk 0.1–0.2 mm long; blade narrowly elliptic, 2.5–7.2 by 0.7–2.2 cm, 2.4–4.2 times longer than wide, chartaceous, symmetric, base obtuse, margin entire, flat (to slightly revolute), without glands, apex acute to obtuse, adaxially initially with scattered trichomes (more dense near large veins), glabrescent, abaxially with scattered distinct trichomes, epidermis visible; venation distinct, basally slightly to not triplinerved, secondary veins 4–6 pairs. *Inflorescences* thyrsoid, solitary per apical node, unisexual, 0.5–2.5 cm long; bracts triangular-ovate, c. 0.5 by 0.5 mm, slightly pubescent, caducous. *Staminate flowers* c. 3 mm diam; pedicel 1–2 mm long, round, subglabrous; sepals triangular-ovate, 1–1.5 by 0.5–1 mm, subglabrous outside, with a patch of simple trichomes on apex; petals ensiform, c. 1.8 by 0.3 mm, outside glabrous, lanate on margin and inside; stamens 10 or 11, free, filaments c. 1.5 mm long, anthers c. 0.4 by 0.5 mm, connective pilose. *Pistillate flowers* c. 3 mm diam; pedicel 1–2 mm long, sulcate, densely pubescent; sepals triangular, c. 1.4 by 0.8 mm, fused at the base, spreading at the apex, outside slightly pubescent (denser near base), with a patch of simple trichomes on apex, as high as to slightly shorter than ovary; petals absent; ovary 3-lobed, subglobose, c. 1.2 by 1.4 mm, densely yellowish pubescent; style absent; stigmas c. 2 mm long, fused at base, once divided to c. 1.6 mm from apex. *Capsules* unknown, columella c. 4.5 mm long. *Seeds* young, likely with small caruncle.

Distribution — *Malesia*: Endemic to Sumatra (Sumatera Barat).

Habitat & Ecology — Habitat unknown. Altitude: c. 500 m. Flowering and fruiting: only known from August.

Affinities — Riau pocket group (Van Ee et al. 2015).

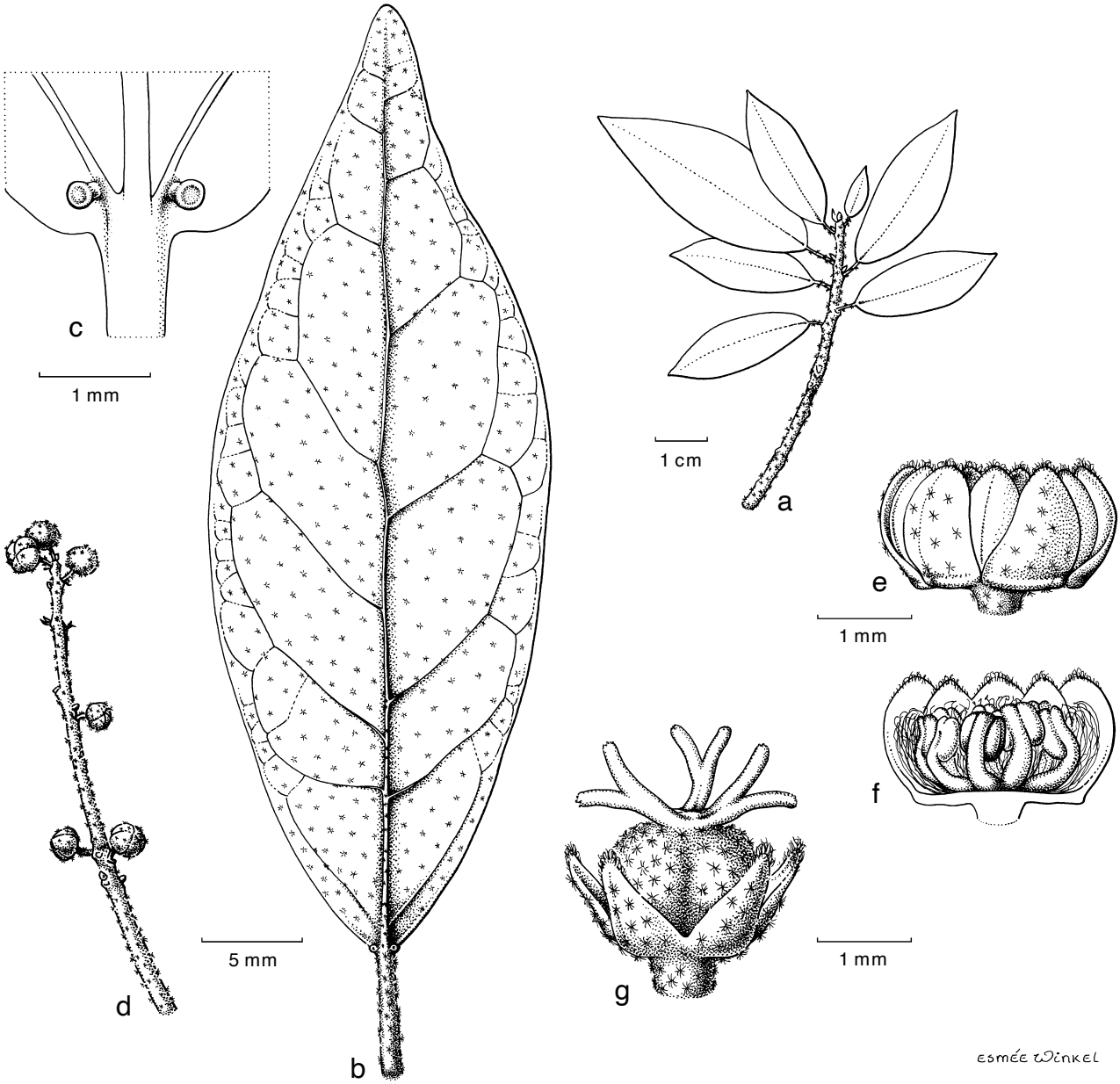

Fig. 7 *Croton viridifolius* J.Beyer. a. Habit; b. abaxial leaf surface; c. extrafloral nectaries abaxially; d. part of inflorescence; e. staminate flower; f. staminate flower with part of sepals removed showing androecium; g. pistillate flower (*Kleinhoonte 460*, L). — Illustration by Esmée Winkel, 2022.

Notes — 1. Only known from one specimen, originally identified by Van Steenis as *Croton verreauxii* Baill. But the specimen shows limited to no similarity with the Australian specimens of *C. verreauxii*.

2. Most similar species are *C. gageianus* (also having short inflorescences and a narrow leaf blade) and *C. simalurensis* (due to similar indumentum and location of leaf glands) but *C. viridifolius* can easily be distinguished by the small leaves and few secondary veins.

3. The inflorescences appear as unisexual, but this is likely typical for this specimen.

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IDENTIFICATION LIST OF *CROTON* SPECIMENS OF SUMATRA EXAMINED

The numbers after the collector numbers are the same ones used in the text and refer to the following species:

1 = *Croton adumbratus* Croizat
2 = *Croton argyratus* Blume
3 = *Croton beccarii* J.Beyer
4 = *Croton cascarilloides* Raeusch.
5 = *Croton caudatus* Geiseler
6 = *Croton coriifolius* Airy Shaw
7 = *Croton gageianus* P.T.Li
8 = *Croton griffithii* Hook.f.
9 = *Croton heterocarpus* Müll.Arg.
10 = *Croton hirtus* L'Hér.
11 = *Croton laevifolius* Blume
12 = *Croton macrocarpus* Ridl.
13 = *Croton scalaeus* J.Beyer
14 = *Croton simalurensis* J.Beyer
15 = *Croton tiglium* L.
16 = *Croton viridifolius* J.Beyer

Achmad 99: 14; 286: 14; 298: 14; 299: 14; 482: 14; 870: 14; 1100: 14; 1780: 14 – Afstriastini 1932 A: 8; 2732: 8; 2750: 11 – Alston 15234: 1 – Amjah 754: 9; 958: 9.

Bakhuizen van den Brink Jr 966: 10 – Bakhuizen van den Brink Sr 3173: 2 – Barlett 8710: 5 – Bartlett & la Rue 43: 5 – Beccari PS 527: 2; PS 973: 3 – Blume 1473: 11 – Bruinier 10: 6 – Bünnemeijer 1443: 1; 1912: 1; 1994: 11; 7263: 8 – Burkill 6519: 12 – Burley Turkirin et al. 1468: 2; 1888: 2 – Buwalda 6315: 11; 6681: 13.

Chew 82: 8 – Chin & Mustafa 3350: 5 – Cockburn KEP FRI 8270: 8 – Cuming 1384: 4 – Curtis 1585: 8.

De Fretes 5758: 15 – De Raadt 67: 5; 68: 5 – De Vogel 1446: 2; 2758: 1; 3003: 4 – De Vogel & Vermeulen 7534: 11 – De Wilde & De Wilde-Duyfjes 12409: 2; 12603: 2; 12608: 2; 16461: 2; 18103: 7; 19604: 1; 20147: 1; 20590: 12; 20725: 1; 21178: 5 – Diepenhorst HB 2094: 2; HB 2527: 2 – Dirksen 28: 2 – Dorst 83.T.1P 144: 2.

Elmer 12872: 2; 21011: 1; 21201: 2; 21559: 2.

Forbes 2989: 5; 3002: 5; 3200: 5.

Gardette 1517: 5; 1526: 5 – George et al. S 58358: 13 – Gianno 239: 5 – Grashoff 864: 6; 1114: 1 – Griffith 1166: 5; 2518: 5; KD 4775: 5; KD 4778: 8; KD 4781: 8; KD 4783: 9; KD 4784: 5.

Hallier 347 b: 10 – Harmand 631: 4 – Haviland & Hose 1846: 13 – Hermann Herb. 2: 6, no. 343: 15; Herb. 2: 76, no. 343: 15; Herb. 3: 6, no. 343: 15; Herb. 4: 10 no. 343: 15 – Huc 254: 1.

Iboet 314: 2 – Iwatsuki, Murata, JDransfield & Saerudin 284: 9.

James et al. S 33740: 8.

Kadim & Noor KN 162: 8 – Kerr 21309: 5 – King's Collector 1115: 8; 4484: 8; 4629: 8; 4820: 8; 6157: 8 – Kleinhoonte 460: 16 – Kochummen KEP FRI 2220: 8 – Koelz 22687: 5 – Koop 99: 2 – Koorders 14426: 15; 19643: 11 – Kornassi 561: 15 – Kostermans S 69: 10 – Kostermans & Anta 2: 11; 859: 5; 885: 5; 910: 11; 967: 11; 1103: 5; 1245: 1; 1339: 1 – Krukoff 4010: 1; 4022: 1; 4281: 1.

Lam 2290: 2 – Laumonier TFB 3980: 2; TFB 4087: 7; TFB 4190: 7 – Lörzing 3216: 9; 5176: 2; 9669: 5; 13910: 9.

Maingay 1406: 8; KD 1376: 5 – Mamit S 35130: 8 – Maxwell 82-286: 5; 86-487: 4; 95-1297: 4 – Meijer 3697: 2; 7294: 2 – Meijer & Amiroeddin et al. 35: 11 – Meijer & Vermeulen 5400: 11 – Merrill Species Blancoanae 308: 15 – Middleton, Suddee & Hemrat 1209: 4 – Mollema 818/132: 10 – Motley 758: 2.

Ngadiman bin Ismail SFN 34737: 8 – Ngamasu 3167: 7; 3248: 1.

Ouwehand 273: 15.

Pereira et al. 835: 13 – Pierre 6233: 4 – Poilane 793: 2; 1725: 4; 10273: 2 – Posthumus 788: 1; 1003: 15; 1080: 6 – Purseglove 5609: 6.

Rahayu 327: 15 – Rahayu & Maskuri 386: 4 – Rahmat si Boeea 377: 2; 3512: 6; 3959: 2; 5241: 2; 9364: 14; 9519: 14; 9947: 15; 10029: 14 – Ramos & Edaño BS 43977: 2 – Ridley 12176: 7; 12194: 7 – Rutten 243: 2; 1884: 2.

Samat bin Abdullah 193: 8 – Scortechini 1423: 8 – Sinclair SFN 39510: 7 – Smitinand & Sleumer et al. 1162: 4.

Teijsmann HB 3499: 11; HB 4188: 9; HB 11033: 1 – Torquebiau 87: 2.

Van Balgooy 2722: 8 – Van Borssum Waalkes 1770: 4 – Verboom 32: 10.

Wallich numerical list 7754: 8; 8938: 5 – Whitmore & Sidiyasa 3297: 2 – Winckel 1789 B: 11; 1842 B: 11 – Worthington 12294: 10.

Yates 2227: 13.

Zollinger 642: 5; 963-Z: 2; 3212: 2; 3809: 2; 3982: 9.

Appendix Samples of *Croton* (*Euphorbiaceae*) and related genera used in the phylogenetic analysis.

Taxon; locality; voucher (herbarium); GenBank accession number ITS. All sequences from GenBank were previously used in Van Ee et al. (2015). Newly generated sequences, indicated with an *, are split up into two separate sequences due to the used primers: GenBank accession numbers ON000835–ON000846 are for ITS1, GenBank accession numbers ON004098–ON004110 are for ITS2 (— = missing).

Astraea lobata (L.) Klotzsch; Costa Rica, Guanacaste; *Van Ee 296* (WIS); EF421720. ***Brasiliocroton mamoninha*** P.E.Berry & Cordeiro; Brazil, Maranhão; *Lobo et al. 340* (NY); AY971174. ***Croton acronychioides*** F.Muell.; Australia, Queensland; *Forster PIF29213* (WIS); KP878314. ***C. acutifolius*** Esser; Thailand, Chiang Mai; *Wongprasert & Khaoiam isolate 0212-33*; AB375078. ***C. adenophorus*** Baill.; Comoros, Mayotte; *Hladik 6558* (P); KP878316. ***C. adumbratus*** Croizat; Indonesia, Sumatra; *Krukoff 402* (L); ON000845*, ON004108*. Indonesia, Sumatra; *de Wilde & de Wilde-Duyfjes 19604* (L); ON000846*, ON004110*. ***C. arboreus*** Millsp.; Mexico, Quintana Roo; *Van Ee 472* (WIS); EU478029. ***C. argyratus*** Blume; Malaysia, Selangor; *Van Ee & Sugumaram 790* (A); HM564075. Thailand, Nara Thiwas; *Pooma et al. 1901*; AB375093. ***C. aridus*** P.I.Forst.; Australia, Western Australia; *Mitchell PRP1823* (BRI); KP878317. ***C. arnhemicus*** Müll.Arg.; Australia, Queensland; *Fell DGF10501* (BRI); KP878319. ***C. bastardii*** Leandri; Madagascar, Mahajanga; *Van Ee 1035* (MICH); KP878324. ***C. billbergianus*** Müll. Arg.; Costa Rica; *Van Ee 342* (WIS); EU477998, ***C. brachypus*** Airy Shaw; Australia, Queensland; *Forster PIF15441* (BRI); KP878325. ***C. bracteatus*** Lam.; Madagascar, Fianarantsoa; *Schatz 3185* (MO); AY971186. ***C. capitis-york*** Airy Shaw; Australia, Queensland; *Forster et al. PIF10331* (BRI); KP878326. ***C. cassinoides*** Lam.; Madagascar, Toliara; *Van Ee* 919 (MICH); KP878328. ***C. caudatus*** Geiseler; Philippines, Palawan; *Soejarto 7728* (MO); AY971192. Australia, Queensland; *Forster et al. PIF13570* (BRI); KP878329. Indonesia, Sumatra; *Rahmat Si Boeea 377* (L); ON000844*, ON004107*. ***C. cascarilloides*** Raeusch.; Thailand, Chanthaburi; *Esser 2001-1* (WIS); AY971191. *Suddee et al. isolate 2129*; AB375088. ***C. choristadenius*** K.Schum.; Australia, Queensland; *Forster et al. PIF21326* (BRI); KP878330. ***C. chrysodaphne*** Baill. [= ***C. lepidotus*** Aug. DC.]; Madagascar, Toamasina; *Van Ee 998* (MICH); HM564085. ***C. consanguineus*** Müll.Arg.; Philippines, Western Visayas; *Nickrent et al. 5540* (A); KP878333. ***C. columnaris*** Airy Shaw; Thailand, Udon Thani; *Rinthong isolate 05001*; AB375080. ***C. consanguineus*** Müll.Arg.; Philippines, Western Visayas; *Nickrent et al. 5540* (A); KP878333. ***C. cordatulus*** Airy Shaw; France, New Caledonia; *McKee 39152* (A); KP878334. ***C. coriifolius*** Airy Shaw; Malaysia, Sarawak (Borneo); *Van Ee & Wurdack s.n.* (US); KP878383; Malaysia, Sarawak (Borneo); Eerwog s.n.; AY971199. ***C. cotoneaster*** Müll.Arg.; Madagascar, Toliara; *Van Ee et al. 870B* (MICH); KP878335, ***C. crassifolius*** Geiseler; Thailand, Nong Khai; *Esser 98-157* (A); AY971200. Thailand, Nakhon Pathom; *Rinthong isolate 05002*; AB375089. ***C. decalvatus*** Esser; Thailand, Chantaburi; *Chayamarit 1961*; AB375075. Thailand, Srakeaw; *Greijmans 70-98*; AB375076. ***C. densivestitus*** C.T.White &W.D.Francis; Australia, Queensland; *Forster et al. PIF28215* (WIS); KP878336. ***C. dichogamus*** Pax; Kenya, Coast Province; *Morawetz 406* (MICH); KP878337. ***C. dockrillii*** Airy Shaw; Australia, Queensland; *Sankowsky 1444* (BRI); KP878384. ***C. emeliae*** Baill.; Comoros, Mayotte; *Barthelat 1315* (P); KP878340. ***C. euryphyllus*** W.W.Sm.; China, Yunnan; *npccDNA10*; KC758673. ***C. farinosus*** Lam.; Madagascar, Toliara; *Van Ee 917* (MICH); KP878341. ***C. fluviatilis*** Esser; Thailand, Kaeng Lam Duan; *Pooma 7386* (BKF); KP878385. ***C. gageianus*** P.T.Li; Indonesia, Sumatra; *Laumonier TFB 4087* (L); ON000838*, ON004101*. Indonesia, Sumatra; *Nagamasu 3167* (L); ON000840*, ON004103*. Indonesia, Sumatra; *de Wilde & de Wilde-Duyfjes 18103* (L); ON000842*, ON004105*. ***C. glabellus*** L. [= ***C. lucidus*** sensu auct]; Cuba, Habana; *Van Ee 378* (WIS); EF421765. ***C. grangerioides*** Bojer ex Baill.; Mauritius; *Haevermans 561* (P); KP878342. ***C. gratissimus*** Burch. [= ***C. zambesicus*** Müll.Arg.]; *Wurdack D536* (US); Cultivated, New York Botanical Garden, native to Africa; AY971214. ***C. griffithii*** Hook.f.; Indonesia, Sumatra; *Afriastini 1932 A* (L); ON000839*, ON004102*. Malaysia, Malaya; *van Balgooy 2722* (L); ON000841*, ON004104*. ***C. haumanianus*** J. Léonard; Congo; *Amsini 337* (DAV); KP878343. ***C. heterocarpus*** Müll.Arg.; Indonesia, Sumatra; *Iwatsuki 284* (L); ON000835*, ON004098*. ***C. hirtus*** L'Her; unknown; *van Ee 481*; EU478071. ***C. hutchinsonianus*** Hosseus; Thailand, Kamphaeng Phet; *Esser 99-8* (WIS); AY971218. ***C. humilis*** L.; Mexico, Yucatán; *Van Ee 1773* (MAPR); KP878371. ***C. kerrii*** Airy Shaw; Thailand, Uttaradit; *Esser 98-233* (WIS); AY971221. ***C. macrocarpus*** Ridl.; Indonesia, Sumatra; *de Wilde & de Wilde-Duyfjes 20590*, sheet 1 (L); ON000836*, ON004099*. Indonesia, Sumatra; *de Wilde & de Wilde-Duyfjes 20590*, sheet 2 (L); ON000837*, ON004100*. ***C. microtiglium*** Burkill; Tonga; *Drake 375* (BISH); AY971234. ***C. rheophyticus*** Airy Shaw; Malaysia, Sabah (Borneo); *S.A.N. 147988* (KLU); KP878387. ***C. schultzii*** Benth.; Australia, Northern Territory; *Forster & Russell-Smith PIF5918* (BRI); KP878389. Australia, Northern Territory; *Russell-Smith & Lucas 8123* (BRI); KP878390. ***C. simalurensis*** J.Beyer; Indonesia, Sumatra; *Rahmat Si Boeea 9364* (L); ON004109*, —. ***C. tiglium*** L.; Thailand; *Suddee et al. 2134*; AB375092. China; *PS0167MT02*; GU441808. China, Yunnan; *npccDNA12*; KC758676. ***C. verreauxii*** Baill.; Cultivated, Sydney Botanical Garden, native to Australia; *Berry 7683* (WIS); AY971257. ***C. viridifolius*** J.Beyer; Indonesia, Sumatra; *Kleinhoonte A 460* (L); ON000843*, ON004106*.