

CRYPTERONIACEAE (R. J. van Beusekom-Osinga, Leyden)

Evergreen trees. Twigs terete to quadrangular, the younger ones mostly with four narrow ribs or wings, with thickened nodes, petiole-bases mostly connected by a faint line. *Leaves* with minute or rudimentary stipules, opposite, simple, entire, penninerved, shortly petioled, with arched or almost straight nerves mostly anastomosing in a marginal vein. *Inflorescence* terminal or axillary, sometimes below the leaves, paniculate, copiously branched to extremely depauperate, branched up to the third order, with decussate side axes which are sometimes arranged (sub)verticillately or subumbellately by contraction, either ending in profuse to very poor racemules, or in cymoid florescences. Bracts mostly small to minute, sometimes with rudimentary stipules. *Flowers* (very) small, shortly pedicelled, bisexual, sometimes by reduction unisexual and then trees dioecious, actinomorphic, peritogynous, (4-)5(-6)-isomerous, sometimes with twice the number of stamens; receptacle widely campanulate. *Sepals* valvate, triangular to deltoid, mostly persistent. *Petals* more or less rudimentary, sometimes absent, alternisepalous, inserted on the margin of the receptacle, inflexed and enveloping the stamens, valvate, rarely imbricate, sometimes cohering, soon caducous. *Stamens* if isomerous epipetalous, (alternisepalous), inserted on the margin of the receptacle, inflexed in bud, persistent or caducous; filaments sometimes very short; connective wide, with or without a tendency to conduplication, or completely conduplicate, sometimes with a dorsal tubercle or a large outgrowth; anthers adnate, marginal or submarginal, linear to semiorbicular, lengthwise dehiscent, introrse to latrorse. *Ovary* superior or inferior, 2-4(-5)-carpellate, 1-6-locular, septs not, or rarely partly, connate; style terminal, rather long to short, \pm terete, mostly persistent; stigma capitate or punctate. *Ovules* situated in horizontal or vertical position, 1, 2, 3, or many per locule, anatropous; placentation parietal, septal, or basal. *Fruit* superior or $1/2$ - or $3/4$ -inferior, a chartaceous or woody capsule, subglobose to ellipsoid, small to big, loculicidally dehiscent with 2-6 valves, on the top often with the persistent style and stigma. *Seeds* few or many, flat, usually small, depressed-ellipsoid, situated basally, apically, centrally, or laterally in its membranous wing in which the raphe is running freely; endosperm none; embryo straight.

Distribution. Pantropical, 5 genera and 11 *spp.*, 3 genera in Indo-Malesia (of which one endemic in Borneo), one monotypic genus in S. Africa (*Rhynchoalyx*) and one in Peru and Bolivia (*Alzatea*).

Ecology. Lowland and hill tropical forest, up to 1300 (-1700) m, mostly in rain-forest, but *Crypteronia paniculata* not shunning a more or less seasonal climate.

Dactylocladus stenostachys is a characteristic peat swamp forest tree.

Young branches of *Crypteronia macrophylla* are frequently inhabited by ants.

Young foliage seems often bright coloured: in *Axinandra* innovations are mauve, while in *Crypteronia paniculata* young leaves and twigs are deep blue or violet turning pinkish brown then green (CORNER), in other species they are purplish.

Morphology. In all genera the nodes of the twigs are thickened and a characteristic transversal ridge or line, sometimes faint (absent in *Rhynchoalyx*), connects the leaf-bases. On the internodes four lengthwise raised lines or narrow wings occur, especially distinct in the upper part of young twigs; they wear off later.

The leaves offer no significant characters, but interesting is the occurrence of ephemeral rudimentary stipules which can only be observed on innovations. These are common among

Myrtalean families, but obviously absent in *Melastomataceae*, where these structures were not found in a sampling of fifteen genera.

The petals in *Crypteroniaceae* are reduced to a varying degree or are even totally absent (in *Crypteronia*). Moreover, they are always soon caducous, except in *Alzatea* where they are almost invisible and mucilaginous. In all genera they are conduplicate and enveloping the inflexed stamens as a hood. In *Dactylocladus* and *Rhynchochalyx* they are minute and unguiculate; in *Axinandra* they are proportionally bigger, and have a broad instead of an unguiculate base. The petals of *Axinandra* are complicated and show a highly interesting specialization; they are coherent to connate, together having the shape of an umbrella or a mushroom. Their wide, tapering basal parts together form the awning of the umbrella, the narrow, coherent, median parts form the stem of the umbrella, and often there are wider, frayed, reflexed, apical parts of the petals together forming the handle of the umbrella (or the 'root' of the mushroom). This whole structure envelops the stamens very closely, and drops when the flower opens and the inflexed stamens stretch. It is, furthermore, interesting that these petals of *Axinandra*, depending on the species, can be valvate-connate, valvate- (or somewhat imbricate-)conduplicate, or imbricate-contorted.

Several petal characters of *Crypteroniaceae* are found again scattered in other Myrtalean families. Reduction, absence, as well as caducousness of petals occurs sporadically in almost all of these families. Unguiculate petals are more or less characteristic for *Lythraceae*, but are also found in *Sonneratiaceae* (*Duabanga*), and in *Rhizophoraceae* (e.g. *Carallia*). Connate petals with a broad base, sometimes fused to a 'cap' occur in *Myrtaceae*. Coherence of petals is also present in *Rhizophoraceae* (*Ceriops*). Valvate and imbricate petals, both found in one genus, *Axinandra*, are usually family characters in *Myrtales*. Contorted petals are, apart from *Axinandra*, only found in *Melastomataceae*.

The enveloping of the stamens by the petals in all petal-bearing Crypteroniaceous genera is almost unique in *Myrtales*, being only found in a few *Rhizophoraceae* (*Rhizophora* and *Bruguiera*). However, in the latter family the petals do not cover the stamens as a hood, as is the case in *Crypteroniaceae*. This is one of the characters upon which the identity of *Crypteroniaceae* as a family is based.

The stamens in *Crypteroniaceae* are arranged in one isomerous epipetalous (alternisepalous) whorl, except in *Axinandra*, where one diplostemonous whorl is present. In general number and position of the stamens in *Myrtales* can be derived from a situation with two isomerous whorls, either by reduction or by polymerisation ('dédoublement') and multiplication. Arrangement of stamens in two isomerous whorls, the diplostemonous androecium, is mostly considered to represent the basic structure of the androecium in *Myrtales*. MELCHIOR (in Engl. Syllabus 2, 1964, 345) distinguished for the androecium in *Myrtales* two progressive trends both starting from the diplostemonous androecium, viz multiplication into many stamens in many whorls and reduction towards the haplostemonous state and even eventually to 3, 2, or 1 stamen(s).

In all Crypteroniaceous genera the stamens are inflexed in bud. This is a widespread character in *Myrtales*, being rather typical for this order. In some families (*Myrtaceae*, *Rhizophoraceae*) it is not present in all genera, and *Lythraceae*, *Onagraceae*, and *Haloragidaceae* are the only families in which it is totally absent. The total absence of inflexed stamens in the *Lythraceae* is another fact which militates against inclusion of Crypteroniaceous genera in that family.

The gynoecea of the Crypteroniaceous genera are distinguished by cells which are divided by interrupted septa, though these may touch each other in the centre of the gynoeceum. This (hemi)synplicate condition is very rare and assumed to be primitive within the *Myrtales*, in which it is only found in *Crypteroniaceae* and in a few genera of *Myrtaceae*.

The capsules of *Crypteronia* and *Axinandra* show interesting specialized structures with a functional significance with regard to opening and closing of the capsule. The mechanisms for this are based upon hygroscopical properties of fibres in vascular bundles.

The morphology of the seed in the *Crypteroniaceae* is peculiar. The seed-coat forms a flat, membranous wing, through which the raphe is running from the insertion to the top where it usually takes a more or less sharp turn, and runs back towards the seed proper, which either takes a central, apical, lateral, or basal position in the wing. This is another assumedly primitive character within *Myrtales*, again only found in *Crypteroniaceae* and in a few genera of *Myrtaceae*.

This character is also rare in other orders. It was first discovered in the *Trochodendraceae* and is, therefore, indicated by me as the Trochodendraceous seed type.

Summarizing, we find that almost the whole variety of floral characters in the *Crypteroniaceae* is also found scattered in other Myrtalean families. In this respect the *Crypteroniaceae* are rather heterogeneous, though not more than for instance the *Myrtaceae* and the *Melastomataceae*. On the other hand, the family is unique in the *Myrtales* by having petals enveloping the stamens as a hood. Moreover, the presence of one whorl of epipetalous (alternisepalous) stamens, characteristic for four out of the five Crypteroniaceae genera, is very rare in other Myrtalean families, being restricted to one or two genera of the *Myrtaceae* and of the *Lythraceae*, and to the monotypic *Oliniaceae*. Finally, the conduplication of the connective or the tendency to it in all *Crypteroniaceae* except *Dactylocladus*, is another important family character, in other *Myrtales* only found in a few *Melastomataceae*. Apart from the above-mentioned characters *Crypteroniaceae* are also characterized by the septation of the gynoeceum and by the Trochodendraceous seed-structure, both being only found in other *Myrtales* in a few *Myrtaceae* genera. They are, however, from a practical viewpoint, less useful for easy diagnosis. — C. F. VAN BEUSEKOM.

Taxonomy. *Crypteroniaceae* belong undoubtedly to *Myrtales*. Though the family concept in this order is fairly satisfactory, it can be observed from the above-made remarks that there are not many exclusive characters, most of them breaking down occasionally in one family, or occurring also sporadically in another family. Each family in *Myrtales* seems to be characterized by a unique character combination in addition to one or two exclusive characters.

For *Crypteroniaceae* this combination and characters are: swollen nodes with transversal line, internodes with lengthwise raised lines or wings, petals in bud hood-like enveloping the stamens, soon caducous (in *Crypteronia* absent), stamens inflexed in bud and in one epipetalous whorl (except in *Axinandra* in two whorls), absence of a perianth tube or of any space between the insertion of petals and stamens, and furthermore the presence of a (hemi)synpicate gynoeceum and seeds of the Trochodendraceous or related type, both assumedly primitive characters, and almost exclusive within *Myrtales*.

Palynological evidence does not fully sustain the recognition of *Crypteroniaceae* as a distinct family; it could be accepted, but the evidence may allow other possibilities (MULLER, *Blumea* 22, 1975, 275).

Anatomical evidence is not much in favour of the family concept as proposed; the genera could in this respect be divided up among *Melastomataceae* and *Lythraceae*, but it remains to be seen in how far anatomical characters clearly sustain other current family concepts in *Myrtales*.

Myrtales are certainly a very ancient complex and during their evolution advanced characters have evolved, reduction series occurred in more lines, and primitive characters may have incidentally persisted in various branchings of ancestral tree in taxa which are not necessarily viewed as closely related. This would also explain the 'reticulate character distribution', a condition found in several families of *Myrtales*.

None of the Myrtalean families is really homogeneous, but from this can and should not be concluded that these families are unnatural. For tracing ancestry and evolution naturalness is more important than homogeneity which, properly, increases always with decreasing taxonomic rank.

The main subdivision of two subfamilies is supported by wood-anatomical characters (VAN VLIET, *J. Micr.* 104, 1975, 65), but other anatomical characters (VAN VLIET & BAAS, *Blumea* 22, 1975, 175) and palynological data (MULLER, *l.c.*) do neither support it, nor militate against it. At tribal level morphological, anatomical and palynological data appear not to agree. The subdivision adopted here is based on morphology. — C. F. VAN BEUSEKOM.

Anatomy. VAN VLIET, *J. Microscopy* 104 (1975) 65–82 (wood anatomy and relationships); VAN VLIET & BAAS, *Blumea* 22 (1975) 175–195 (leaf, nodal and twig anatomy). These two papers contain a full bibliography to the older literature.

The anatomy of *Crypteroniaceae sensu lato* is heterogeneous. Distinctive characters are: cuticle granular (*Axinandra*, *Crypteronia*) or smooth (*Dactylocladus*); stomata paracytic (*Axinandra*, *Crypteronia*) or anomocytic (*Dactylocladus*); hypodermis present (*Axinandra*, *Crypteronia*) or absent (*Dactylocladus*); petiole with arc-shaped vascular bundle (*Axinandra*) or with \pm closed system (*Crypteronia*, *Dactylocladus*); phloem with styloid crystals (*Axinandra*, *Crypteronia*) or

crystal sand (*Dactylocladus*); cork arising in pericycle (*Axinandra*, *Crypteronia*) or subepidermal (*Dactylocladus*); node complex, with complete girdling trace (*Axinandra*, *Crypteronia paniculata*) or with common gaps (other species of *Crypteronia*, *Dactylocladus*); cortical bundles present (*Axinandra p.p.*) or absent (other taxa); vesturing of vessel pits in wood confined to the pit chamber (*Axinandra*, *Dactylocladus*) or also on pit apertures (*Crypteronia*); vessel-ray pits alternate (*Axinandra*, *Crypteronia*) or reticulate to scalariform and larger (*Dactylocladus*); parenchyma aliform with narrow wings (*Axinandra*, *Dactylocladus*) or chiefly diffuse in aggregates (*Crypteronia*); rays heterogeneous Kribs type I (*Axinandra*, *Crypteronia*) or Kribs type III (*Dactylocladus*); intercellular canal-like spaces present in rays (*Crypteronia*, *Dactylocladus*) or absent (*Axinandra*).

The entire evidence from vegetative anatomy supports affinities between *Crypteronia* and *Axinandra* — both genera sharing salient features with a number of *Melastomataceae*. *Dactylocladus* resembles several *Melastomataceae* in its anatomy more closely than it does *Axinandra* or *Crypteronia*. The inclusion of *Alzatea* from S. America and *Rhynchocalyx* from S. Africa in the *Crypteroniaceae* adds to the anatomical heterogeneity of the family. On anatomical grounds, *Rhynchocalyx* fits better in *Lythraceae*, and *Alzatea* could also be accommodated in that family with its trilacunar nodes as only aberrant character. The existence of a considerable overlap of the anatomical range in *Melastomataceae* with that of *Lythraceae*, *Sonneratiaceae* and *Oliniaceae*, forbids, however, formal taxonomic decisions on anatomical grounds only. — P. BAAS.

Palynology. Pollen grains are small, ranging in size from 11 μm in *Crypteronia paniculata* to 20 μm in *Rhynchocalyx lawsonioides*, and thin-walled with a smooth or finely verrucate outer surface. In *Alzatea* they are tricolporate, in *Axinandra*, *Dactylocladus* and *Rhynchocalyx* heterocolpate, while *Crypteronia* is characterized by bilaterally flattened bisyncolporate grains (MULLER, 1975).

The subdivision of the family according to the pollen types is not correlated with those based on morphological or anatomical characters.

The relatively unspecialized *Alzatea* type occurs in many dicotyledonous families. The heterocolpate type is found in *Combretaceae*, *Lythraceae*, *Melastomataceae*, *Oliniaceae*, and *Penaeaceae*. Pollen grains similar to the *Crypteronia* type only occur in *Cunoniaceae*, but differ in sculpture and an affinity with this family, as suggested by ERDTMAN (1952), appears remote. — References: ERDTMAN, Pollen morphology and plant taxonomy. Angiosperms. Stockholm (1952); MULLER, Note on the pollenmorphology of *Crypteroniaceae s.l.* Blumea 22 (1975) 275. — J. MULLER.

Uses. *Crypteronia paniculata*, which may attain a height of 30 m, is said to have durable, reddish heartwood and is sometimes used in West Java for house-building; also in S. Sumatra reports are favourable (HEYNE, Nutt. Pl. 1927, 1158), but occurrence is too scattered to have come into general use.

Dactylocladus stenostachys is one of the most important export timber trees of Sarawak and Sabah; see under that species.

KEY TO THE GENERA

1. Flowers sustained by 1 bract. Stamens as many as sepals; connective not or only slightly conduplicate. Capsule small, chartaceous. Seed situated (latero-)centrally in its wing. Tribe CRYPTERONIEAE.
2. Petals absent. Ovary superior with many ovules per cell. Capsule with many seeds per cell. Nerves distinct, ascending and often anastomosing into a looped marginal nerve 1. *Crypteronia*
2. Petals present, soon caducous. Ovary at least half-inferior, the lower part immersed in the receptacle, with 3 ovules per cell. Capsule with 1–3 seeds per cell. Leaves coriaceous with vague venation 2. *Dactylocladus*
1. Flowers sustained by 3 bracts, the two lateral ones often minute. Stamens twice as many as petals. Connective completely conduplicate. Ovary inferior, with 1 or 2 ovules per cell. Capsule large, woody, half-inferior. Seed situated basally in its wing. Nerves ascending and anastomosing into a looped marginal nerve. Tribe AXINANDREAE 3. *Axinandra*

1. CRYPTERONIA

BL. Bijdr. (1826) 1151; HASSK. Cat. Hort. Bog. (1844) 232 ('*Crypterhonia*'); BL. Mus. Bot. Lugd. Bat. 2 (1856) 123, t. 42; B. & H. Gen. Pl. 1 (1867) 782; DC. Prod. 16, 2 (1868) 677; CLARKE in Hook. f. Fl. Br. Ind. 2 (1879) 573; KOEHNE, Verh. Bot. Ver. Brandenburg 22 (1881) 69; O. K. Rev. Gen. Pl. 1 (1890) 250 ('*Cryptoneria*'); NIEDENZU, Bot. Jahrb. 15 (1892) 161; in E. & P. Nat. Pfl. Fam. 3, 7 (1892) 21, t. 8; HALL. f. Abh. Naturw. Ver. Hamb. 18 (1903) 90; Med. Rijksherb. 1 (1911) 31; *ibid.* 35 (1918) 17; HUTCH. Gen. Fl. Pl. 2 (1967) 33; BEUS.-OSINGA & BEUS. Blumea 22 (1975) 258. — *Henslowia* WALL. Pl. As. Rar. 3 (1831) 13, t. 221, non BL. 1850. — *Quilamum* BLANCO, Fl. Filip. 1 (1837) 851; ed. 2, 1 (1845) 136; ed. 3, 1 (1877) 245; cf. MERR. Sp. Blanc. (1918) 282. — Fig. 1, 2, 6.

Leaves elliptic or ovate to (ovate-)lanceolate, glabrous or slightly pubescent; midrib flat or slightly impressed above, prominent beneath; nerves ascending and often anastomosing in a looped marginal nerve, flat above, \pm prominent beneath, intramarginal nerve mostly present. *Panicles* terminal or axillary, sometimes on leafless older nodes or ramiflorous, erect to usually pendulous, poorly to rather copiously branched; axes terete to more or less angular, puberulous; racemules with very numerous flowers. Flower-bracts persistent. *Flowers* bisexual or by reduction unisexual and then trees dioecious, 4–5(–6)–isomerous, pedicelled. *Receptacle* in- and outside puberulous, inside sometimes minutely tomentose, hardly or not accrescent. *Sepals* deltoid to triangular, persistent. *Petals* absent. *Stamens* persistent, in $\text{\textcircled{f}}$ flowers staminodial and mostly permanently inflexed; filaments filiform, somewhat flattened, connective about orbicular, with or without a tendency to conduplication, dark when dry, anthers apically or laterally on the connective, semiorbicular to broad-linear, latrorse or \pm introrse. *Ovary* superior or almost so, the lower part adhering to the receptacle, (sub)globose to pyramidal, 2–4-carpellate, 2–4-celled, with free or only basally connate septa, badly developed in $\text{\textcircled{m}}$ flowers; style filiform to subulate, somewhat longer to shorter than the ovary, more or less puberulous, persistent; stigma punctate to capitate. *Ovules* many, either in horizontal position on the septa or in \pm vertical position basally between the septa. *Capsule* superior or almost so, (sub)globose or more or less (ob)ovoid, puberulous, upper part dehiscent with 2–4 valves, inside split as far as the basal connation of the septa; valves at the top kept together by the non-dehiscent part of style and stigma. *Seeds* many, very small, in horizontal or vertical position; seed ovoid-ellipsoid, situated latero-centrally in its narrow, membranous wing, which has a shorter or longer apical and basal extension, raphe running closely along the embryo (microscopical!).

Distr. 4 spp., of which one ranges through tropical SE. Asia (Assam, Bengal, Lower Burma, Thailand, and Indo-China) to *Malesia*, the other three endemic in *Malesia*. Fig. 3.

Ecol. Lowland and montane rain-forests below c. 1300 m; *C. paniculata* also rather frequent in areas with a more or less seasonal climate. *Fl. fr.* in almost all taxa Jan.–Dec.

Uses. *C. paniculata* seems to yield a fairly good timber, but is never found in quantity.

KEY TO THE SPECIES

1. Ovary (and capsule) 2-celled with ∞ ovules *eq.* seeds on the septa. Dioecious tree: flowers by reduction unisexual, rarely bisexual. Leaves papyraceous. *Sect. Crypteronia* 1. *C. paniculata*
 1. Ovary (and capsule) 3- or 4-celled with ∞ ovules (seeds) inserted basally. Flowers bisexual. Leaves usually coriaceous. *Sect. Basispermia*.

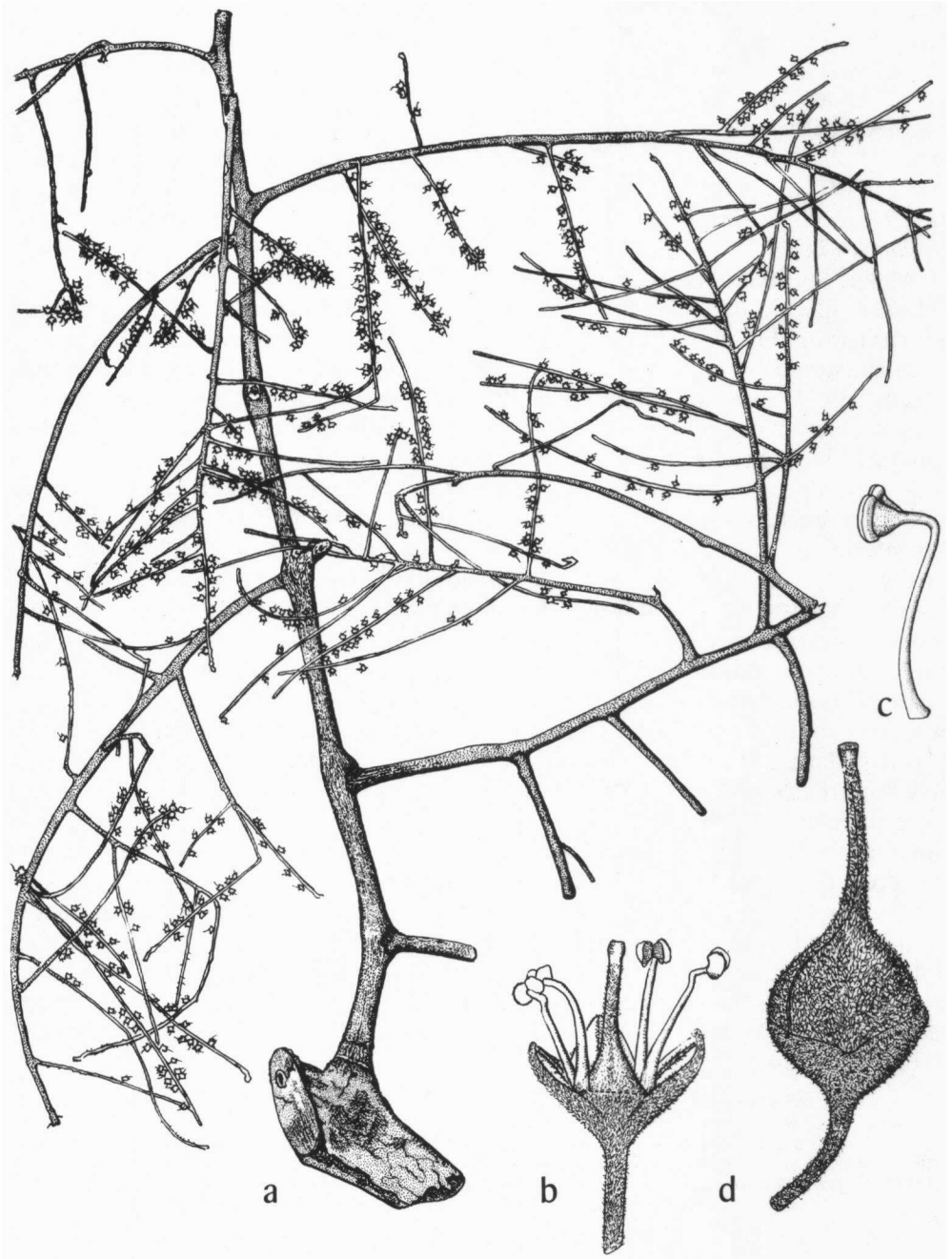


Fig. 1. *Crypteronia macrophylla* BEUS.-OSINGA. a. Inflorescence, $\times \frac{1}{2}$, b. flower, $\times 10$, c. stamen, $\times 15$, d. fruit, $\times 10$ (ASHTON S 19372).

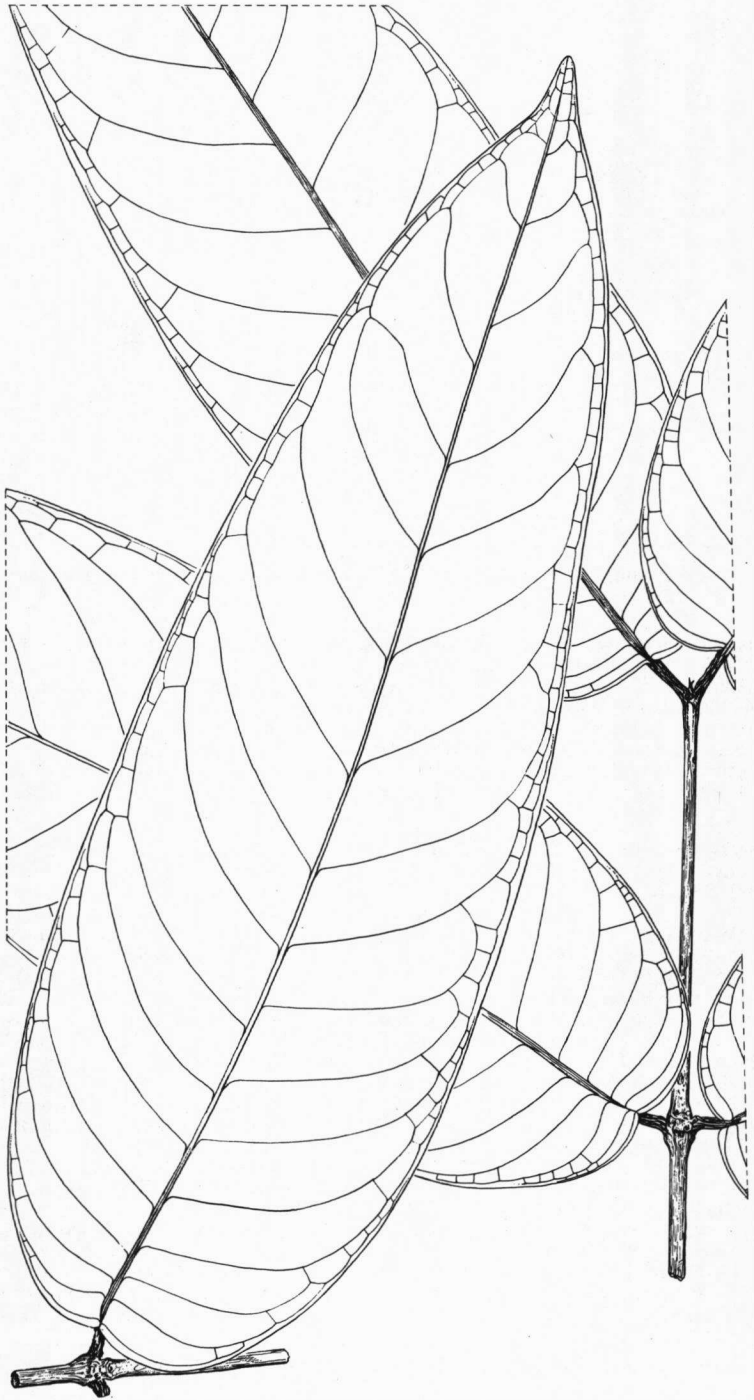


Fig. 2. *Crypteronia macrophylla* BEUS.-OSINGA. Young twig with leaves, $\times \frac{1}{3}$ (ASHTON S 19372).

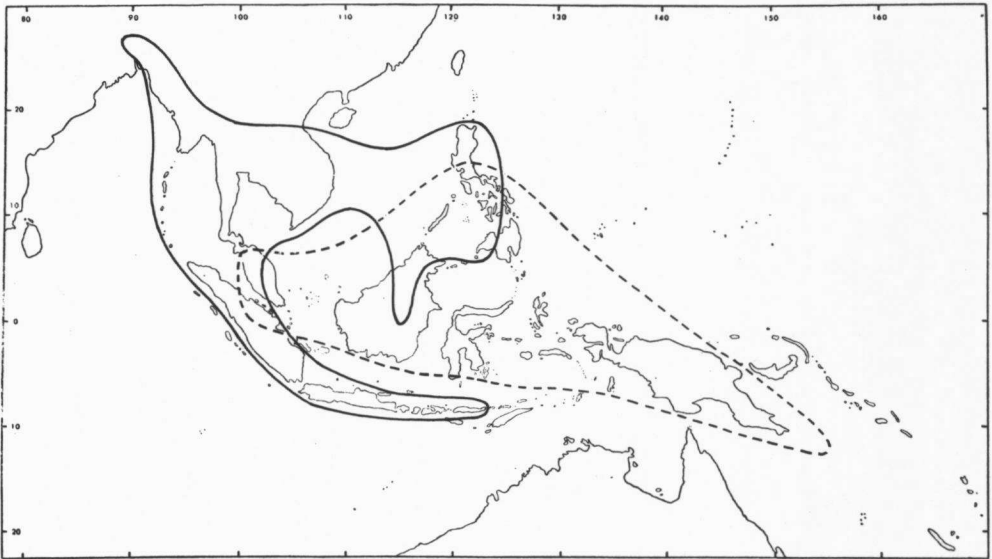


Fig. 3. Range of the genus *Crypteronia* BL.; sect. *Crypteronia* unbroken line, sect. *Basispermia* broken line.

2. Inflorescences terminal at main or side twigs, 10–25(–40) cm. Ovary (capsule) 3-locular¹. Sepals usually with longitudinal crest at the inside 2. *C. cumingii*
2. Inflorescences axillary below the leaves on older nodes, or ramiflorous, 15–90 cm. Ovary (capsule) 3- or 4-celled. Sepals with or without longitudinal crest at the inside.
3. Inflorescences below the leaves on older nodes, 15–50 cm, only with primary, very rarely with a few secondary side-axes near the base. Ovary (capsule) 3-celled. Sepals without crest 3. *C. griffithii*
3. Inflorescences ramiflorous, 45–90 cm², with primary, secondary and tertiary side-axes. Ovary (capsule) 4-celled. Sepals with a longitudinal crest at the inside 4. *C. macrophylla*

1. *Crypteronia paniculata* BL. Bijdr. (1826) 1151; Mus. Bot. Lugd. Bat. 2 (1856) 123, t. 42; DC. Prod. 16, 2 (1868) 679; KURZ, J. As. Soc. Beng. 46, ii (1877) 86, incl. var. *glabra* (WALL.) KURZ et var. *pubescens* (WALL.) KURZ; Fl. Burma 1 (1877) 519; CLARKE, Fl. Br. Ind. 2 (1879) 574; NIEDENZU, Bot. Jahrb. 15 (1892) 177; K. & V. Bijdr. 1 (1894) 203, incl. var. *leptostachya* (PLANCH.) K. & V.; KING, J. As. Soc. Beng. 67, ii (1898) 5; RIDL. Agr. Bull. Str. & F. M. S. n.s. 1 (1902) 180 ('*Cryptorania*'); MERR. Philip. J. Sc. 1 (1906) Suppl. 102; BRANDIS, Ind. Trees (1906) 341; KOORD. Exk. Fl. Java 2 (1912) 664; Atlas 2 (1914) 318; MERR. Sp. Blanc. (1918) 282; GAGNEP. & GUILLAUMIN, Fl. Gén. I.-C. 2 (1920) 696, t. 70; RIDL. Fl. Mal. Pen. 1 (1922) 821; MERR. En. Philip. 3 (1923) 140; CRAIB, Fl. Siam. En. 1 (1931) 729; OCHSE & BAKH. Ind. Groent. (1931) 182, f. 111; BURK. Dict. 1 (1935) 693; CORNER, Ways. Trees (1940) 197, pl. 48, f. 51; KRAEMER, Trees W. Pacif. Region (1951) 330; LECOMPTE, Fl. Camb. Laos & Vietn. 4 (1965) 57; BEUS.-OSINGA & BEUS. Blumea 22 (1975) 259. — *Henslowia glabra* WALL. Pl. As. Rar. 3 (1831) 14;

Cat. (1831–32) n. 4903; PLANCH. Hook. Lond. J. Bot. 4 (1845) 478; MIQ. Fl. Ind. Bat. 1, 1 (1856) 716. — *C. glabra* (WALL.) PLANCH. ex ENDL. Gen. Pl. Suppl. 4, 2 (1847) 39; BL. Mus. Bot. Lugd. Bat. 2 (1856) 123; DC. Prod. 16, 2 (1868) 678; CLARKE, Fl. Br. Ind. 2 (1879) 574; F.-VILL. Nov. App. (1880) 91; VIDAL, Synopsis (1883) 27, t. 52, f. E; Phan. Cuming. (1885) 48; Rev. Pl. Vasc. Filip. (1886) 138. — *Henslowia pubescens* WALL. Pl. As. Rar. 3 (1831) 14, t. 221; Cat. (1831–32) n. 4904; PLANCH. Hook. Lond. J. Bot. 4 (1845) 477, t. 14 B, f. 1–4; GRIFF. Not. 4 (1854) 404; Ic. Pl. As. 4 (1854) t. 562 f. 3, t. 564 f. 2; MIQ. Fl. Ind. Bat. 1, 1 (1856) 716. — *Quilamum luteum* BLANCO, Fl. Filip. 1 (1837) 851; ed. 2, 1 (1845) 136; ed. 3, 1 (1877) 245; NIEDENZU, Bot. Jahrb. 15 (1892) 177. — *Henslowia affinis* PLANCH. Hook. Lond. J. Bot. 4 (1845) 477; MIQ. Fl. Ind. Bat. 1, 1 (1856) 716. — *Henslowia leptostachys* PLANCH. Hook. Lond. J. Bot. 4 (1845) 478; MIQ. Fl. Ind. Bat. 1, 1 (1856) 716. — *Henslowia hookeri* WALL. Cat. (1847) n. 8566, nomen. — *C. affinis* (PLANCH.) PLANCH. ex ENDL. Gen. Pl. Suppl. 4, 2 (1847) 39. — *C.*

(1) Rarely a few 4-locular ovaries may be found among the predominant 3-locular ones in one inflorescence.

(2) One should be aware that of the big inflorescences of *C. macrophylla* usually only fragments have been collected.

pubescens (WALL.) PLANCH. ex ENDL. *l.c.*; BL. Mus. Bot. Lugd. Bat. 2 (1856) 123; DC. Prod. 16, 2 (1868) 678, incl. var. *affinis* (PLANCH.) DC.; CLARKE, Fl. Br. Ind. 2 (1879) 574, incl. var. *hookeri* (WALL. ex DC.) CLARKE; F-VILL. Nov. App. (1880) 91; NIEDENZU, Bot. Jahrb. 15 (1892) 176, incl. var. *typica*. — *C. leptostachys* (PLANCH.) PLANCH. ex ENDL. Gen. Pl. Suppl. 4, 2 (1847) 39; BL. Mus. Bot. Lugd. Bat. 2 (1856) 123; DC. Prod. 16, 2 (1868) 679; BAILL. Hist. Pl. 6 (1877) 436, f. 414, 415 (*'leptostachya'*); VIDAL, Phan. Cuming. (1885) 53; Rev. Pl. Vasc. Filip. (1886) 139; NIEDENZU, Bot. Jahrb. 15 (1892) 175; MERR. En. Philip. 3 (1923) 140. — *Henslowia paniculata* (BL.) MIQ. Fl. Ind. Bat. 1, 1 (1856) 716. — *C. lutea* (BLANCO) BL. Mus. Bot. Lugd. Bat. 2 (1856) 123; DC. Prod. 16, 2 (1868) 679. — *C. hookeri* WALL. ex DC. *l.c.* — *C. wallichii* DC. *l.c.*; HANCE, J. Bot. 14 (1876) 259.

Tree up to c. 30 m. Twigs glabrous or puberulous. Leaves elliptic or oblong or ovate-oblong, (5-)10-15(-25) by (3-)5-10(-12) cm, rounded to cuneate at the base, acuminate to cuspidate at the top, tip usually obtuse, sometimes acute, glabrous or puberulous, chartaceous to herbaceous, usually finely and distinctly reticulate beneath; nerves 8-10(-12) pairs; petiole 5-10 mm, 1-2 mm \varnothing , glabrous or puberulous. Panicle axillary or terminal, also on leafless older nodes, (5-)10-30 cm, branched up to the second order, without definite peduncle, more or less pendulous, not woody; main axis more or less angular; primary axes 2-5 pairs, the lower ones usually with 1-3 pairs of 5-25 cm long racemes. Bracts of axes triangular or narrowly triangular, 1-6 mm, usually caducous. Bracts of the flowers narrowly triangular to linear, $\frac{1}{2}$ -1 mm, persistent. Pedicels 1-3 mm, c. $\frac{1}{4}$ mm \varnothing . Receptacle c. $\frac{1}{2}$ mm high, c. 2 mm wide, puberulous, inside sometimes minutely tomentose. Sepals deltoid to triangular, ($\frac{1}{4}$ -) $\frac{1}{2}$ -1 $\frac{1}{4}$ mm. Stamens

5 (4), reduced and mostly permanently inflexed in \varnothing flowers; filaments 2 $\frac{1}{2}$ -3 $\frac{1}{2}$ mm, glabrous; connective c. $\frac{1}{2}$ (- $\frac{3}{4}$) mm, not conduplicate; anthers linear, $\frac{1}{4}$ - $\frac{1}{2}$ by c. $\frac{1}{4}$ mm, latrorse. Ovary reduced in σ flowers, subglobose, 2(-3)-locular, 1-2 mm, puberulous; style 1-2 mm, c. $\frac{1}{4}$ mm \varnothing , puberulous; stigma capitate, c. $\frac{1}{4}$ mm. Ovules inserted on the surface of the septa. Capsule (sub)globose or more or less obovoid, 2-3 mm, usually recurved; valves 2, rarely 3. Seeds $\frac{1}{2}$ -1 by c. $\frac{1}{4}$ mm; acute apical part of the wing half as long as the seed proper, basal part mostly short.

Distr. Continental SE. Asia (Assam: Khasya Hills, Sylhet, Lushai Hills; Bengal; Burma: Arakan Div. to Rangoon; S. Indo-China) and West Malesia: eastwards to the Philippines, Borneo, and Flores. Fig. 4.

Note. Two replacing varieties are distinguished but it should be mentioned that in Penang and in the Rangoon area, where the ranges coincide, more or less intermediate specimens are found which have almost or practically glabrous leaves and twigs.

KEY TO THE VARIETIES

1. Leaves and branches glabrous. Receptacle inside more or less puberulous. Sepals c. 1 mm long. Capsules (sub)globose var. *paniculata*
1. Leaves at least beneath, and young twigs puberulous. Receptacle inside tomentose. Sepals $\frac{1}{4}$ - $\frac{1}{2}$ (- $\frac{3}{4}$) mm long. Capsules (sub)globose to obovoid var. *affinis*

var. *paniculata*. — *C. paniculata*, incl. var. *glabra* et var. *leptostachya* — *C. glabra* — *Quilamum luteum* — *C. leptostachys* — *C. lutea* — *C. wallichii*.

Leaves (5-)10-15(-25) by (3-)5-10(-12) cm, glabrous; petiole glabrous. Buds glabrous. Inflorescence up to c. 30 cm; racemes up to 25 cm. Receptacle inside puberulous. Sepals c. 1 mm long. Staminodes $\frac{1}{2}$ -1 mm long. Capsule (sub)globose.

Distr. Continental SE. Asia: E. Bengal (Chittagong), Assam (Khasya Hills, Lushai Hills), Andaman Is., Burma (Arakan, Rangoon, Pegu, Tenasserim); in Malesia: Malay Peninsula (Kedah, Perak, Langkawi I., Pahang, Selangor, incl. Penang I.), Sumatra (Sibolangit, Pajakumbuh, Painan, Palembang), Java, Lesser Sunda Is. (Bali, Sumbawa, Flores), Borneo (Sabah, W. Kutai), Philippines. Fig. 4.

Ecol. Primary and secondary forests on hills and mountains up to 1700 m. Reported from riverbanks, ridges, ravines and forest borders. Scattered, locally fairly common.

Field notes. Bole up to 15 m, often crooked. Buttresses sometimes present. Bark smooth or rough, scaling off. Young twigs and leaves deep blue or violet (CORNER), when dried blackish. Flowers white, pale green, or greenish yellow.

Uses. The timber is reported as of good quality, used amongst others for house-building purposes and cart-wheels. In the Philippines the bark is sometimes used against skin-eruptions. In Java the young shoots are eaten with rice as lalab (HASS-KARL).

Vern. Sumatra: *kayu kapas*, *médang ajam*, M; Malaya: *békoi*, *békwoi*, *berkol*, *bua babi*, *mènkuah*, *rupal*, *tukoi*, M; Java: *kibanèn*, *kijèngklak*, S, *kayu babi*, *kigandik*, *ponggonan* (Jakarta, M),

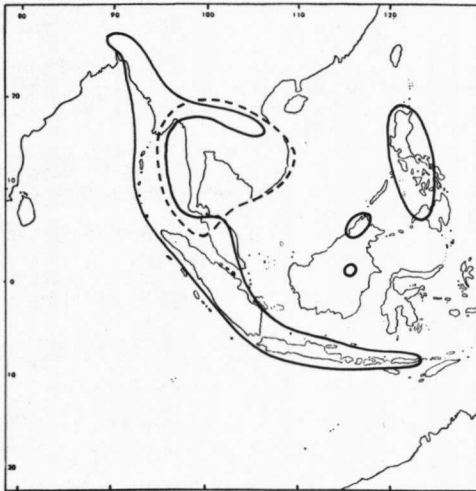


Fig. 4. Range of *Crypteronia paniculata* BL. var. *paniculata* (unbroken line) and var. *affinis* (PLANCH.) BEUS.-OSINGA (broken line).

kibakko, *kidjarak* (Priangan), *bang-kongan* (Banten), *blis* or *blisan*, *kayu tjèlèng* (Banjumas), *mungur* (Madiun), *wungu lubu* (Kediri), *tjèlèng(an)*, *wrakas* or *kwakas* (Pekalongan), *glingsing* (Pasuruan), *sépat* (Besuki), all J; Flores: *maja*; Sumbawa: *sarowe*; Borneo: *kinkidon mantok*, Dusun; Philippines: *balinog*, *bitog*, *bitok*, *bongari*, *bongau*, *bungaing*, *kilamo*, *malabayánas*, *salasan*, *tiaui*, *tua*, Tag., *agidai*, *agudai*, *barabok*, *barabak*, *bungaing*, Ilk., *banujo*, *tolan-manók*, P.Bis., *baroga*, *baruga*, *kodai*, *kudai*, *ladao*, Ig., *kamanok*, Bis., *malabióng*, Sbl.

var. affinis (PLANCH.) BEUS.-OSINGA, *comb. nov.* — *Henslowia affinis* PLANCH. Hook. Lond. J. Bot. 4 (1845) 477. — *C. affinis* — *C. pubescens*, *incl. var. affinis* (PLANCH.) DC. Prod. 16, 2 (1868) 678. — *C. hookeri*.

Leaves (2)5–10(–16) by (1½)3–6(–8) cm, sometimes sparsely puberulous above, more or less puberulous beneath especially on the nerves; petiole puberulous. Buds puberulous. Inflorescence up to c. 20 cm; racemes up to 20 cm. Receptacle inside tomentose. Sepals ¼–½(–¾) mm long. Stamens 0.1–0.3 mm long. Capsule (sub)globose to obovoid.

Distr. Continental SE. Asia: Burma (Rangoon, Pegu, Tenasserim Div.), Thailand, Laos, Cambodia, S. Vietnam; in *Malesia*: Malaya (Kedah; Penang I.). Fig. 4.

Ecol. Several times reported from riverbanks and ridges, 90–300 m.

2. *Crypteronia cumingii* (PLANCH.) PLANCH. ex ENDL. Gen. Pl. Suppl. 4, 2 (1847) 39; Bl. Mus. Bot. Lugd. Bat. 2 (1856) 123; DC. Prod. 16, 2 (1868) 678; F.-VILL. Nov. App. (1880) 91; VIDAL, Phan. Cuming. (1885) 20; Rev. Pl. Vasc. Filip. (1886) 138; NIEDENZU, Bot. Jahrb. 15 (1892) 179; MERR. Philip. J. Sc. 1 (1906) Suppl. 102; En. Philip. 3 (1923) 139; MERR. & PERRY, J. Arn. Arb. 12 (1941) 270. — *Henslowia cumingii* PLANCH. Hook. Lond. J. Bot. 4 (1845) 478, t. 14, f. C 1–4. — *C. javanica* BAILL. Hist. Pl. 6 (1877) 435, f. 412, 413, *nomen*. — *C. laxa* ELMER, *nomen in sched.*, cf. MERR. En. Philip. 3 (1923) 140.

Tree up to 40 m. Twigs glabrous. Leaves elliptic to ovate-oblong, (5)–8–25 by (3)–4–14 cm, usually emarginate sometimes rounded or acute at the base, acute, sometimes acuminate at the top, tip mostly obtuse, glabrous, coriaceous, distinctly and slightly prominently reticulate beneath; nerves 6–12(–15) pairs; petiole 2–10(–15) mm, 1–4 mm Ø, glabrous. Inflorescence terminal, at the end of main or side twigs, 10–25(–35) cm, branched up to the first, second or third order, whether or not peduncled, erect, with flaccid to stiff and subliguose axes; main axis more or less flattened; primary axes 5–25, paired or irregular, sometimes in whorls of 4; racemes up to 15 cm. Bracts of axes triangular, 2–10 mm, sometimes present as small or reduced leaves, persistent or caducous. Bracts of flowers narrowly triangular, ½–1½ mm, persistent. Pedicels 1½–2 mm, c. ½ mm Ø. Receptacle ½–1¼ mm high, 1½–2½ mm wide, densely whitish papillose inside. Sepals 5, triangular, 1–1¼(–1½) mm, inside mostly with a longitudinal densely puberulous crest. Stamens 5; filaments 1–2½ mm, glabrous; connective c. ¼ mm, slightly conduplicated;

anthers linear or semiorbicular, c. ¼(–½) by 0.1–0.2 mm, ± latrorse. Ovary subglobose, 3-celled, 1–1½ mm, whitish papillose and/or puberulous; style (1)–1½–2½ mm, 0.2–0.4 mm Ø, more or less shortly puberulous to papillose; stigma punctate to slightly capitate. Ovules inserted on the somewhat conically elevated edges between the bases of the septa. Capsule (sub)globose, more or less episeptally impressed, c. 2 mm; valves 3. Seeds c. ¾ by c. ¼ mm, apical and basal part of wing from ½ to 1 times as long as the seed proper.

Distr. *Malesia*: Borneo (Sarawak), Philippines (Luzon), Celebes, Moluccas (Morotai, Halmahera), New Guinea (incl. Misool and Louisiades: Rossel I.). Fig. 5.

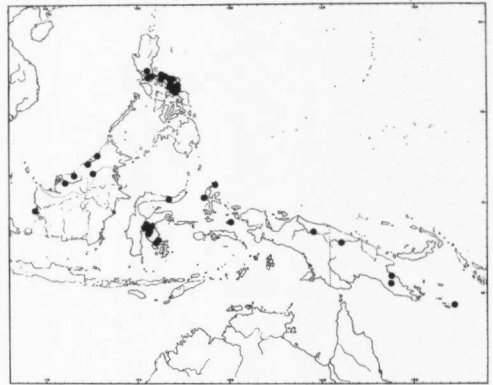


Fig. 5. Range of *Crypteronia cumingii* (PLANCH.) PLANCH. ex ENDL.

Ecol. Primary and secondary forests, on ridges, slopes, and along riverbanks, usually at low altitude, but also in the hills to 1200 m, once even found at 1800 m (Central Celebes, Malili area: B. Takale Kadju).

Vern. Borneo: *ubah*, Iban, Sarawak; Philippines: *andalai*, Tag., *ugdu*, *tigduon*, Bik.; Central Celebes, Malili area: *kumba-a*, *langori tauru*, *longari*, *tomo wanna*.

Notes. As appears from his drawings, *C. javanica* BAILL. must be referred here: bisexual flower with basal ovules; very probably they were made after a Philippine specimen.

In a depauperate collection from New Guinea (NGF 2958) the panicles are axillary.

In specimens from the Moluccas frequently 6-merous flowers occur among the normally 5-merous ones.

In specimens from New Guinea there are usually some 4-celled ovaries and 4-celled fruits present among the predominantly 3-celled ones.

3. *Crypteronia griffithii* CLARKE in Hook. f. Fl. Br. Ind. 2 (1879) 574; KING, J. As. Soc. Beng. 67, ii (1898) 5; RIDL. Agr. Bull. Str. & F. M. S. n.s. 1 (1902) 180; Fl. Mal. Pen. 1 (1922) 821; WATSON, Mal. For. Rec. 5 (1928) 176; BURK. Dict. 1 (1935) 693; CORNER, Ways. Trees (1940) 198. — *Henslowia sp.*, GRIFF. Not. 4 (1845) 404; Ic. Pl. As. 4 (1845) t. 564, f. 1. — Fig. 6.

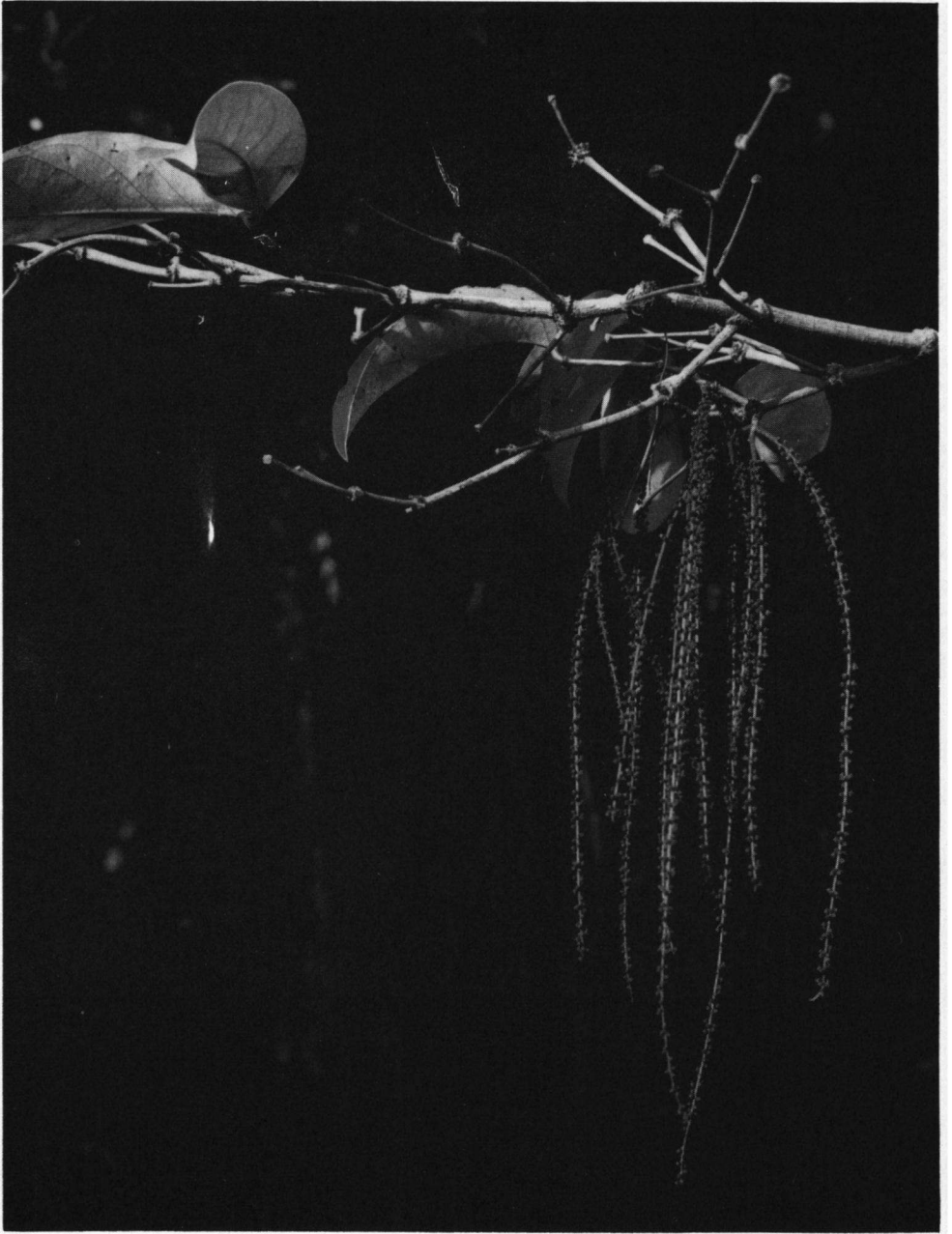


Fig. 6. *Crypteronia griffithii* CLARKE, Singapore watercatchment area, Dec. 1969 (Photogr. VAN BEUSEKOM).

Tree up to 40 m, 60 cm \varnothing . Twigs glabrous. *Leaves* elliptic-oblong to ovate-oblong, (5-)10-25 (-35) by 5-12(-15) cm, rounded or emarginate at the base, acute, sometimes acuminate at the top, tip usually obtuse, sometimes acute, glabrous, coriaceous, distinctly and slightly prominently reticulate beneath; nerves (8-)10-15(-18) pairs; petiole (2-)5-10 mm, 2-5 mm \varnothing , glabrous. *Inflorescence* axillary, one or a few together below the leaves on older nodes, 15-50 cm, only with primary side axes, very rarely with a few secondary side axes near the base, without distinct peduncle, subligulate, often ferruginously pubescent, with pendulous axes; main axis terete or somewhat flattened, finely ribbed; primary axes 8-12(-15), not always paired, finely ribbed; racemes up to 50 cm. Bracts of axes triangular, c. 1 mm, mostly caducous. Bracts of flowers subulate, c. 1 mm, persistent. Pedicels $\frac{1}{2}$ -1(- $\frac{1}{2}$) mm, c. $\frac{1}{2}$ mm \varnothing . *Receptacle* c. 1 mm high, 2-3 mm wide, densely whitish papillose inside. *Sepals* triangular, $1\frac{1}{2}$ -2 mm. *Stamens* 5; filaments 3-4 mm, glabrous; connective $\frac{1}{4}$ - $\frac{1}{2}$ mm, slightly conduplicated; anthers linear, $\frac{1}{4}$ - $\frac{1}{2}$ by c. 0.1 mm, \pm latrorse. *Ovary* (sub)globose to pyramidal, 3-celled, c. 1 mm, more or less fine whitish papillose whether or not with longer hairs in between; style ($1\frac{1}{2}$ -)3-4(-5) mm, c. $\frac{1}{4}$ mm \varnothing , sparsely puberulous; stigma slightly capitate. *Ovules* inserted on the somewhat conically elevated edges between the bases of the septa. *Capsule* (sub)globose, c. 2 mm; valves 3. *Seeds* 0.3-0.4 by c. 0.2 mm, apical and basal part of wing about $1\frac{1}{2}$ times as long as the seed proper.

Distr. Burma (Moulmein, one coll.); in *Malesia*: Central Sumatra (one coll.), Malay Peninsula (incl. Penang I.), Borneo (W. Sarawak, Sandakan, Gaya I., E. Kutai, Nunukan I.). Fig. 7.

Ecol. In primary lowland forests, often on sandy soils, up to 500 m.

Field notes. Bole usually straight. Bark surface

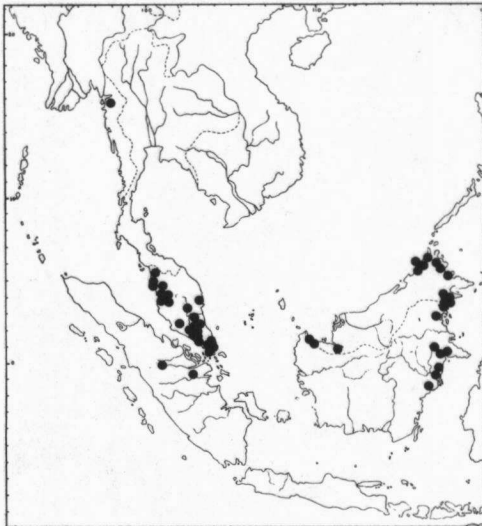


Fig. 7. Range of *Crypteronia griffithii* CLARKE.

smooth or rough and scaly. Twigs strongly swollen at the nodes. Young leaves purplish. Flowers dark blue to purple or magenta, sometimes noted yellow or yellowish reddish.

Uses. RIDLEY (1902) reported the wood to be durable and used for house-building.

Vern. Sumatra: *panarahan*; Malay Peninsula: *békwoi*, *kélat tampoi*, *nyirék bukit*, *sémbo*, *sérumpu*, *simpoh*, *sumpu(t)*, *télingga badak*; Borneo: *engkolot*, *rambai rambai*, Gaya I., *ubah sémus*, Iban.

4. *Crypteronia macrophylla* BEUS.-OSINGA, *Blumea* 22 (1975) 261. — Fig. 1, 2.

Tree up to 20 (?) m. Twigs glabrous. *Leaves* ovate-oblong to lanceolate, (20-)25-45 by 7-15 cm, usually emarginate, sometimes rounded at the base, acute to \pm acuminate at the top, tip obtuse, glabrous, coriaceous, distinctly and \pm prominently reticulate beneath; nerves 15-25 pairs; petiole 5-10(-15) mm, 2-5 mm \varnothing , glabrous. *Inflorescence* ramiflorous, 45-90 cm, always branched up to the third order, without distinct peduncle, pendulous, woody, with spreading axes; main axis terete; primary axes many, not always paired; racemes up to 30 cm. Bracts of axes triangular, c. 1 mm, caducous. Bracts of the flowers subulate, c. 1 mm, persistent. Pedicels 1-3 mm, c. $\frac{1}{2}$ mm \varnothing . *Receptacle* \pm flat, 1- $1\frac{1}{2}$ mm wide, puberulous, not densely papillose inside. *Sepals* deltoid, c. 1 mm, inside with a longitudinal densely puberulous crest. *Stamens* 4; filaments $1\frac{1}{2}$ -3 mm, glabrous, at the very base puberulous; connective c. $\frac{1}{2}$ mm, more or less conduplicated; anthers \pm linear, $\frac{1}{2}$ by 0.1-0.2 mm, \pm introrse. *Ovary* pyramidal, 4-celled, 1-2 mm, puberulous, more or less epistepally impressed; style (1-) $1\frac{1}{2}$ -2 $\frac{1}{2}$ (-3) mm, c. $\frac{1}{4}$ mm \varnothing , puberulous; stigma truncate, hardly wider than the style. *Ovules* inserted on the somewhat conically elevated edges between the bases of the septa. *Capsule* (sub)globose to pyramidal, 2-2 $\frac{1}{2}$ by 2-2 $\frac{1}{2}$ mm; valves 4. *Seeds* c. $\frac{1}{2}$ by c. $\frac{1}{4}$ mm, apical and basal part of wing as long as or slightly longer than the seed proper.

Distr. *Malesia*: Borneo: Sarawak (Kuching, Sibul), Kutai (several localities), Sambas region. Fig. 8.

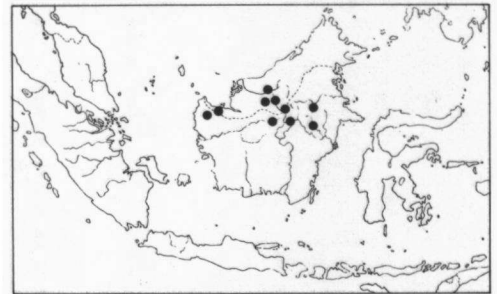


Fig. 8. Range of *Crypteronia macrophylla* BEUS.-OSINGA.

Ecol. In primary forest up to 1200 m. Locally frequent. Young branches are often inhabited by ants.

Field notes. Tree with semi-pendent branches. Bark surface smooth. Young leaves rich purplish. Flowers greenish with purple-brown stamens. Fruits dark green.

Note. The large, complex, woody inflorescence which is always produced below the leaves on older nodes is characteristic.

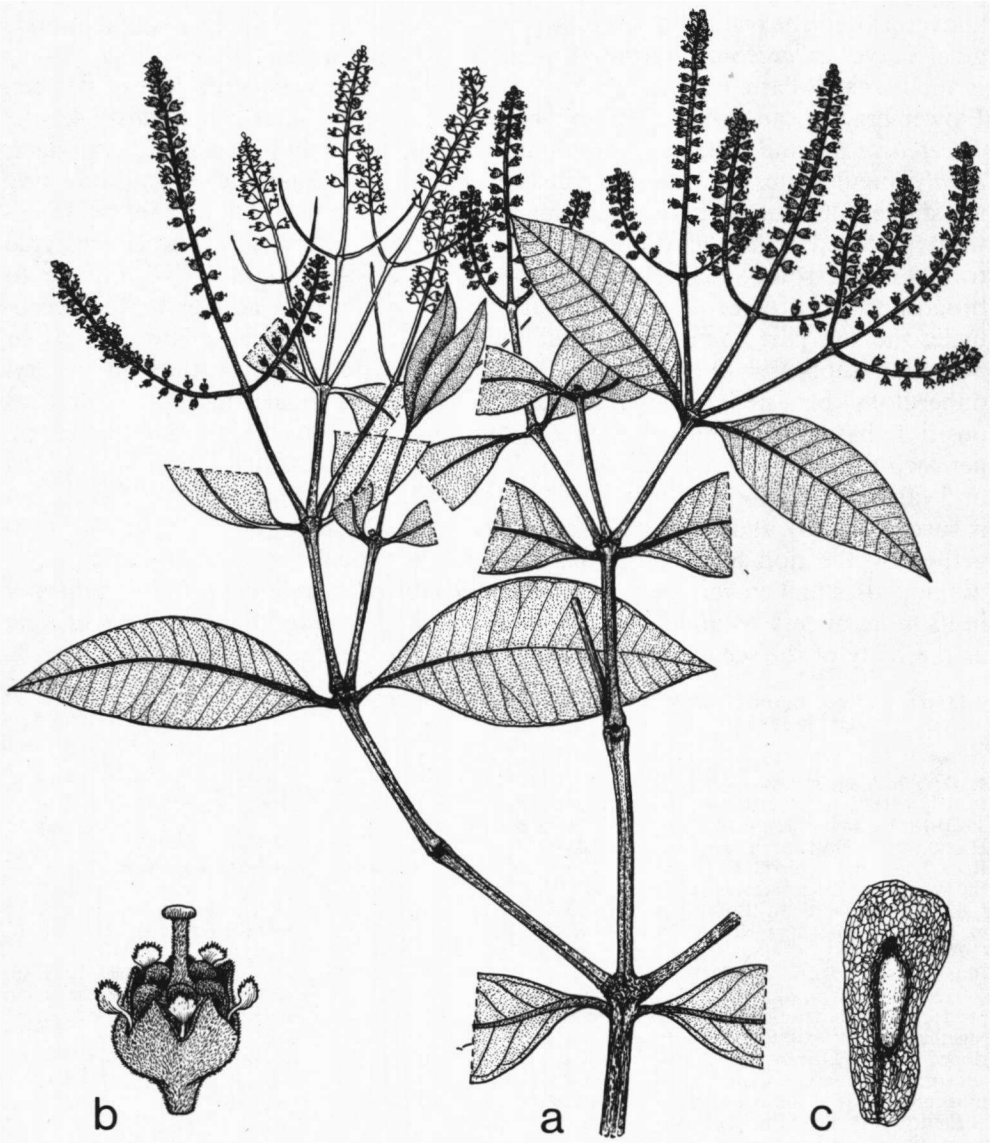


Fig. 9. *Dactylocladus stenostachys* OLIV. a. Habit, $\times \frac{2}{3}$, b. flower, $\times 10$, c. seed, $\times 16$ (a, b FUCHS 21186, c S 9261).

2. DACTYLOCLADUS

OLIV. in Hook. Ic. Pl. (1895) t. 2351; GILG in E. & P. Nat. Pfl. Fam. Nachtr. 1 (1897) 267; HALL. f. Med. Rijksherb. 35 (1918) 18; BAKH. f. Rec. Trav. Bot.

Néerl. 40 (1943) preprint 329; BEUS.-OSINGA & BEUS. *Blumea* 22 (1975) 261. — Fig. 9.

Leaves elliptic or obovate to (obovate-)oblong, glabrous; midrib thickish, \pm flat above, prominent beneath; nerves \pm straight, anastomosing in an indistinct marginal nerve. *Inflorescence* terminal or axillary to the highest leaves, erect, poorly branched; axes flattened, puberulous; racemes with at least a few tens of flowers. Flower-bracts caducous. *Flowers* bisexual, 5-(4)-isomerous, almost sessile. *Receptacle* in- and outside puberulous, accrescent. *Sepals* triangular, persistent. *Petals* unguiculate, with suborbicular, irregularly lobed lamina, in bud covering the stamens as a hood, soon caducous. *Stamens* persistent; filaments terete, somewhat flattened; connective about orbicular, not conduplicate; anthers inserted transversally, somewhat below the upper margin of the connective, oblong to broad-linear, introrse. *Ovary* half-inferior, the lower part adnate to the receptacle, the top part semiglobose, puberulous, (3-), 4- or 5-carpellate, (3-), 4- or 5-locular, septa not connate; style subulate, somewhat longer than the ovary, puberulous, persistent; stigma capitate. *Ovules* 3 per locule, inserted in vertical position, basally between the septa. *Capsule* almost inferior, broad-ellipsoid, small, pericarp chartaceous, puberulous, inside dehiscent down to the bottom with (3) 4 or 5 valves of which only the upper $\frac{1}{4}$ protrudes from that part of the pericarp that is surrounded by and fused with the enlarged receptacle, at the top often kept together by the non-splitting stigma. *Seeds* 3 per locule (1 or 2 sometimes not developed), small, in vertical position; seed narrow-ellipsoid, flat, situated centrally in its more or less rectangular, narrow, membranous wing almost 2 times as long as the body of the seed; raphe running close to the embryo.

Distr. *Malesia*: Borneo and W. New Guinea (sterile coll.). Fig. 10.
Ecol. Lowland peat swamp forest.

1. *Dactylocladus stenostachys* OLIV. in Hook. Ic. Pl. IV, 4 (1895) t. 2351; HALL. f. Med. Rijksherb. 35 (1918) 18; MERR. En. Botn. (1921) 452; DIELS & HACKENBERG, Bot. Jahrb. 60 (1926) 312; BAKH. f. Rec. Trav. Bot. Néerl. 40 (1943) preprint 329; BROWNE, For. Trees Sarawak & Brunei (1955) 261, t. 33; ANDERSON, Gard. Bull. Sing. 20 (1963) 178, pl. 1, 2, 6, 7; MEIJER, Field Guide Trees W. Mal. (1974) 205, f. 51, pl. 14; BEUS.-OSINGA & BEUS. *Blumea* 22 (1975) 262. — Fig. 9.

Tree up to 40 m, dbh up to $1\frac{1}{4}$ m, at the base producing pneumatophores. Twigs often several together per leaf-axil, the younger ones often with ribbed angles. *Leaves* 4-8(-16) by $2\frac{1}{2}$ -4(-6) cm, with revolute margin, cuneate at the base, sometimes emarginate, usually rounded up to acuminate at the top with acute tip, coriaceous; nerves 11-15 pairs, usually rather obscure, flat to prominent above and beneath; petiole 3-5 mm, 2-3 mm \varnothing . *Inflorescence* when axillary 1-3 together, erect, up to 14 cm, consisting of 3 racemes; peduncle up to 6 cm, (sub)glabrous; axes finely ribbed; racemes c. 8 cm, from 1 cm above the base \pm densely set with flowers. Bracts of axes minute, soon caducous. Bracts of the flowers linear or narrowly triangular, c. 1 mm. Pedicels up to $\frac{1}{2}$ mm. *Receptacle* c. 2 mm high, c. $2\frac{1}{2}$ mm wide. *Sepals* c. 1 mm. *Petals* c. 1 mm, puberulous outside and

on the margin. *Filaments* c. 1 mm, 0.2 mm wide, puberulous; connective $\frac{1}{4}$ - $\frac{1}{2}$ mm; anthers 0.2 by 0.1 mm. *Style* $1\frac{1}{2}$ -2 mm, c. 0.2 mm \varnothing ; stigma $\frac{1}{4}$ - $\frac{1}{2}$ mm. *Capsule* 3-4 by 2-3(- $3\frac{1}{2}$) mm. *Seed* c. 1.4 by 0.2-0.3 mm, including wing $2\frac{1}{2}$ -3 by $\frac{3}{4}$ - $1\frac{1}{4}$ mm.

Distr. *Malesia*: widely distributed in Borneo. It was by error incidentally reported from Malaya (Fl. Mal. Bull. p. 1696, p. 2375). Fig. 10.

Ecol. DURANT (For. Rep. Brunei, 1933, 6, photogr.) reported this species (under the name *Crypteronia*) to occur in Brunei as an associate of

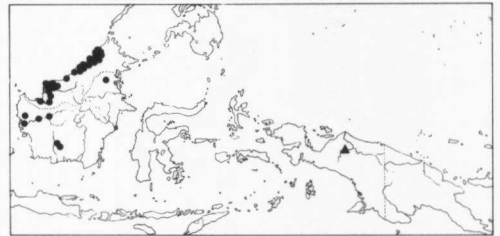


Fig. 10. Range of the genus *Dactylocladus* OLIV.; *D. stenostachys* OLIV. dots, *D. sp.* triangle.

Dryobalanops and *Combretocarpus* in considerable quantity over large areas of freshwater swamp, often with 12 mature trees (over 30 cm Ø) per ha. DIELS & HACKENBERG (*l.c.*) mentioned its occurrence in the Sampit swamp forest area in SW. Borneo together with *Combretocarpus*, *Campnosperma*, etc. BROWNE (*l.c.*) stated that it occurs in practically all types of peat swamp forest in Sarawak. He found its frequency somewhat lower than DURANT did; he found sometimes 8, but averagely 3 mature trees per ha, but he said that locally, between Balingian and Bintulu, it was the dominant tree of the swamps of Sarawak.

BROWNE recorded that the vernacular names *jongkong* and *tabak* allude to characteristic qualities: *jongkong* referring to the rather stout yellowish pneumatophores at the stem-base, while *tabak* would refer to the characteristic minute perforations of the wood from radial vessels.

ANDERSON (*l.c.*) confirmed BROWNE's observation that it is one of the most characteristic swamp forest trees, the only species represented in all communities throughout Sarawak and Brunei. He produced photographs of the *Gonystylus-Dactylocladus-Neoscortechinia* (*l.c.* pl. 1 & 2) and the *Combretocarpus-Dactylocladus* associations (*l.c.* pl. 6 & 7).

Its wide range in the peat swamps is also confirmed palynologically in the peat according to ANDERSON & MULLER (Rev. Palaeobot. & Palyn. 19, 1975, 314-316) where it figures in phases 1-6. In a Miocene deposit in Brunei, near Berakas, MULLER reported also its occurrence (*l.c.* f. 5, diagram) with the associates as today. It must be added that its pollen can be confused with that of *Axinandra* and some *Melastomataceae* of which the latter also occur in peat swamps, albeit in small numbers.

It is remarkable that whereas this type of peat forest ranged unbrokenly at least from the Miocene to the Present, *Dactylocladus* is not yet found in Sumatra and Malaya, provinces with which Borneo was joined, during the Pleistocene Glacial period, by a huge lowland riverine area (now the South China Sea); this would have made dispersal and exchange very probable, as it was for its associate *Combretocarpus* and some species of

Gonystylus. It may yet be discovered in the peat swamps of Malaya and Sumatra, but must then be very rare.

Uses. According to BROWNE (*l.c.*) it is the fourth important export timber tree of Sarawak. Extraction is facilitated by the fact that the logs float in water. MEIJER (*l.c.*) termed it a general utility timber in Sabah where it is, besides *Gonystylus*, the most important export timber from the Klias Peninsula.

Vern. *Jongkong*, *tabak* (the most common names), *ëntibu*, *garu buaja*, *jinjang*, (*médang*) *bélaai*, *m. miang*, *mélinkat kérangas*, *mérébong*, *téréngangan*.

Dactylocladus sp. — Cf. MEIJER, Field Guide Trees W. Mal. (1974) 205, in note.

Distr. *Malesia*: West New Guinea: in peat forest along Rouffaer R., the only large tree in this forest type, c. 175 m alt., DOCTERS VAN LEEUWEN 9973 (BO, L, etc.), sterile, distributed as *Memecylon* sp. Fig. 10.

Notes. Through MEIJER (*l.c.*) attention was drawn to this collection which was pre-identified through the uncanny form knowledge of Mr. NEDI at Bogor. Mr. G. VAN VLIET, Leyden, has examined the leaves anatomically and found no difference with the Bornean species. Dr. VAN STEENIS, who unearthed the Leyden duplicate, has found that it shares a small but significant vegetative character with the Bornean species, viz the occurrence of a shallow, rimmed cavity-like depression at the extreme base of the petiole, similar to that in *e.g.* *Garcinia*; the two small cups together envelop the terminal bud. This is not found in *Memecylon*.

Though in fact he found the sterile macromorphology exactly matching, we like to postpone judgement on specific status until flowers and fruit are available.

About the considerable geographical gap between Borneo and West New Guinea it can be said that true peat forest is not known from this gap at the present time. This is no explanation, however, as the same gap occurs in the genus *Koompassia* (*Leg.-Caes.*) which is not a peat-forest tree genus; in that genus the New Guinean species is distinct from the two of the Sunda shelf.

3. AXINANDRA

THW. in Hook. J. Bot. 6 (1854) 66, t. 1 C; En. Pl. Zeyl. (1859) 122; B. & H. Gen. Pl. 1 (1867) 784; BEDD. Fl. Sylv. 2 (1869) t. 207; BAILL. Adansonia 12 (1876) 84; CLARKE in Hook. f. Fl. Br. Ind. 2 (1879) 581; COGNIAUX in DC. Mon. Phan. 7 (1891) 1113; KRASSER in E. & P. Nat. Pfl. Fam. 3, 7 (1893) 142, 196; BAKH. f. Rec. Trav. Bot. Néerl. 40 (1943) preprint 332; MEIJER, Ceyl. J. Sc. (Biol. Sc.) 10 (1972) 72; BEUS.-OSINGA & BEUS. Blumea 22 (1975) 262. — *Naxiandra* (BAILL.) KRASSER in E. & P. Nat. Pfl. Fam. 3, 7 (1893) 197, f. 182 A. — Fig. 11.

Leaves elliptic to oblong, sometimes ovate, glabrous; midrib impressed above, prominent beneath; nerves ascending and anastomosing in a looped marginal nerve, intramarginal nerve present. *Inflorescence* terminal or axillary and then at the end of the twigs, erect, poorly branched; axes more or less angular, puberulous; racemes with up to some tens of flowers. Flower-bracts 3 per flower, the outer

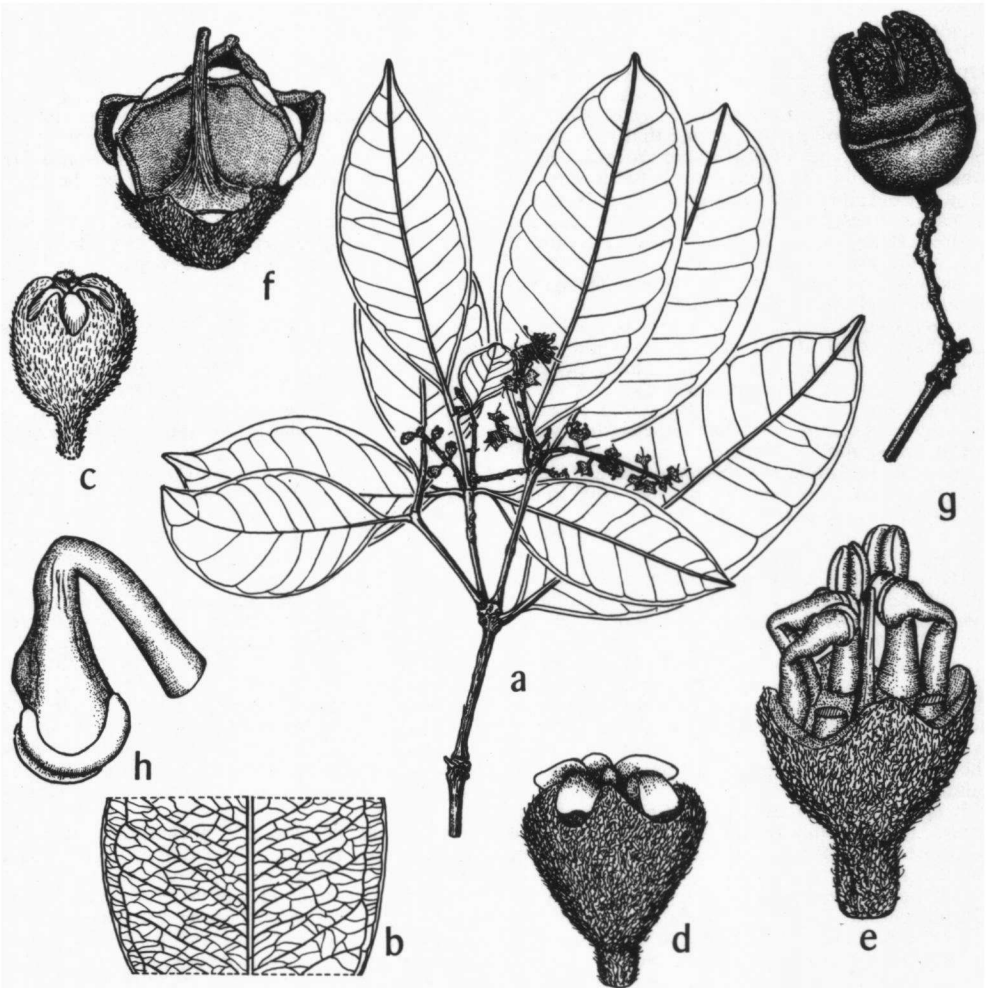


Fig. 11. *Axinandra coriacea* BAILL. a. Habit, $\times \frac{1}{2}$, b. venation undersurface of leaf, nat. size, c. bud, d. older bud, style protruding, petals separating, e. mature flower, petals dropped, f. old flower, petals and stamens dropped, all $\times 7\frac{1}{2}$, g. ripe capsule, $\times \frac{3}{4}$, h. stamen, $\times 15$ (a SAN 57276, c-f, h S 14489, g MEIJER SAN 49845).

ones often minute, persistent during anthesis. *Flowers* bisexual, 5(-4)-merous, pedicelled. *Receptacle* puberulous outside only, glabrescent in fruit, much accrescent and lignified in fruit. *Sepals* 5 (4), deltoid, more or less acuminate, evanescent in fruit. *Petals* 5 (4), valvate-connate or valvate- (or somewhat imbricate-)conduplicate or imbricate-contorted, more or less connate or cohering and soon dropping simultaneously in the shape of an umbrella, flimsy, consisting of a wide basal part tapering into a narrower median part which widens into a whether or not well-developed, frayed apical part, induplicate and enveloping the stamens which are situated in pairs between two longitudinal lamellae on the inside of each petal. *Stamens* 10 (8), epi- and alternisepalous, (sub)equal, caducous; filaments (rather) thick and short, terete, to more or less flattened, tapering upwards; connective

wide, large, conduplicate, mostly provided with a more or less distinct dorsal tubercle; anthers marginally at the apex of the connective, broad-linear, introrse. *Ovary* inferior, immersed in the receptacle, 3-(2)-carpellate, 6-(4)-celled, with free or towards the base somewhat connate septa, glabrous; style (subulate-) terete, shorter to distinctly longer than the receptacle, and whether or not protruding from the ripe bud, glabrous, evanescent in fruit; stigma punctate, minute. *Ovules* 1 or 2 per cell, two (one) by two (one) in vertical position inserted basally on either side of the 3 (2) stouter ones of the 6 (4) septa. *Capsule* half-inferior, big and woody, globose to ellipsoid, (sub)glabrous, when young provided with a fragment of the style, inside dehiscent down to the bottom with 2-6 valves of which only the upper parts protrude from that part of the capsule which is surrounded by and fused with the enlarged receptacle of which the rim often remains visible as an irregular more or less conspicuous rib; visible part of the valves triangular, coarse, solid, deltoid at cross-section, glabrous. *Seeds* few, in vertical position; seed depressed-ellipsoid, situated basally and obliquely in its thin, (narrow-)oblong wing 2-3 times as long as the body of the seed; raphe running from the basal insertion all along the wing margin back to the embryo.

Distr. Ceylon (1 sp.) and *Malesia*: Malay Peninsula (one record) and Borneo (3 spp.) but nowhere common. Fig. 12.

A. zeylanica was also mentioned to occur in Borneo by BAKHUIZEN f. (Rec. Trav. Bot. Néerl. 40, 1943, preprint 332) but HALLIER f. 2683, on which this was based, belongs to *A. coriacea*. The same author (i.c.) recorded *A. borneensis* BAKH. f. (= *A. beccariana*) from Billiton I.; the sheet TEYSMANN s.n. was collected, however, on Mt Bliotong in Borneo.

As with *Dactylocladus* the extreme rarity of the genus on the Sunda-shelf west of Borneo is remarkable and remains unexplained; so far known *Axinandra* is not bound to a rare or very specialized biotope.

Ecol. Lowland and submontane rain-forest, up to 1200 m.

KEY TO THE SPECIES

1. Connective pear- or drop-shaped. Filaments $1\frac{1}{2}$ -2 mm. Style 2-5 mm. Ovules 2 per cell. *Sect. Naxian-dra* BAILL.
2. Internodes winged upwards. Leaf-base rounded to emarginate. Inflorescences distinctly longer than 5 cm 1. *A. alata*
2. Internodes not winged. Leaf-base shortly attenuate. Inflorescences shorter, or distinctly longer than 5 cm.
3. Leaves chartaceous. Tip of leaf-apex acute. Inflorescence 5-20 cm. Petals c. 3 mm. Fruit $1\frac{1}{2}$ -2 by $1-1\frac{1}{2}$ cm; rim of enlarged receptacle about median 2. *A. beccariana*
3. Leaves coriaceous. Tip of leaf-apex obtuse. Inflorescence stunted, (1-)-2-4(-5) cm. Petals c. 6 mm (fig. 11d). Fruit 2-3(- $3\frac{1}{2}$) by $1\frac{1}{2}$ - $2\frac{1}{2}$ cm; rim of enlarged receptacle infra-median (fig. 11g) 3. *A. coriacea*
1. Connective quadrate-elliptic. Filaments c. $\frac{1}{2}$ mm. Style shorter than $\frac{1}{2}$ mm. Ovules 1 per cell. *Sect. Axinandra*. Species of Ceylon *A. zeylanica* THW.

1. *Axinandra alata* BAILL. *Adansonia* 12 (1876) 86; Bull. Soc. Linn. Paris (1877) 128; COGNIAUX in DC. Mon. Phan. 7 (1891) 1114; MERR. En. BORN. (1921) 452; BEUS.-OSINGA & BEUS. *Blumea* 22 (1975) 263.

Tree. Twigs glabrous; internodes terete at the base, growing acutely quadrangular upwards with 4 gradually widening wings towards the nodes, (sub)glabrous; wings 1-3 mm (or more?) wide at the top, ending in an acute process often curved upwards, wearing off when older. *Leaves* 5-10 by 3-5 cm, rounded at the base, cuspidate at the top and with acute tip, chartaceous to subcoriaceous, distinctly reticulate; nerves c. 12 pairs, flat above, prominent beneath; petiole 3-5 mm, $1-1\frac{1}{2}$ mm \varnothing . *Inflorescence* 8-13 cm, consisting of main axis with 1 or 2 pairs of 4-12 cm long primary axes each

bearing 10-35 flowers. Bracts of axes deltoid to triangular, c. 1 mm, acute at the top, minutely puberulous, mostly caducous. Floral bracts small, the middle one only slightly exceeding the lateral ones, narrowly triangular, c. 1 mm. Pedicels 1-2 mm, c. $\frac{1}{2}$ mm \varnothing . *Receptacle* c. 2 mm high, c. 3 mm wide, ribbed, densely puberulous. *Sepals* c. $\frac{3}{4}$ mm. *Petals* c. $3\frac{1}{2}$ -4 mm, $1-1\frac{1}{4}$ mm wide at the base, valvate to imbricate at the base, valvate-conduplicate for the rest, more or less connate especially in the median part, almost completely enveloping the stamens. *Filaments* c. 2 mm, $\frac{1}{2}$ - $\frac{3}{4}$ mm wide at the base, glabrous. Connective pear- or drop-shaped, c. 1 mm, with dorsal swelling. Anther-cells c. 1 mm, c. $\frac{1}{4}$ mm wide. *Style* 3-5 mm, $\frac{1}{4}$ mm \varnothing , protruding from mature bud. *Ovules* 2 per cell. *Fruit* not seen.

Distr. *Malesia*: Borneo (Sarawak), only known from the type.

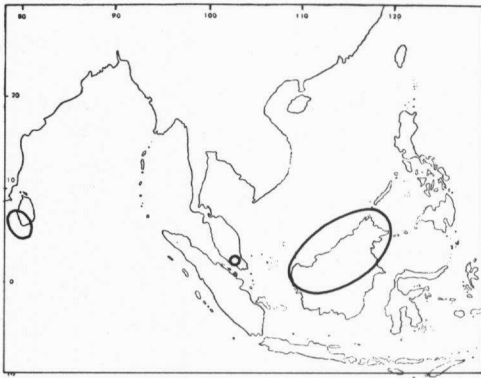


Fig. 12. Range of the genus *Axinandra* THW. In Ceylon 1 sp., in Borneo 3 spp. of which one once found in Malaya.

2. *Axinandra beccariana* BAILL. *Adansonia* 12 (1876) 85; *Bull. Soc. Linn. Paris* (1877) 127; COGNIAUX in DC. *Mon. Phan.* 7 (1891) 1114; MERR. *En. Born.* (1921) 452; BEUS.-OSINGA & BEUS. *Blumea* 22 (1975) 263. — *A. maingayi* CLARKE, *Fl. Br. Ind.* 2 (1879) 581; COGNIAUX in DC. *Mon. Phan.* 7 (1891) 115; RIDL. *Fl. Mal. Pen.* 1 (1922) 826. — *A. borneensis* BAKH. *f. Rec. Trav. Bot. Néerl.* 40 (1943) preprint 332.

Tree. Twigs glabrous or very minutely puberulous. *Leaves* 5–10 by 2–5 cm, shortly attenuate at the base, acuminate to cuspidate at the top, with acute tip, chartaceous, faintly reticulate; nerves 8–12 pairs, flat above, prominent beneath; petiole 5–8 mm, 1–2 mm \varnothing . *Inflorescence* 5–20 cm, branched up to the second order, with slender axes each bearing up to c. 15 flowers; primary axes up to 4 pairs, 4–15 cm. Bracts of the axes deltoid to narrowly triangular, 1–3 mm, acute at the top, subglabrous, mostly caducous, sometimes partly present as small or reduced leaves. Floral bracts small, the middle one triangular to linear-lanceolate, $\frac{1}{2}$ –4 mm, the lateral ones minute. Pedicels 1–2 $\frac{1}{2}$ mm, c. $\frac{1}{2}$ mm \varnothing . *Receptacle* c. 2 mm high, c. 3 mm wide, sometimes faintly ribbed, sparsely minutely puberulous. *Sepals* c. $\frac{1}{2}$ mm. *Petals* c. 3 mm, c. 1 mm wide at the base, valvate, almost completely connate, only enveloping the dorsal and part of the apical side of the stamens. *Filaments* c. 1 $\frac{1}{2}$ mm, c. $\frac{1}{2}$ mm wide at the base, glabrous. Connective pear- or drop-shaped, c. 1 $\frac{1}{2}$ mm, with dorsal swelling. Anther-cells c. 1 by c. $\frac{1}{4}$ mm. *Style* c. 2 mm, c. $\frac{1}{2}$ mm \varnothing , hardly or not protruding from mature bud. *Ovules* 2 per cell. *Capsule* 1 $\frac{1}{2}$ –2 by 1–1 $\frac{1}{4}$ cm, faintly 10-ribbed, rim of enlarged receptacle about median; valves c. $\frac{3}{4}$ cm. *Seeds* not seen.

Distr. *Malesia*: Borneo and Malay Peninsula (Malacca, one old record). Fig. 13.

Ecol. Lowland forests.

Note. From the Malay Peninsula only one collection is known (MAINGAY 654–2, type of

A. maingayi). The differences between this specimen and the material from Borneo as mentioned by CLARKE *l.c.* are in my opinion of minor importance; consequently, I have included *A. maingayi* in the synonymy of *A. beccariana*.

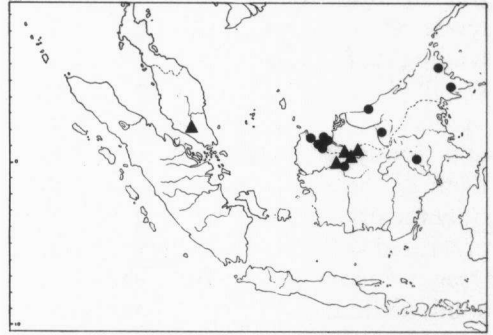


Fig. 13. Localities of *Axinandra beccariana* BAILL. (triangles) and *A. coriacea* BAILL. (dots).

3. *Axinandra coriacea* BAILL. *Adansonia* 12 (1876) 85; *Bull. Soc. Linn. Paris* (1877) 127; *Hist. Pl.* 7 (1880) 28, f. 43; COGNIAUX in DC. *Mon. Phan.* 7 (1891) 1114; MERR. *En. Born.* (1921) 452; BEUS.-OSINGA & BEUS. *Blumea* 22 (1975) 264. — *Naxiandra coriacea* (BAILL.) KRASSER in E. & P. *Nat. Pfl. Fam.* 3, 7 (1893) 197. — Fig. 11.

Tree up to 35 m, 50 cm \varnothing . Twigs glabrous. *Leaves* 5–10(–12) by (1 $\frac{1}{2}$)–2–5(–6) cm, shortly attenuate, sometimes acute at the base, acuminate to cuspidate at the top, with obtuse tip, coriaceous, conspicuously reticulate; nerves 8–12 pairs, flat above, prominent beneath; petiole 5–8 mm, c. 1–2 mm \varnothing . *Inflorescence* (1–)2–4(–5) cm, consisting of a few, sometimes one 1–5 cm long rather coarse, sometimes stunted axes, each bearing 0–15 flowers. Bracts of the axes deltoid to triangular, c. 1 mm, obtuse at the top, subglabrous, mostly caducous. Floral bracts small, the middle one deltoid to triangular, c. 1 mm, the lateral ones minute. Pedicels 1–2 $\frac{1}{2}$ mm, c. 1 mm \varnothing . *Receptacle* c. 3 mm high, 3–4(–5) mm wide, densely puberulous. *Sepals* c. 1 mm. *Petals* c. 6 mm, c. 1 $\frac{1}{2}$ mm wide at the base, valvate at the base, conduplicate-valvate for the rest, more or less connate in the median part, mostly almost completely enveloping the stamens. *Filaments* 1 $\frac{1}{2}$ –2 mm long, $\frac{3}{4}$ –1 mm wide at the base, glabrous. Connective pear- or drop-shaped, c. 1 $\frac{1}{2}$ mm, with dorsal swelling. Anther-cells c. 1 $\frac{1}{2}$ mm, c. $\frac{1}{4}$ mm wide. *Style* 2–5 mm, c. $\frac{1}{2}$ mm \varnothing , protruding from mature bud. *Ovules* 2 per locule. *Capsule* 2–3 $\frac{1}{2}$ by 1 $\frac{1}{2}$ –2 $\frac{1}{2}$ cm; rim of enlarged receptacle infra-median; valves $\frac{1}{2}$ –1(–1 $\frac{1}{2}$) cm. *Seeds* 0.7–0.8(–1) by 0.3–0.4(–0.5) cm; wing c. $\frac{1}{2}$ cm wide.

Distr. *Malesia*: Borneo. Fairly rare. Fig. 13.

Ecol. Primary (dipterocarp) forest at low and medium altitude, up to 1200 m, also recorded from ultrabasic red-brown soil.

Field notes. Buttresses when present up to 1 $\frac{1}{2}$ –2 m vertically. Bark surface flaky. Stamens pale yellow. Flowers greenish; corolla white.

Vern. *Ubah*, Iban, Sarawak, *obah*, Sabah.