

**PERACEAE**  
**(formerly EUPHORBIACEAE s.l.**  
**subfam. ACALYPHOIDEAE tribes CLUTIEAE,**  
**POGONOPHOREAE, CHAETOCARPEAE and PEREAE)**

(P.C. van Welzen, Leiden, The Netherlands

&

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*Peraceae* (Baill.) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin (1859) 246. — *Peridae* Baill., Étude Euphorb. (1858) 433. — *Prosopidoclineae* Klotzsch, Arch. Naturgesch. 7 (1841) 176. — *Acalyphoideae* Asch. tribus *Pereae* (Baill.) Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiii (1919) 1; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 65; Racl.-Sm., Gen. Euphorbicearum (2001) 117. — Type: *Pera* Mutis.

*Hippomaneae* A.Juss. ex Bartl. subtribus *Chaetocarpeae* Müll.Arg., Linnaea 34 (1865) 202. — *Acalyphoideae* Asch. tribus *Chaetocarpeae* (Müll.Arg.) G.L.Webster, Taxon 24 (1975) 595; Ann. Missouri Bot. Gard. 81 (1994) 64; Radcl.-Sm., Gen. Euphorbicearum (2001) 115. — Type: *Chaetocarpus* Thwaites.

*Hippomaneae* A.Juss. ex Bartl. subtribus *Clutiae* Müll.Arg., Linnaea 34 (1865) 202. — *Acalyphoideae* Asch. tribus *Clutiae* (Müll.Arg.) Pax in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 3 (5) (1890) 81 ('*Clutiae*'); G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 63; Racl.-Sm., Gen. Euphorbicearum (2001) 112. — *Acalyphoideae* Asch. tribus *Clutiae* (Müll.Arg.) Pax subtribus *Cluytiinae* Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 49. — Type: *Clutia* L.

*Hippomaneae* A.Juss. ex Bartl. subtribus *Pogonophoreae* Müll.Arg., Linnaea 34 (1865) 202. — *Acalyphoideae* Asch. tribus *Pogonophoreae* (Müll.Arg.) G.L.Webster, Taxon 24 (1975) 595; Ann. Missouri Bot. Gard. 81 (1994) 64; Racl.-Sm., Gen. Euphorbicearum (2001) 114. — Type: *Pogonophora* Miers ex Benth.

Trees or shrubs, in *Clutia* also shrublets or woody herbs, dioecious (or monoecious in some *Clutia* and *Pera*). *Indumentum* simple hairs, stellately arranged in *Trigonopleura*, malpighiaceous in inflorescences of *Pogonophora*, mainly stellate and lepidote in *Pera*. *Stipules* small or absent. *Leaves* alternate, often distichous, (to very rarely opposite in *Pera*), simple, entire, penninervid, often pellucid-punctate, eglandular. *Inflorescences* axillary fascicles (or also short panicles or thyrses in *Pogonophora*), pistillate flowers in *Clutia* often solitary, usually bracteate or in *Pera* flowers involucrate and buds even completely enclosed by the 2 involucre-like bracts. *Flowers* small, actinomorphic, unisexual, pedicellate or sessile. *Staminate flowers*: in *Pera* calyx 2–4-fid or absent, in other genera sepals usually 4–5, imbricate, sometimes in 2 series; petals absent or 5, valvate or imbricate, inside centrally barbate in *Pogonophora*; disc generally extrastaminal (*Chaetocarpus*, *Clutia*, *Trigonopleura*), annular or glandular, in 1–3 series

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1) With contributions by P. Baas (wood anatomy) and R.W.J.M. van der Ham (pollen morphology). — Drawings by Jan van Os. Photos on page 124 were published with permission from Phonsak Phonsena.

in *Clutia*, absent in *Pera*, intrastaminal glands in *Pogonophora*, forming a cup under the pistillode; stamens 5–15, filaments only free in *Pogonophora*, basally united in an androphore in all other genera, anthers splitting off in 1–2 layers, basifixed, opening introrse, latrorse or extrorse via lengthwise slits, connective often apiculate; pistillode present, but absent in *Pera*, but there each staminate flower surrounded by remnants of 3–4 pistillate flowers. *Pistillate flowers* pedicellate, but (sub)sessile and without perianth in *Pera*; sepals 4–8, imbricate; petals absent or 5, free, inside centrally barbate in *Pogonophora*; disc annular, often cupular to urceolate; ovary (seldom in *Trigonopleura* 2-), 3- (or some *Clutia* 4-)locular, per locule 1 anatropous ovule, style absent to short, stigmas apically split to apically fimbriate in *Pogonophora*. *Fruits* rhegmas, dehiscing septically and partly loculicidally into 2-valved mericarps except almost drupaceous in *Pera* and tardily also completely dehiscing loculicidally, in *Pera* mericarps remaining attached to the persistent columella; septa thin, membranous and without visible vascularisation. *Seeds* ellipsoid to globular, black, shiny, always carunculate; testa with a tracheoidal exotegmen; endosperm copious but scanty in *Trigonopleura*; cotyledons much longer and broader than the radicle except somewhat longer in *Clutia*. n = 18.

#### DISTRIBUTION

The family is pantropical. Five genera are distinguished: *Chaetocarpus* (c. 13 spp.) occurs in all tropics and subtropics of S and C America, Africa and S and SE Asia with 1 species in W Malesia; *Clutia* with c. 75 species is African; *Pera* with 30–40 species is present in the Caribbean and tropical South America; *Pogonophora* has 2 neotropical and one W African species; and *Trigonopleura* Hook.f. is found with 3 species in W Malesia.

#### TAXONOMY

The most recent classification of the Euphorbiaceae s.l. (APG III 2009) divides it into five families (Euphorbiaceae s.s., Pandaceae, Phyllanthaceae, Picrodendraceae, Putranjivaceae) with a note on the possible split off of the Peraceae, the most basal clade in the phylogeny of the Euphorbiaceae s.s. (e.g., Wurdack et al. 2005, Tokuoka & Tobe 2006). Phylogenetic analyses (Davis et al. 2007) of 111 Malpighiales (plus 22 outgroups) for eight DNA markers attached the Rafflesiaceae at the base of the Euphorbiaceae (s.s.), just above the Peraceae clade. Including the Rafflesiaceae in the Euphorbiaceae (s.s.) would, on the one hand, render one of the few extremely recognisable families, Rafflesiaceae, unrecognisable and, on the other hand, it would add inferior ovaries with many ovules per locule to the description of the Euphorbiaceae, making them extremely indistinguishable. Therefore, it is prudent to split off the genera at the base of the Euphorbiaceae cladogram as a separate family, the Peraceae. Then the Rafflesiaceae and Euphorbiaceae (s.s.) remain monophyletic. Also positive is that the Peraceae have a typical character combination: woody, dioecious (rarely monoecious), leaves simple, entire and without any glands, unisexual flowers generally in axillary fascicles, ovaries mainly 3-locular with one anatropous ovule per locule, fruits with

usually 3 conspicuously shiny black seeds, and the testa of the seeds with a tracheoidal exotegmen. Because of the monophyly of the Euphorbiaceae and the recognisability of the Peraceae we accept the family for Flora Malesiana. The Peraceae are part of the Malpighiales and sister to the Euphorbiaceae (s.s.) together with Rafflesiaceae.

We refrain from an infrafamily classification for two reasons. Maintaining the four tribes as in the classification of the Euphorbiaceae s.l. (Webster 1994, Radcliffe-Smith 2001) of which three tribes are monotypic and only one contains two genera (*Chaetocarpeae* with *Chaetocarpus* and *Trigonopleura*) is over the top for such a small family. Moreover, the backbone phylogenies of the Euphorbiaceae (Wurdack et al. 2005, Tokuoka & Tobe 2006) do not include representatives of all genera and this makes a subclassification premature. Webster (1994) and Radcliffe-Smith (2001) used the four tribes as the position of the genera in their classifications was still uncertain.

*References:* APG (Angiosperm Phylogeny Group), An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161 (2009) 105–121. — Davis, C.C., M. Latvis, D.L. Nickrent, K.J. Wurdack & D.A. Baum, Floral gigantism in Rafflesiaceae. Science 315 (2007) 1812. — Radcliffe-Smith, A., Gen. Euphorbiacearum (2001) 112–119. — Tokuoka, T. & H. Tobe, Phylogenetic analyses of Malpighiales using plastid and nuclear DNA sequences, with particular reference to the embryology of Euphorbiaceae sens.str. J. Pl. Res. 119 (2006) 599–616. — Webster, G.L., Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81 (1994) 33–144. — Wurdack, K.J., P. Hoffmann & M.W. Chase, Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcl* and *trnL-F* DNA sequences. Amer. J. Bot. 92 (2005) 1397–1420.

#### WOOD ANATOMY

(P. Baas)

Wood anatomically the Peraceae constitute an interesting clade. *Pera*, *Chaetocarpus* and *Trigonopleura* are wood anatomically quite similar. They share diffuse-porous wood with vessels solitary and in radial multiples, simply perforated vessels with large, alternate intervessel pits (9–15  $\mu\text{m}$ ) and vessel-ray pits round or elongate or of irregular shape and simple or with much reduced borders (with in addition also some bordered pits similar to intervessel pits in shape and size). Tyloses frequent in heartwood, and sclerotic in some species of *Chaetocarpus* and *Pera*. Fibres non-septate, ranging from thin- to thick-walled with minutely to distinctly bordered pits confined to the radial walls; pit-chambers in *Trigonopleura* 3–5  $\mu\text{m}$ , in *Chaetocarpus* and *Pera* 2–3(–4)  $\mu\text{m}$ . Parenchyma typically in narrow lines and/or diffuse in aggregates and scanty paratracheal, in long strands of (3–)8(–12) cells. Rays heterocellular with procumbent body ray cells and a varying number (1 to > 4) marginal square to erect cells; 1–2(–3)-seriate in *Pera* and *Trigonopleura*, 1–3(–5)-seriate in *Chaetocarpus* (varying with the specimen and stem diameter). Crystals solitary prismatic in chambered axial parenchyma cells in all three genera, but also occasionally in ray cells in *Pera* and *Chaetocarpus*. Radial canals/laticifers recorded in four species of *Pera* by D tienne & Jacquet (1983), but absent from reference slides in Leiden and the materials studied by Hayden & Hayden (2000). *Clutia* and *Pogonophora* differ significantly in their wood anatomy from the other Peraceae. Both have simple fibres pits; *Pogonophora* has parenchyma mainly vasicentric to confluent and in marginal bands, intervessel pits (5–7  $\mu\text{m}$ ), and silica

grains; *Clutia* has intervessel pits of 7–10  $\mu\text{m}$ , very scanty parenchyma, fusiform or in short strands, and lacks crystals.

Although the close wood anatomical similarities of the Malesian *Chaetocarpus* and *Trigonopleura* with Neotropical *Pera* testify to their inclusion in the same family, their wood anatomical syndrome also betrays very close affinities with Euphorbiaceae where similar wood anatomies are not uncommon (Metcalf & Chalk 1950, Stern 1967, Ilic 1991, Sosef et al. 1998, InsideWood 2002 onwards, Westra & Koek-Noorman 2004), especially in the Acalyphoideae as pointed out by Hayden & Hayden (2000).

*References:* D tienne, P. & P. Jacquet, Atlas d'identification des bois de l'Amazonie et des regions voisines (1983). CTFT, Nogent-sur-Marne. — Hayden, W.J. & S.M. Hayden, Wood anatomy of the Acalyphoideae (Euphorbiaceae). IAWA J. 21 (2000) 213–235. — Ilic, J., CSIRO Atlas of hardwoods (1991). Springer-Verlag, Berlin. — Insidewood database, <http://insidewood.lib.ncsu.edu> (2002 onwards). — Metcalfe, C.R. & L. Chalk, Anatomy of the Dicotyledons (1950). Clarendon Press, Oxford. — Sosef, M.S.M., L.T. Hong & S. Prawirohatmodjo (eds.), Plant Resources of South-East Asia 5, 3, Timber Trees: Lesser known timbers (1998) 612. Backhuys Publishers, Leiden. — Stern, W.L., Kleinodendron and xylem anatomy of Cluytieae (Euphorbiaceae). Amer. J. Bot. 54 (1967) 663–676. — Westra, L.Y.Th. & J. Koek-Noorman, Wood Atlas of the Euphorbiaceae. IAWA J., Suppl. 4 (2004).

#### POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Using light microscopy, Punt (1962) described all five genera of the Peraceae. The generic pollen descriptions in the overview by Radcliffe-Smith (2001) are largely based on those in Punt's study. Webster (1994) provided pollen data of the four tribes (Chaetocarpeae, Clutieae, Pereae, Pogonophoreae) in which the genera were accommodated. The most detailed account, being based on light, scanning electron and transmission electron microscopy, is that by Nowicke et al. (1998), from which the following summary was drawn.

The pollen grains are shed as monads. They are mostly medium-sized (P by E = 21–52 by 19–39  $\mu\text{m}$ ), sometimes small (*Pera parvifolia* type: P by E = 14–25 by 14–26  $\mu\text{m}$ ) or relatively large (*Pera distichophylla* type: P by E = 47–60 by 34–49  $\mu\text{m}$ ). Pollen grain shape is oblate spheroidal to subprolate (P/E = 0.97–1.24), though mostly prolate in *Clutia* (P/E = 1.19–1.53). The aperture system is generally 3-colporate in all five genera; 4-colporate grains occur rarely in *Pera*. The colpi are inoperculate and usually long, sometimes relatively short (*Pera* p.p.). The endoapertures are nearly always lalongate pores. Mostly, the exine is tectate (intectate in *Pera arborea* type) and has a distinct columellate infratectum. The columellae are distally branched in *Clutia* pollen. The tectum is perforate to finely reticulate or diversely scabrate (*Chaetocarpus*, *Pera parvifolia* type p.p.).

According to Nowicke et al. (1998) the pollen data support the monogeneric concept of the tribe Clutieae and suggest that *Trigonopleura* may be more closely related to *Pogonophora* than to *Chaetocarpus*.

*References:* Nowicke, J.W., M. Takahashi & G.L. Webster, Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae). Part 1. Tribes Clutieae (*Clutia*), Pogonophoreae (*Pogonophora*), Chaetocarpeae (*Chaetocarpus*, *Trigonopleura*), Pereae (*Pera*), Cheiloseae (*Cheilosa*,

Neoscortechinia), Erismantheae pro parte (Erismanthus, Moultonianthus), Dicoelieae (Dicoelia), Galearieae (Galearia, Microdesmis, Panda) and Ampereae (Amperea, Monotaxis). Rev. Palaeobot. Palynol. 102 (1998) 115–152. — Punt, W., Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7 (1962) 1–116. — Radcliffe-Smith, A., Gen. Euphorbiacearum (2001) 112–119. — Webster, G.L., Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81 (1994) 33–144.

#### KEY TO THE GENERA

- 1a. Petals absent (though inner sepal may be petal-like, then single); fruits covered with glochidiate (long stinging) hairs; hairs simple . . . . . **1. Chaetocarpus**  
 b. Petals 5; fruits tomentose with normal hairs; hairs simple and stellately bundled . . . . . **2. Trigonoleura**

### 1. CHAETOCARPUS

*Chaetocarpus* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6 (1854) 300; Baill., Étude Euphorb. (1858) 323; Thwaites, Enum. Pl. Zeyl. (1861) 274; Müll.Arg. in DC., Prodr. 15, 2 (1866) 1121; Kurz, Forest Fl. Burma 2 (1877) 408; Hook.f., Fl. Brit. India 5 (1887) 460; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 89; Nat. Pflanzenfam. Nachtr. II-IV. Teil (1897) 212; Craib, Contr. Fl. Siam, Aberdeen Univ. Stud. 57 (1912) 194; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iv (1912) 7; Ridl., Fl. Malay Penins. 3 (1924) 310; Gagnep. in M.H.Lecomte, Fl. Indo-Chine 5 (1926) 471; Airy Shaw, Kew Bull. 26 (1972) 231; Whitmore, Tree Fl. Malaya 2 (1973) 76; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 67; Kew Bull. 36 (1981) 275; Welzen, Rheedea 4 (1994) 94; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 65; Welzen, Thai Forest Bull., Bot. 28 (2000) 56, f. 3; Radcl.-Sm., Gen. Euphorbiacearum (2001) 116. — Type: *Chaetocarpus pungens* Thwaites [= *Chaetocarpus castanocarpus* (Roxb.) Thwaites].

*Regnaldia* Baill., Adansonia 1 (1860) 187; Müll.Arg. in DC., Prodr. 15, 2 (1866) 1257. — Type: *Regnaldia chuytioides* Baill. [= *Chaetocarpus castanocarpus* (Roxb.) Thwaites].

Trees or shrubs, dioecious. *Indumentum* consisting of simple, hirsute to sericeous hairs, glabrescent. *Stipules* very asymmetric, early caducous. *Leaves* simple, distichous; petiole not to slightly pulvinate; blade (a)symmetric, coriaceous, punctate, base broadly attenuate, margin entire (to laxly sinuate), apex acuminate (to cuspidate), both surfaces (sub)glabrous; venation pinnate, looped and closed at the margin, indistinctly reticulate. *Inflorescences* dense axillary clusters of flowers (reduced thyrses), brachyblasts increasing in size with age. *Bracts* on brachyblasts, 4 surrounding each flower. *Flowers* actinomorphic; sepals 4(–5), 2 outside (outside sericeous), and 2(–3; see note) inside (outside with central sericeous band), spreading horizontally or reflexed, inside glabrous, third inner sepal petal-like, often with claw; petals absent (see note). *Staminate flowers*: pedicels with abscission zone; disc annular, lobed, toothed; stamens 8–15, absent in pistillate flowers (see note 2 under the species), in Malesia with an androphore from which the filaments branch alternately, androphore apically with a pilose, 3-lobed pistillode; anthers basifixed, opening laterally with a slit, bend upwards. *Pistillate flowers*: pedicels elongating in fruit; disc with more numerous and narrower teeth than staminate flowers; pistil: ovary (on short gynophore), 3(–4)-locular, densely hirsute; ovules one per locule, descending, epitropous, anatropous, attached halfway to column; styles 3, short, hirsute; stigmas divided up to the style, above with dendritic papillae, on

lower surface hirsute. *Fruit* a rhagma, subglobose, in Malesia outside densely echinate with glochidiate hairs, inside glabrous, dehiscent septically into 3(–4) segments, latter almost loculicidally split to the base; wall thin, woody. *Seeds* ovoid, flattened, 1–3 per fruit, black, glossy, covered in upper third by a thin aril; endosperm absent.

Distribution — 10 or 11 species pantropical, one species in W Malesia.

Notes — 1. The third (and very seldom a fourth) inner sepal is placed within the other two sepals and is alternisepalous and thinner than the sepals. Therefore, it might as well be described as a petal (see also Fig. 1b). Petals are reported to be absent in *Chaetocarpus* and this character is considered to be the main difference with the genus *Trigonopleura*. Obviously, the difference between both genera is not in the complete absence or presence of petals, but in the reduced number of petals in *Chaetocarpus*.

2. The New Guinean specimens (*Docters van Leeuwen 10234* and *Takeuchi et al. 15939*), identified as *C. pubescens* (Thwaites) Hook.f. (a species so far only known from Sri Lanka), are not added to this treatment, because the material is too poor to ascertain their identification.

### 1. *Chaetocarpus castanocarpus* (Roxb.) Thwaites

*Chaetocarpus castanocarpus* (Roxb.) Thwaites, Enum. Pl. Zeyl. (1861) 275; Müll.Arg. in DC., Prodr. 15, 2 (1866) 1122; Kurz, Forest Fl. Burma 2 (1877) 409; Hook.f., Fl. Brit. India 5 (1887) 460; Gamble, Man. Ind. Timb. (1902) 623; Craib, Contr. Fl. Siam, Aberdeen Univ. Stud. 57 (1912) 194; Pax & K.Hoffm. in Engl., Pflanzenz. IV.147.iv (1912) 8; Ridl., Fl. Malay Penins. 3 (1924) 310; Gagnep. in M.H.Lecomte, Fl. Indo-Chine 5 (1926) 471, f. 59: 12–16; Corner, Wayside Trees Malaya 1 (1940) 244 ('*castaneicarpus*'); Airy Shaw, Kew Bull. 26 (1972) 231; Whitmore, Tree Fl. Malaya 2 (1973) 76; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 67; Kew Bull. 36 (1981) 275; Jarvie & Perumal, Tropics 3 (1994) 159; Welzen, Rheede 4 (1994) 98, f. 1, map 1; Welzen in Sosef et al., PROSEA 5, 3 (1998) 156. — *Adelia castanicarpa* Roxb., Fl. Ind. 3 (1832) 848. — *Chaetocarpus castanocarpus* (Roxb.) Thwaites var. *genuina* Müll.Arg. in DC., Prodr. 15, 2 (1866) 1122, nom. inval. — *Gaedawakka castanocarpa* (Roxb.) Kuntze, Revis. Gen. 2 (1891) 606, nom. superfl. (see note 1). — Type: *Icones Roxburghianae* (holo K), India, Bengal, Boolkokra.

[*Casearia ? coriacea* Wall., Cat. (1847) 7196 (K, L), nom. nud.]

[*Bradleya ? coriacea* Wall., Cat. (1847) 7872 (BM, K, NY), Malaysia, Penang, nom. nud.]

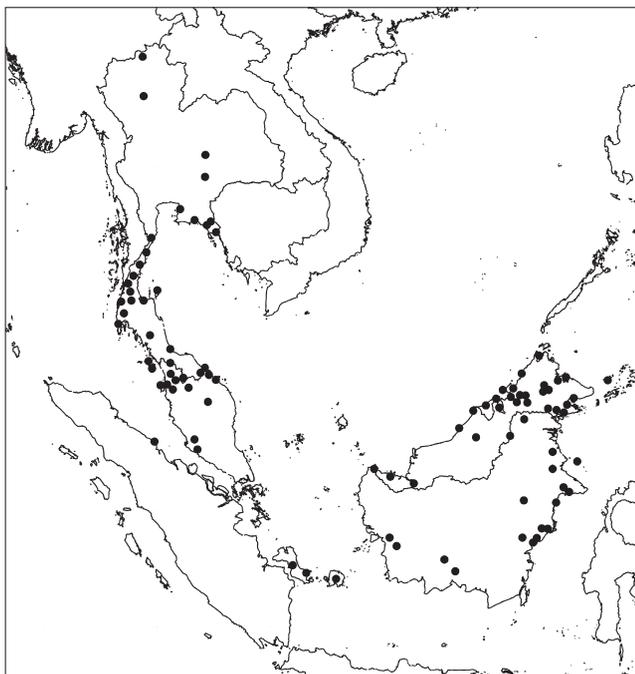
*Chaetocarpus pungens* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6 (1854) 301, f. 10A: 1–5, p.p., excl. description of fruit + f. 10A: 6–9 (Thwaites 1861). — Type: *CP (Thwaites) 2641* (holo K, n.v.; iso L, UC), Ceylon.



Plate 1. *Chaetocarpus castanocarpus* (Roxb.) Thwaites. a. Pistillate flowers with dendritic papillae on the stigma; b. fruits. © Phonsak Phonsena.

Trees (or shrubs) up to 45 m high, girth up to 3 m, dbh up to 60 cm; buttresses usually absent or indistinct, up to 1.2 m long, c. 7.5 cm thick; flowering branches 1–4 mm thick. *Outer bark* (smooth to) flaky, finely fissured, peeling off in 1–2 cm wide strips, coarsely granular, white to brown-grey to reddish brown to deep purple-brown, up to 2 mm thick; inner hard, gritty, salmon to red to purplish brown, up to 1 cm thick; cambium white to pale yellow; sapwood white to yellow-brown, heartwood pale reddish brown. *Stipules* falcate, obovate, 3–6.5 by 0.6–2.2 mm, subglabrous to subsericeous. *Leaves*: petiole 3–17 mm long, reniform in transverse section, with grooves across; blade ovate (to elliptic), 3.5–18.5 by 1.5–8 cm, length/width ratio 1.8–3.5, very apex narrowly rounded to mucronulate, nerves 7–9 per side. *Inflorescences* densely hirsute; bracts triangular, c. 0.8 by 1 mm. *Flowers* greenish yellow to white-yellow to yellow, slightly fragrant, sweet; pedicels woolly; sepals ovate to rounded, 1.5–3 by 1.5–3.3 mm; disc pink to red. *Staminate flowers* 2.2–3.7 mm diam.; pedicel 3.8–4.6 mm long; stamens: androphore 2.8–5 mm long, hairy, white, filaments 0.4–1 mm long, anthers triangular to elliptic, 0.5–1.2 by 0.4–0.6 mm, (hairy), yellow. *Pistillate flowers* up to 7.5 mm diam.; pedicel 3.3–5 mm long; pistil: (gynophore up to 0.4 mm high), ovary ovoid, 1–1.3 mm high, styles 3, 0.3–1.2 mm long, stigma lobes 1–2 mm long. *Fruits* 8–18 by 80–18 mm, yellow turning reddish brown, glochidiate hairs c. 3 mm long. *Seeds* 5.2–5.5 by 3.5–5 by 2.7–3.5 mm; aril red. *Embryo* ovoid, flattened, c. 4.3 by 3 mm; plumule and radicle c. 0.7 mm long. — **Fig. 1; Plate 1; Map 1.**

Distribution — Sri Lanka, India, Assam, Andamans, Burma, Cambodia, Vietnam, Thailand; in *W Malesia*: Peninsular Malaysia (not recorded for Singapore), Sumatra, and Borneo.



Map 1. Distribution of *Chaetocarpus castanocarpus* (Roxb.) Thwaites.

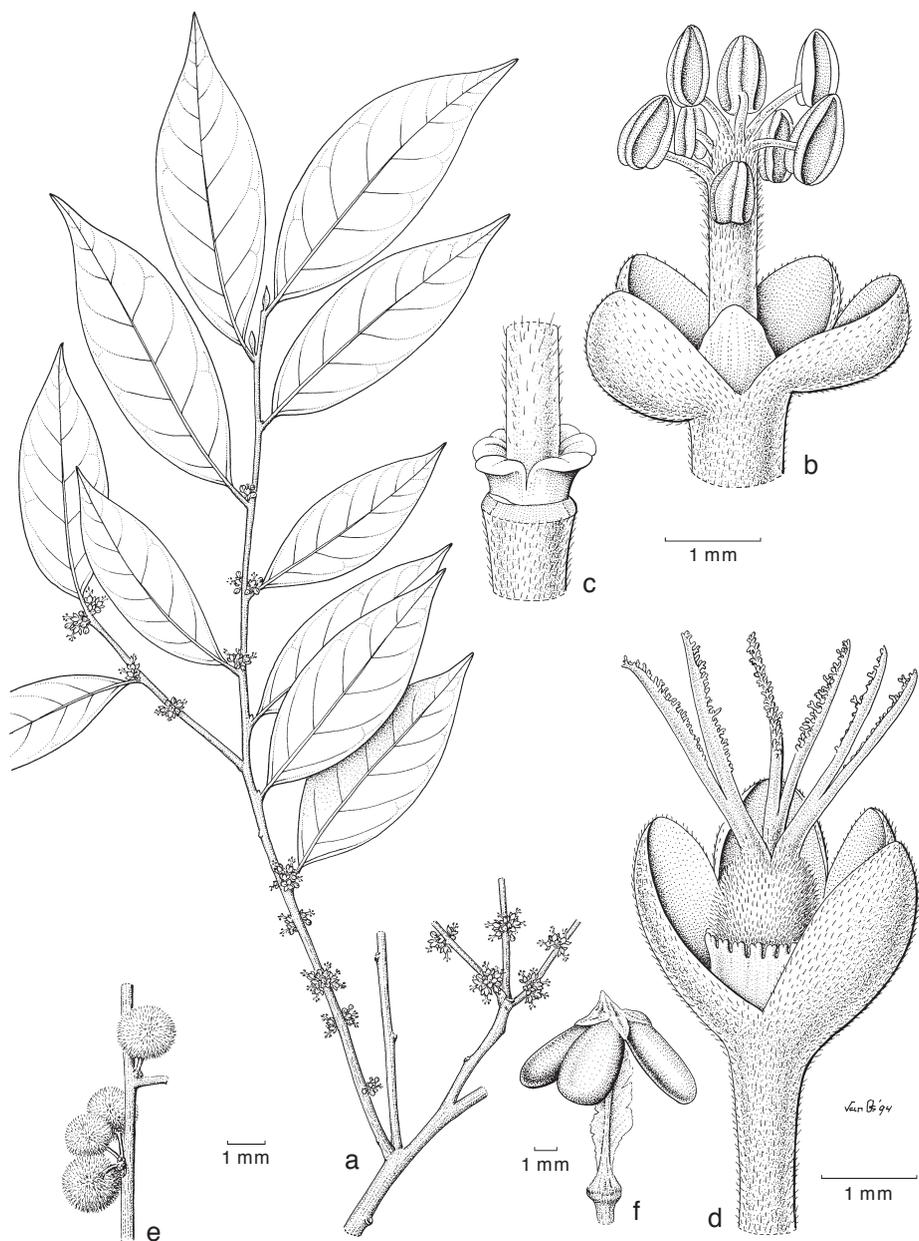


Fig. 1. *Chaetocarpus castanocarpus* (Roxb.) Thwaites. a. Habit; b. staminate flower showing fifth, petal-like sepal; c. idem, sepals removed showing disc and androphore; d. pistillate flower; e. fruit with stinging hairs; f. dehiscent fruit leaving columella and carunculate seeds (a–c: Ambriansyah & Arifin W 901; d: SAN (Gibot) 35970; e: Simpson 2009; f: SAN (Lantoh) 73395; all L).

**Habitat & Ecology** — Often common, but scattered in (hilly) primary and secondary lowland forest, mixed dipterocarp forest, coastal peat-swamp forest (kerangas), seasonally swampy forest, *Schima*-bamboo forest, along beaches and river banks, and in submontane scrubs. Soil: yellow, brown or black sandy soil, sandy loam, sandstone, yellow clay, clay-loam, rocky coral, or granite. Altitude: sea level up to 500 m. (Partly after Airy Shaw 1972, 1975, 1981.) According to Whitmore (1973) a calcifuge, because it is common along the coast in NE Malaysia and the inland collections may reflect old Pleistocene shore lines. However, the plants are also found in a far more acid surrounding, therefore, *Ch. castanocarpa* is more likely to be a very tolerant species capable of growing in a wide variety of soils. Flowering and fruiting throughout the year.

**Uses** — In NE Malaysia (Kelantan and Trengganu) the young leaves are cooked and eaten as spinach or chopped up with rice (Corner 1940). The wood is used as a non-construction timber by the Iban, Sarawak, Borneo (Jarvie & Perumal 1994), for building purposes in Ceylon (Gamble 1902), and for sampans and columns in Indochina (Gagnepain 1926). The wood is said to be light red, moderately hard, close-grained, pores small, scanty, in short radial lines, medullary rays very fine, very numerous, narrow wavy concentric bands fairly regular and prominent (Gamble 1902, Welzen 1998).

**Malesian vernacular names** — Malaysia: Batu, Membatu (Corner 1940). Sumatra: Besie, Kaju besi(e) (Malay). Borneo: Dengin-bobok (Bassap-Mapulu); Dusun bukit (Tidong); Kaju dusun, Nampadu (Malay); Masam (Serawak-Dyak); Mauhi (Bajar Malay); Medang serukan (Brunei Dusun); Pingas (Sungei); Rr'teh r'teh (Medong Serokan); Boekir, Djamilas, Djentian, Oebar bantan, Perupuk batu (Kalimantan area); Obah nasih (Sandakan Prov.).

**Notes** — 1. Kuntze (1891) made a new combination in the genus *Gaedawakka* L. (Fl. Zeyl. 1747: 203). This combination is superfluous, because the description of *Gaedawakka* predates the starting date of 1 May 1753 (art. 13.1a, I.C.B.N. 1988).

2. One specimen with pistillate flowers (*Forest Guard* 3, Malaysia, BM) showed 3 filaments attached to the gynophore, all other pistillate flowers were devoid of stamens.

3. The species is fairly constant, the infraspecific variation is quite narrow. Leaves on the Malay Peninsula are usually much larger than those on Sumatra, with the Bornean specimens in between. The pilosity varies, plants in Malaysia are (early) glabrous, while on Sumatra and especially in NE Borneo the leaves can be subpilose and the branches pilose, although glabrescent. On Borneo the leaves tend to be more elliptic than ovate (Malaysia, Sumatra). The staminate flowers in the Malay Peninsula are usually much larger than those on Sumatra, also with the Bornean specimens in between.

## 2. TRIGONOPLEURA

*Trigonopleura* Hook.f., Fl. Brit. India 5 (1887) 399; Pax in Engl. & Prantl, Pflanzenfam. 3, 5 (1890) 84; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 95; Pflanzenr. IV.147.xiv (1919) 42; Whitmore, Tree Fl. Malaya 2 (1973) 134; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 201; Kew Bull. 36 (1981) 350; Alphabet. Enum. Euphorb. Philipp. Isl. (1983) 46; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 65; Bulalacao & On, Natl. Mus. Pap. (Philippines) 3 (1992) 67; Welzen, Bulalacao & On, Blumea 40 (1995) 368; Radcl.-Sm., Gen. Euphorbicearum (2001) 115. — Type: *Trigonopleura malayana* Hook.f.

*Peniculifera* Ridl. (Sterculiaceae), J. Straits Branch Roy. Asiat. Soc. 82 (1920) 173; Fl. Malay Penins. 1 (1922) 290. — Type: *Peniculifera penangensis* Ridl. [= *Trigonopleura malayana* Hook.f.].

Trees, dioecious. *Indumentum* consisting of simple and stellately bundled, tomentose to hirsute hairs, latter deciduous. *Stipules* falcate, early caducous, tomentose. *Leaves* simple, distichous; petiole not to completely slightly pulvinate, below with transverse grooves when dry; blade symmetric (to slightly asymmetric), coriaceous, punctate, base emarginate to attenuate, margin entire, apex acuminate to caudate, very apex obtuse, both surfaces smooth, lower surface variously hirsute to glabrous; venation pinnate, at most slightly raised above, distinct below, nerves looped and joined at the margin, tertiary nerves slightly scalariform, veinlets reticulate. *Inflorescences* dense axillary clusters of 2–many flowers (reduced thyrses), tomentose, brachyblasts increasing in size with age; bracts on brachyblasts minute, triangular, hirsute. *Flowers* actinomorphic; pedicels with abscission zone, tomentose; sepals 5, imbricate, succulent, margin entire, apex (emarginate to) acute, outside keeled, tomentose, inside subglabrous; petals 5, valvate, more or less clawed, margin entire, apex emarginate to rounded, especially inside long hirsute; disc annular, consisting of 5 lobes, obovate to square, more or less triangular in transverse section, thick, glabrous, orange. *Staminate flowers*: stamens with a hirsute androphore from which the filaments branch in two bundles, a lower with 5 anthers and an upper with 3, anthers basidorsally fixed, opening latero-extorse with a slit, connective hirsute outside, apically often elongated into an appendix; pistillode 3-lobed, between upper stamens. *Pistillate flowers*: ovary (seldom 2–)3-locular, tomentose; ovules one per locule, descending, epitropous, anatropous, attached half-way to column; style 1, short, hirsute; stigmas 3, deeply divided, above with dendritic papillae, on lower surface hirsute. *Fruits* globose rhegmas, outside densely tomentose, reticulately wrinkled when dry, with 6 raised lines, dehiscing completely septically and partly loculicidally into 3 bifid pieces; inside smooth, glabrous; wall thin, woody. *Seeds* ovoid, flattened, 1–3 per fruit, black, glossy, abaxially covered up to 2/3rd by a thin, sometimes lobed aril, lobes sometimes touching adaxially; hilum V-shaped. *Embryo* ovoid, flattened, endosperm scanty.

Distribution — The genus comprises 3 species, all found in Malesia. One is widespread in W Malesia (Peninsular Malaysia, Sumatra, Borneo, Sulawesi; not known from Singapore), the others are endemics in Sarawak or in the Philippines.

#### KEY TO THE SPECIES

- 1a. Fruits 1.4–2.1 cm wide by 1.5–1.7 cm high, wall 2.5–4.3 mm thick. Flowers 5–7 by 4–8 mm diam. Aril also covering seed adaxially up to 1/2–2/3rd in the Philippines. — Sarawak, Philippines . . . . . **2**
- b. Fruits 0.9–1.3 cm wide by 1–1.3 cm high, wall 1.5–2.3 mm thick. Flowers 5–6 by 4–7 mm diam. Aril adaxially at most only basally covering seed. — Malay Peninsula, Sumatra, Borneo . . . . . **3. T. malayana**
- 2a. Leaves 7.3–21.5 by 3.8–7.1 cm, margin flat, subglabrous below (microscope!), brown when dry. Fruit wall c. 2.5 mm thick. — Philippines . . . . . **1. T. dubia**
- b. Leaves 5.7–14 by 2.5–5.5 cm, margin revolute, glabrous below, blackish brown when dry. Fruit wall c. 4.3 mm thick. — Sarawak . . . . . **2. T. macrocarpa**

### 1. *Trigonopleura dubia* (Elmer) Merr.

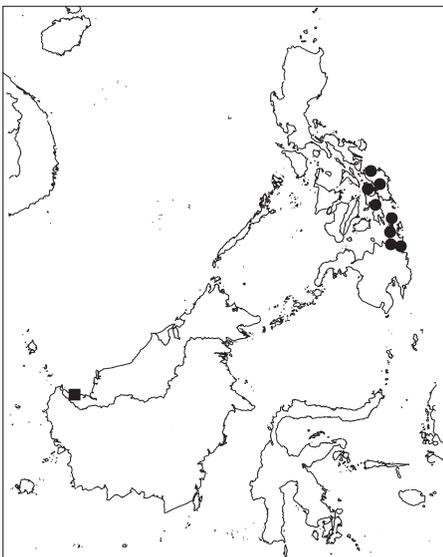
*Trigonopleura dubia* (Elmer) Merr., Philipp. J. Sci., Bot. 11 (1916) 77; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 42; Welzen, Bulalacao & On, Blumea 40 (1995) 369, f. 2b, c; map 1.

— *Alsodeia dubia* Elmer (Violaceae), Leaflet Philipp. Bot. 8 (March 1915) 2875. — Type: *Elmer 13956* (holo PNH<sup>+</sup>; iso L, NSW), Philippines, Mindanao, Agusan Prov., Cabadbaran (Mt Urdaneta).

*Trigonopleura philippinensis* Merr., Philipp. J. Sci., Bot. 10 (July 1915) 275. — Type: *BS (Ramos) 17475* (holo PNH<sup>+</sup>; iso K, L), Philippines, Samar.

*Trigonopleura malayana* auct. non Hook.f.: Airy Shaw, Alphabet. Enum. Euphorb. Philipp. Isl. (1983) 46.

Trees, up to 25 m high, dbh up to 90 cm; flowering branches 3.5–5 mm thick, ribbed to smooth, hirsute when young, descending. *Bark*: outer red or brown on trunk to grey on branches, smooth, c. 2 mm thick; inner reddish brown, c. 0.5 cm thick; wood soft to hard, odourless, slightly bitter; sapwood thin, white tinged reddish. *Stipules* obovate, c. 7 by 2.5 mm. *Leaves* descending; petiole 5–13 mm long, laterally flattened and deeply keeled on upper side with the walls touching, leaving a closed groove; blade ovate to obovate, 7.3–21.5 by 3.8–7.1 cm, length/width ratio 2.5–3.2, darker green above, brown when dry, margin flat, apex ascending, upper surface glabrous (except for the basal part of the midrib), lower surface subglabrous, nerves 8–11 per side. *Bracts* on brachyblasts c. 0.7 by 0.7 mm. *Flowers* 5–7 by 4–8 mm diam., odourless, ascending. *Staminate flowers*: pedicel 9–10 mm long; upper part above abscission zone 3–4 mm long; sepals elliptic to obovate, 3.8–5 by 2.2–3 mm, green; petals elliptic to obovate, 4–5.2 by 1.2–2 mm, cream white; disc lobes 0.9–1.4 by 0.7–0.9 mm; stamens: androphore 4–5.5 mm long, filaments 1–1.3 mm long, cream-white; anthers ± triangular, 0.8–1.1 by 0.7–0.9 mm, dull yellow. *Pistillate flowers* not seen. *Fruits* 1.4–1.6 by 1.5–1.7 cm high, red to purple; wall c. 2.5 mm thick. *Seeds* 5.8–7.5 by 5.3–6.5 mm; aril covering seed also adaxially, pink; hilum 2.8–4 mm broad. *Embryo* 6–6.5 by 5.5–6 mm; plumule and radicle not seen. **Fig. 2b, c; Map 2.**



Map 2. Distribution of *Trigonopleura dubia* (Elmer) Merr. (●) and *T. macrocarpa* Airy Shaw (■).

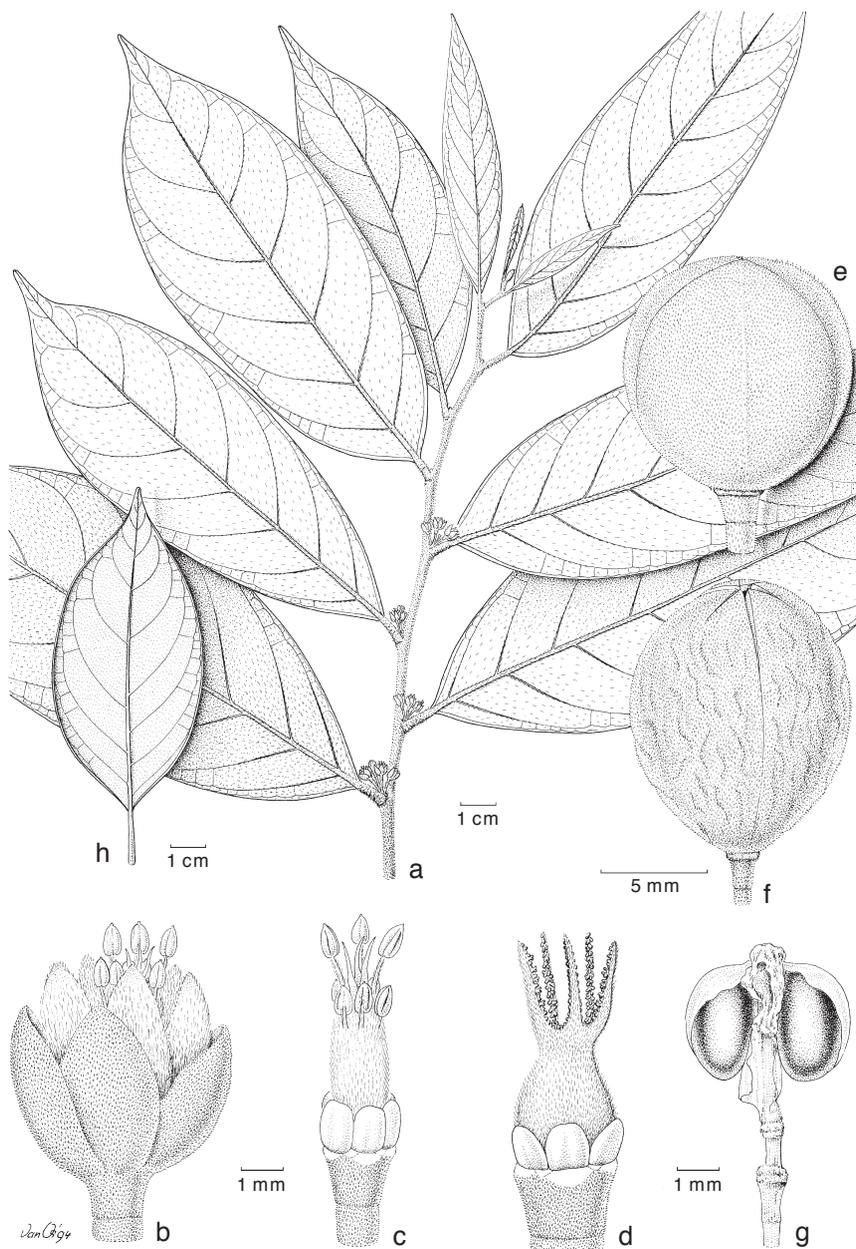


Fig. 2. a, d–g. *Trigonepleura malayana* Hook.f. a. Habit; d. pistillate flower; e. fruit (spirit kept); f. dried, wrinkled fruit; g. dehiscent fruit leaving columella and carunculate seeds. — b, c. *Trigonepleura dubia* (Elmer) Merr. b. Staminate flower with sepals, petals still attached; c. idem, sepals and petals removed, showing disc glands and androphore with stamens and pistillode. — h. *Trigonepleura macrocarpa* Airy Shaw. Leaf with recurved margins (a: Sinclair 10588; b, c: PNH (Sulit) 14357; d: KEP FRI (Chan) 13303; e: Pennington 8001; f, g: SAN (Leopold, Shea & Dewol) 73818; h: S (Nudong & Luang) 25378; all L).

Distribution — *Malesia*: Endemic in the central E Philippines (Samar and Leyte up to NE Mindanao).

Ecology & Habitat — Found in primary dipterocarp forest to logged over forest, on shady to open places like streams and forest margins. Altitude: 200–1250 m. Flowering: March, April (September); fruiting: March to July.

Vernacular name — Badabogan (Manobo language).

Note — Typical for *T. dubia*, just like for *T. macrocarpa*, are the flowers and fruits which are larger than those of *T. malayana*. Unlike *T. macrocarpa*, *T. dubia* does not differ in the leaves from *T. malayana*. The differences noted by Merrill (1915), like different angle of the nerves, disc glands with a different shape, and no mucro on the connective, could not be confirmed. Contrary to what Merrill reported, the connective does show a long appendix, usually much longer than in most specimens of *T. malayana*. *Trigonopleura dubia* is kept separate because the differences in flower and fruit size are correlated with a disjunction in the distribution of the genus.

## 2. *Trigonopleura macrocarpa* Airy Shaw

*Trigonopleura macrocarpa* Airy Shaw, Kew Bull. 36 (1981) 610; Welzen, Bulalacao & On, Blumea 40 (1995) 371, f. 2h; map 1. — Type: *S (Rosli & Galau) 15747* (holo K; iso L), Borneo, Sarawak, Arboretum Semengoh Forest Reserve.

Trees, up to 30 m high, up to 1.5 m girth; flowering branches 2–2.5 mm thick, smooth, hirsute when very young. *Stipules* obovate, 2–2.5 by 0.6–0.7 mm. *Leaves*: petiole 8–15 mm long, laterally flattened and deeply keeled on upper side with the walls touching, leaving a closed groove; blade ovate to elliptic, 5.7–14 by 2.5–5.5 cm, length/width ratio 2.1–3, blackish brown when dry, margin revolute, upper and lower surface glabrous, nerves 6–8 per side. *Bracts* on brachyblasts c. 0.7 by 0.7 mm. *Staminate flowers* c. 6.5 by 6 mm diam., white; pedicels 2–5 mm long; upper part above abscission zone 1–2 mm long; sepals ovate to obovate, 4.8–5.5 by 2–3 mm; petals obovate, 5–5.3 by 1.6–2.4 mm; disc lobes 1.2–1.3 by 0.5–1.3 mm; stamens: androphore c. 5.3 mm long, filaments c. 0.8 mm long; anthers ± triangular, c. 1 by 0.9 mm. *Pistillate flowers* not seen. *Fruits* c. 2.1 by 1.7 cm high; wall c. 4.3 mm thick. *Seeds* c. 7 by 5.7 mm; aril not observed; hilum c. 3.7 mm broad. *Embryo* not full-grown. — **Fig. 2h; Map 2.**

Distribution — *Malesia*: Sarawak, endemic in the Arboretum of Semengoh Forest Reserve near Kuching.

Habitat & Ecology — Found in lowland primary dipterocarp forest on hill slopes. Altitude: c. 100 m. Flowering: September; fruiting: November.

Note — Typical for *T. macrocarpa* are the large flowers and fruits, and the shorter leaves with revolute margins which dry blackish brown. Some Bornean specimens of *T. malayana* resemble *T. macrocarpa* in the lack of indumentum and shape and colour of the dried leaves, however, their fruits and flowers are always smaller than those of *T. macrocarpa*. Some examples of glabrous *T. malayana* are: *S 41134, 46802; SAN 17572, 41933, 44679.*

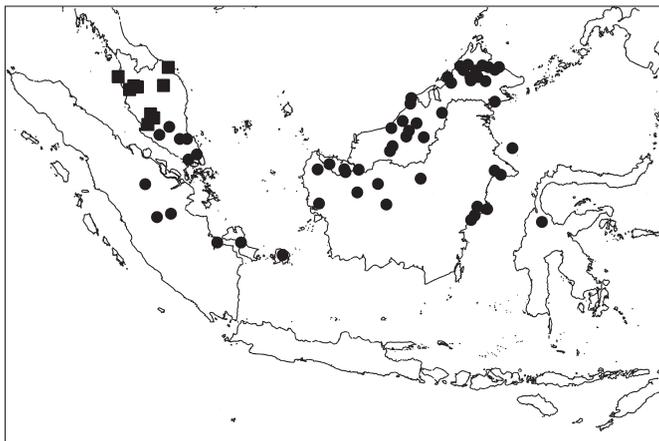
### 3. *Trigonopleura malayana* Hook.f.

*Trigonopleura malayana* Hook.f., Fl. Brit. India 5 (1887) 399; Hooker's Icon. Pl. 18 (1888) t. 1753; Pax & K.Hoffm. in Engl., Pflanzenz. IV.147.iii (1911) 95, f. 1b–d, 30; Ridl., Fl. Malay Penins. 3 (1924) 263; Stern, Amer. J. Bot. 54 (1967) 665, 667, 671, f. 10; Whitmore, Tree Fl. Malaya 2 (1973) 134; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 201; Kew Bull. 36 (1981) 350; Welzen, Bulalacao & On, Blumea 40 (1995) 372, f. 2a, d–g, map 2. — Lectotype (Welzen et al. 1995): *Maingay KD 1452* (holo K), Malaya. (The other two syntypes, *Scortechini* specimens, were sterile.)

*Trigonopleura borneensis* Merr., Philipp. J. Sci., Bot. 11 (1916) 76. — Type: *Hose 676* (holo? PNH†; iso BM, L; photo of BM sheet in A), Borneo, Sarawak, Miri River.

*Peniculifera penangensis* Ridl. (Sterculiaceae), J. Straits Branch Roy. Asiat. Soc. 82 (1920) 173; Fl. Malay Penins. 1 (1922) 290. — Type: *Curtis 3745* (holo K), Malaysia, Penang, Government Hill.

Trees, up to 27 m high; dbh up to 41 cm; buttresses up to 1.5 m long, 80 cm high, 12.5 cm thick; flowering branches 2.5–8 mm thick, ribbed to smooth, hirsute when young. *Indumentum* of white hairs. *Bark* with watery, yellow exudate; outer (red-)brown to chocolate brown to dark grey, smooth to rough and lenticellate, c. 2 mm thick; inner reddish brown to (pale) brown, granular, soft, c. 1 cm thick; cambium yellow; sapwood white to light brown; heartwood dark brown. *Stipules* obovate, 2.5–9 by 0.8–3 mm. *Leaves*: petiole 6–12 mm long, reniform in transverse section to laterally flattened and deeply keeled on upper side with the walls touching, leaving a closed groove; blade (ovate to) elliptic to obovate, 4.8–19.5 by 2–8.2 cm, length/width ratio 2.1–3(–3.8), red when young, darker green above when mature, margin flat (to revolute), upper surface glabrous except for the basal part of the midrib, lower surface subglabrous to hirsute, nerves 8–11 per side. *Bracts* on brachyblasts c. 0.7 by 0.7 mm. *Flowers* 5–6 by 4–7 mm diam., fragrant; pedicels 6–8 mm long; upper part above abscission zone 1.3–2.4 mm long; sepals ovate to elliptic (to obovate), 2.3–4.3 by 1.3–3.5 mm, light green; petals white; disc lobes 0.7–1.4 by 0.3–1.2 mm. *Staminate flowers*: petals obovate, 3–3.8 by 1.1–1.3 mm; stamens: androphore 4–5.2 mm long, filaments 0.5–0.8 mm long, white; anthers ± triangular, 0.7–1 by 0.4–0.8 mm, yellow. *Pistillate flowers*:



Map 3. Distribution of *Trigonopleura malayana* Hook.f., showing two geographical forms in Peninsular Malaysia, a glabrous form with narrow petioles (■) and a hirsute form with broad petioles (●).

petals obovate, 3.8–5.8 by 1.2–3 mm; ovary ± globose, 2.3–2.6 by 1.3–2.3 mm, style 0.3–0.6 mm long, stigmas c. 2.5 mm long, lobes c. 1.8 mm long, glass-like to white. *Fruits* 0.9–1.3 by 1–1.3 cm high, red to purple; wall 1.5–2.3 mm thick. *Seeds* 4.5–5.7 by 4.5–5.2 mm; aril adaxially at most basally touching, pink; hilum 1.6–3.5 mm broad. *Embryo* 4.2–4.8 by 4–4.8 mm; plumule and radicle c. 1 mm long. — **Fig. 2a, d–g; Map 3.**

Distribution — *Malesia*: Peninsular Malaysia, Sumatra, Borneo (Indonesian Kalimantan, Sabah, Sarawak), and one specimen is known from Sulawesi (*bb* 29657).

Habitat & Ecology — Found in primary dipterocarp forest, secondary forest, riverine forest, submontane forest, along ridges and rivers, sometimes slightly swampy. Soil: limestone, sandy loam, granitic sand, sandstone, yellow sandy clay. Occurrence: very rare and scattered. Altitude: sea level up to 450(–1200) m. Flowering: March to October; fruiting: (March to) May to December.

Wood anatomy — See Stern, *Amer. J. Bot.* 54 (1967) 665, 667, 671, f. 10.

Uses — The leaves can be eaten fresh or dried above a fire as a substitute of gambir when chewing sireh. The wood is used as fire wood.

Vernacular names — Peninsular Malaysia: Medang keladi. Sumatra: Gambir oetan; Kaju salak; Tjelangau. Borneo: Kalimantan: Gomi balua; Sabah: Gambir (Kadazan); Gambir (Kadazan, Dusun-kinabatangan); Gambir hutan (Malay); Kadnoi, Kadaloy, Kadoro, Kodoloi, Kodoro (Dusun-kinabatangan); Sarawak: Akil (Malay); Enkunit, Kelali (Kayan); Kayu sedi, Kayu masam, Sedi, Selait, Sidek kayu (Iban); Kratuok (Dayak).

Notes — 1. This species is widespread on the Sunda Shelf and it is somewhat variable. In Peninsular Malaysia two forms are found, in the northern half the plants have narrow, grooved petioles and are almost glabrous, in the southern half the petioles are broad, more flat and the plants are very hairy. Examples of glabrous, narrow-petioled specimens: *Curtis* 1523, 3670, 3743; *KEP* 94455, 104857; *KEP FRI* 4488, 5745, 8324, 13303, 16136; *King's collector* 3610, 3650, 7587, 10178; *Scortechini* 738, 2056. Examples of pilose, broad-petioled specimens: *CF* 1977; *KEP* 105025; *KEP FRI* 7901, 7905, 7985, 16937; *Maingay* 1452; *Maxwell* 82-102; *Sinclair* 10588. No taxonomic distinction has been made, because the southern form is also found on Sumatra and Borneo, where subglabrous specimens are found with often also narrower petioles.

2. On Borneo the specimens can vary between (sub)glabrous (see note under *G. macrocarpa*), and then they are often found at higher altitudes, to hairy in most specimens to extremely hairy. The glabrous and very hairy forms are not geographically restricted. Examples of glabrous specimens are mentioned in the note under *G. macrocarpa*, examples of very hairy specimens are: *Endert* 1960; *Guigonis* 306; *W. de Jong* 445; *Paymans* 78.