

## A TAXONOMIC REVISION OF THE MALESIAN GENUS *TRIGONOPLEURA* HOOK. f. (EUPHORBIACEAE)

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### SUMMARY

*Trigonopleura*, a genus from W Malesia, has three species, the widespread *T. malayana* (Malay Peninsula, Sumatra, Borneo, Sulawesi) and the two endemic species *T. dubia* (Philippines) and *T. macrocarpa* (Sarawak, Kuching). The species differ slightly from each other in leaf size, colour, and margin, flower and fruit size, fruit wall thickness, and aril size.

A phylogenetic analysis was not performed, but it is argued that both endemic species split off separately from *T. malayana*. *Trigonopleura* is probably related to *Chaetocarpus*, in particular to *C. castanocarpus*. Probably, *Chaetocarpus* is a paraphyletic group of species and will be monophyletic when united with *Trigonopleura*, but this will need thorough phylogenetic research. Here, both genera are kept separate, because they are very distinct (see Table 1).

Typical for *Trigonopleura* are the fruits (wrinkled when dry, tomentose), the seeds (arillate), the inflorescences (axillary clusters of flowers), and the flowers (sepals imbricate, petals present, valvate, disc lobed, an androphore, 3 locules with one ovule each).

### INTRODUCTION

The genus *Trigonopleura* is readily recognizable by its tomentose fruits which become typically wrinkled when dry, the black, arillate seeds, the axillary clusters of flowers, the imbricate sepals, valvate petals, the disc consisting of 5 free lobes, and the stamens of which the filaments are united into an androphore. The ovary is 3-locular with one ovule per locule.

Hooker described the genus in 1887. He only recognized one species (*T. malayana*), with which two other later published species appeared to be conspecific, one described by Merrill (*T. borneensis*, 1916) and the other one by Ridley (*Peniculifera penangensis*, 1920). The latter genus is monotypic and was established by Ridley in the family Sterculiaceae. This already indicates the confusion around *Trigonopleura*. Elmer (March 1915) described the Philippine species *Alsodeia dubia* in the Violaceae, whereby the epithet already indicated his doubts about its relation to the Violaceae. Elmer described this second *Trigonopleura* species just a few months earlier than Merrill (July 1915). Merrill interpreting Elmer's species correctly (1916), made the combination *T. dubia* and placed his *T. philippinensis* into its synonymy. Finally,

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Airy Shaw (1981) described the third species in the genus, *T. macrocarpa*, based on a specimen from the Arboretum near Kuching (Sarawak) with larger fruits and different leaves.

The confusion around the position of *Trigonopleura* is not only reflected by descriptions in different families, but also within the Euphorbiaceae its position is not clear. Pax (1890) placed *Trigonopleura* in the subtribe Cluytiinae of the Platylobeae–Crotonoideae–Cluytieae, close to *Trigonostemon*, which it does not resemble at all (Airy Shaw, 1975). In 1911, Pax & K. Hoffmann restricted the delimitation of the Cluytiinae, but it still contained *Trigonopleura* next to *Trigonostemon*. Airy Shaw (1975) remarked on the similarity between *Trigonopleura* and *Chaetocarpus*. He placed them together in the informal group Chaetocarpeae, away from the Cluytiinae (Pax, 1890, who did not consider both genera to resemble each other, had placed *Chaetocarpus* in a different tribe, the Gelonieae instead of Cluytieae). Webster (1994) in the most recent overview of the family, holds an intermediate position, *Chaetocarpus* and *Trigonopleura* in a separate tribe, the Chaetocarpeae, close to the Cluytieae (all belonging to the subfamily Acalyphoideae and not the Crotonoideae!).

Both genera resemble each other in the alternate leaves, falcate stipules, axillary flower clusters, 5 imbricate sepals, disc appendages, presence of an androphore with 8 stamens, ovary 3-locular, 1-ovuled locules, and woody fruits with arillate flattened seeds. They differ in several characters, which are summarized in Table 1. Malaysian *Chaetocarpus* has been revised recently by Van Welzen (1994).

Table 1. Differences between *Chaetocarpus* and *Trigonopleura*.

| Character                            | <i>Chaetocarpus</i>         | <i>Trigonopleura</i> |
|--------------------------------------|-----------------------------|----------------------|
| Stellately bundled hairs             | absent                      | present              |
| Sepals                               | 4                           | 5                    |
| Petals                               | absent (to 1 or 2)          | 5                    |
| Flower size                          | small                       | large                |
| Branching of stamens from androphore | alternately (some together) | 2 whorls             |
| Ovary                                | echinate                    | smooth               |

#### SPECIES DELIMITATION

The species concept in this article is very narrow, the differences between the species are slight. Two considerations were basic to the decision to recognize three species.

The differences between *T. malayana* and *T. macrocarpa* are obvious. The leaves are (usually) different and the flowers and especially the fruits differ in size, those of *T. macrocarpa* being larger. However, *T. dubia*, which in vegetative parts is similar to *T. malayana*, also has larger flowers and fruits like *T. macrocarpa*. Important is the fact that a few Bornean specimens of *T. malayana* have leaves with the same size and almost the same colour as *T. macrocarpa*. Therefore, synonymizing *T. dubia* and *T. malayana*, because they are vegetatively similar, would result in the elimination of two differing characters (flower and fruit size) between *T. macrocarpa* and *T. malayana*, although the fruits of *T. macrocarpa* are somewhat larger than those of *T. dubia*.

Then, because of the few exceptional specimens of *T. malayana*, the remaining difference in leaf shape and texture between *T. macrocarpa* and *T. malayana* becomes questionable and these two species would have to be united.

An additional reason to keep *T. dubia* and *T. malayana* separate, beside some morphological differences, is the disjunct distribution. *Trigonopleura dubia* occurs very locally in the Philippines, an area with a drier climate than that on the everwet Sunda Shelf where *T. malayana* occurs. *Trigonopleura dubia* probably speciated recently from *T. malayana* (see next chapter), while during that short time morphological differences already developed. Therefore it is to be expected that due to a different climate, absence of genetic exchange with *T. malayana*, and a relatively narrow distribution *T. dubia* will change more in the future and it deserves a specific delimitation.

The specimens of *T. malayana* on the Malay Peninsula show two different groups. In the northern half of the peninsula (see Map 2) the specimens are more slender, almost glabrous, and they have a very narrow, high petiole, while in the southern half they are more robust, very hairy, and they have a broad, flat petiole. These differences cannot support a taxonomic delimitation, because specimens on Sumatra, resembling the southern, sturdy form are almost glabrous (not shown on the map). The same variation is present on Borneo, where also hairy specimens with narrow petioles were found. However, in the Malay Peninsula the demarcation between both forms is very conspicuous.

#### PHYLOGENETIC CONSIDERATIONS

The resemblance between species of the families Flacourtiaceae and Euphorbiaceae is often striking, but probably superficial; the ovary of the Flacourtiaceae is unilocular and the placentation is parietal instead of axillary. *Trigonopleura* seems to be 'very similar to *Casearia* (Flacourtiaceae)' (Whitmore, 1973; see also Elmer, 1915; Airy Shaw, 1975), while the hermaphrodite species *Aporosa hermaphrodita* (Euphorbiaceae) can be linked to several other Flacourtiaceae genera (Airy Shaw, 1971). This demonstrates the superficial resemblance between both families, because *Trigonopleura* and *Aporosa* are seemingly not closely related, they are even placed in completely different subfamilies, the Crotonoideae and Phyllanthoideae respectively.

A proper phylogenetic analysis of *Trigonopleura* is quite difficult. The selection of the outgroup is obvious; *Chaetocarpus* is the apparent choice. However, none of the macromorphological characters studied is indicative of the relationships within the genus *Trigonopleura*; *T. macrocarpa* has as autapomorphy the smaller, differently coloured, recurved leaves, while *T. dubia* has a slightly different type of aril. The resemblance between *T. macrocarpa* and *T. dubia* is based on the larger fruits and slightly larger flowers, but probably this is not the same character state, because the fruits of *T. macrocarpa* are larger and their wall is thicker than those of *T. dubia*. This leaves no characters for an analysis and a trichotomy is the result (see Fig. 1a). If we consider the geography of the three species (see Maps 1 and 2), then *T. malayana* is widespread and the other two species are endemics. Therefore, it is very likely that both endemic species originated from *T. malayana* (Fig. 1b), the exact timing being unknown. The isolation mechanism which split off *T. macrocarpa* is not obvious, but with *T. dubia* it is probably a result of glacial periods, during which the Philip-

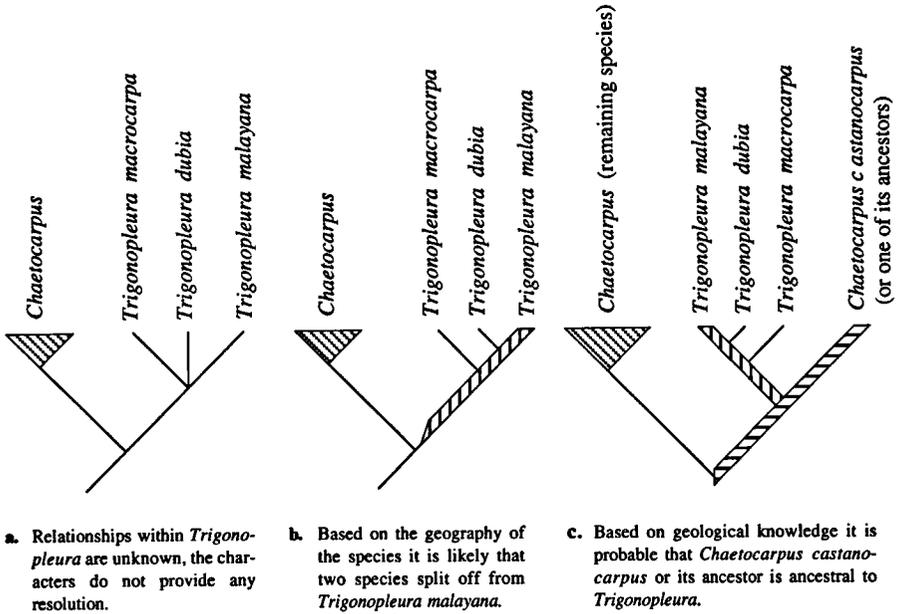
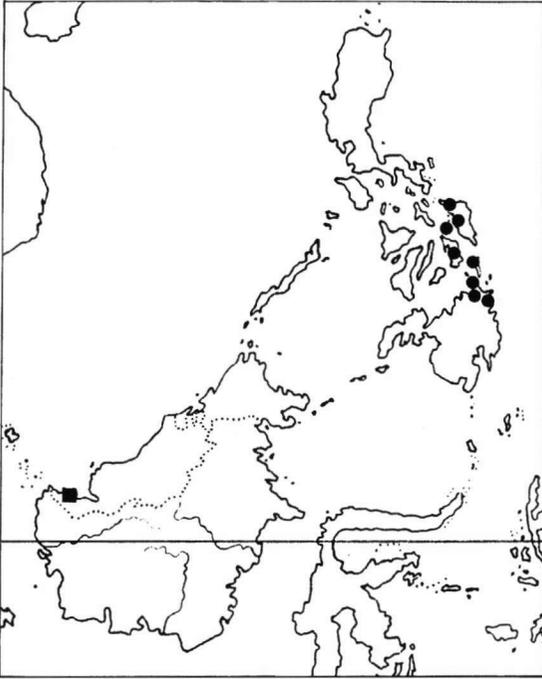


Fig. 1. The presumed phylogenetic relationships between the genera *Chaetocarpus* and *Trigonopleura*.

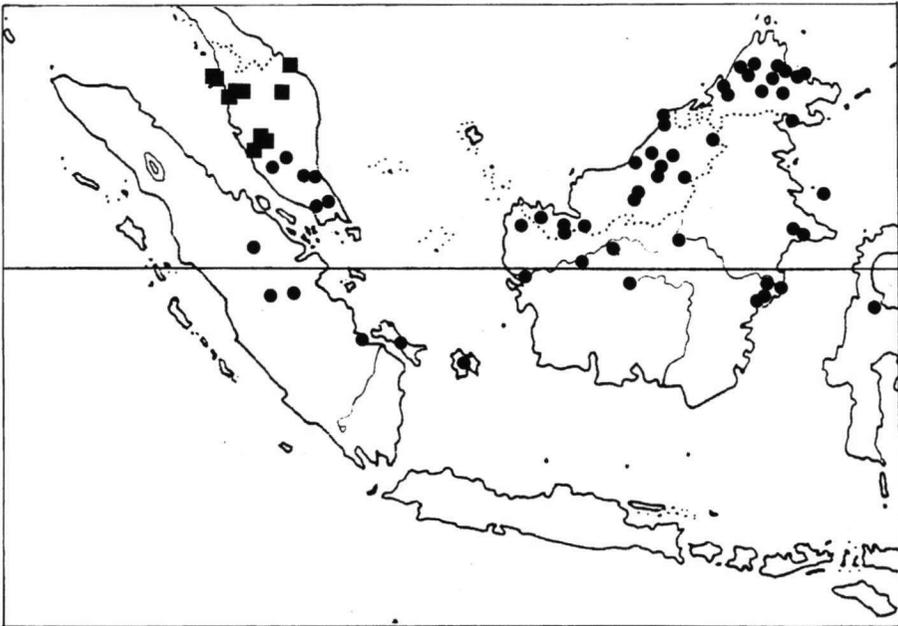
pine islands were connected to Borneo through land bridges (Morley & Flenley, 1987). Then *T. malayana* could extend its distribution over the Philippines, but the distribution became disjunct during interglacial periods, when the land bridges disappeared. The disjunction resulted in speciation. Consequently, *T. dubia* is a very young species, having originated in Pleistocene times.

One more interesting detail about phylogeny: *Chaetocarpus* is thought (probably correctly so) to be related to *Trigonopleura*. A whole genus can never be the ancestor of another genus. Therefore, *Trigonopleura* may have speciated from the ancestor to both *Chaetocarpus* and *Trigonopleura*, in which case both genera are a monophyletic group of species, or *Trigonopleura* speciated from one of the (ancestral) *Chaetocarpus* species, in which case *Chaetocarpus* will be a paraphyletic group of species, only to be monophyletic if *Trigonopleura* would be included. Geographically, the latter seems to be the most logical solution. *Chaetocarpus* comprises many more species than *Trigonopleura* and it has a far wider, even pantropical distribution, which makes it acceptable that this genus is older than *Trigonopleura*. Probably, *Chaetocarpus* originated in Gondwanaland, when S America, Africa, and India were still united and *Chaetocarpus* was transported to SE Asia with the plate tectonic movement of India from where it spread over SE Asia and the Sunda Shelf of Malesia (n.b., this must have been dispersal, because the larger part of SE Asia is of Australian origin; Audley-Charles, 1987). Only one species of *Chaetocarpus*, *C. castanocarpus*, is sympatric with *Trigonopleura*, therefore, this might be the ancestral species to *T. malayana* (Fig. 1c). Otherwise, *Trigonopleura malayana* and *Chaetocarpus castanocarpus* will



share an ancestral species in *Chaetocarpus*, which perhaps dispersed eastwards from India into SE Asia. However, several morphological characters of *Chaetocarpus* suggest that it is a monophyletic group of species, because these characters are seemingly apomorphic, e.g., the loss of petals and the presence of ovarian appendages. As far as the petals are concerned, *C. castanocarpus* is intermediate between *Chaetocarpus* and *Trigonopleura*, because it shows a reduced number of

Map 1. Distribution of *Trigonopleura dubia* (Elmer) Merr. (●) and *T. macrocarpa* Airy Shaw (■).



Map 2. Distribution of *Trigonopleura malayana* Hook. f. with two geographical forms in Peninsular Malaysia, a glabrous, narrow-petioled form in the northern half (■) and a hirsute, broad-petioled form in the southern half (●).

petals (Van Welzen, 1994); this might be a reversal, which continued in *Trigonopleura*. If *Trigonopleura* is derived from *Chaetocarpus*, then the loss of ovarian appendages must be a reversal. In conclusion, *Chaetocarpus* and *Trigonopleura* may have to be united into one genus (to be called *Chaetocarpus* Thwaites, because it is the oldest name, 1854), which without doubt will comprise a monophyletic group of species. However, both genera will be kept separate in this treatment, because a thorough phylogenetic treatment is outside the scope of the present Flora Malesiana revision.

### TRIGONOPLEURA

*Trigonopleura* Hook. f., Fl. Brit. India 5 (1887) 399; Pax in Engl. & Prantl, Nat. Pflanzenfam. III, 5 (1890) 84; Pax & K. Hoffm. in Engl., Pflanzenr. IV, 147, iii (1911) 95; xiv Euph.-Add. 6 (1919) 42; Whitmore, Tree Fl. Malaya 2 (1973) 134; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 201; Kew Bull. 36 (1981) 350; Alphab. Enum. Euph. Philipp. Isl. (1983) 46. — Type species: *Trigonopleura malayana* Hook. f.

*Peniculifera* Ridl. (Sterculiaceae), J. Roy. As. Soc. Str. Br. 82 (1920) 173; Fl. Mal. Penin. 1 (1922) 290. — Type species: *Peniculifera penangensis* Ridl. [= *Trigonopleura malayana* Hook. f.].

Trees, dioecious. *Indumentum* consisting of simple and stellately bundled, tomentose to hirsute hairs, the 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 to many flowers (reduced thyrses), tomentose, brachyblasts increasing in size with age. *Bracts* on brachyblasts minute, triangular, hirsute. *Pedicels* with abscission zone, tomentose. *Flowers* actinomorphic. *Sepals* 5, imbricate, succulent, margin entire, apex (emarginate to) acute, outside keeled, tomentose, inside subglabrous. *Petals* 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. *Stamens* absent in pistillate flowers; in staminate flowers with a hirsute androphore from which the filaments branch in two bundles, a lower with 5 anthers and an upper with 3, between the upper anthers a 3-lobed pistillode; anthers basidorsally fixed, opening latero-extrorse with a slit; connective hirsute outside, apically often elongated into an appendix. *Pistil* in pistillate flower: ovary (seldom 2- or) 3-locular, tomentose; ovules one per locule, descending, epitropous, anatropous, attached halfway to column; style 1, short, hirsute; stigmas 3, deeply divided, above with dendritic papillae, on lower surface hirsute. *Fruit* a globose rhegma, outside densely tomentose, reticulately wrinkled when dry, with 6 raised lines, along which the septicial dehiscence into 3 bifid pieces; inside smooth, glabrous; wall thin, woody. *Seeds* ovoid, flattened, 1–3 per fruit, black, glossy, abaxially covered up to  $\frac{2}{3}$ rd by a thin, sometimes lobed aril, lobes sometimes touching adaxially; hilum V-shaped. *Embryo* ovoid, flattened, endosperm absent.

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  $\frac{1}{2}$ – $\frac{2}{3}$ rd 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. — Malaya, 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. — Fig. 2b, c; Map 1

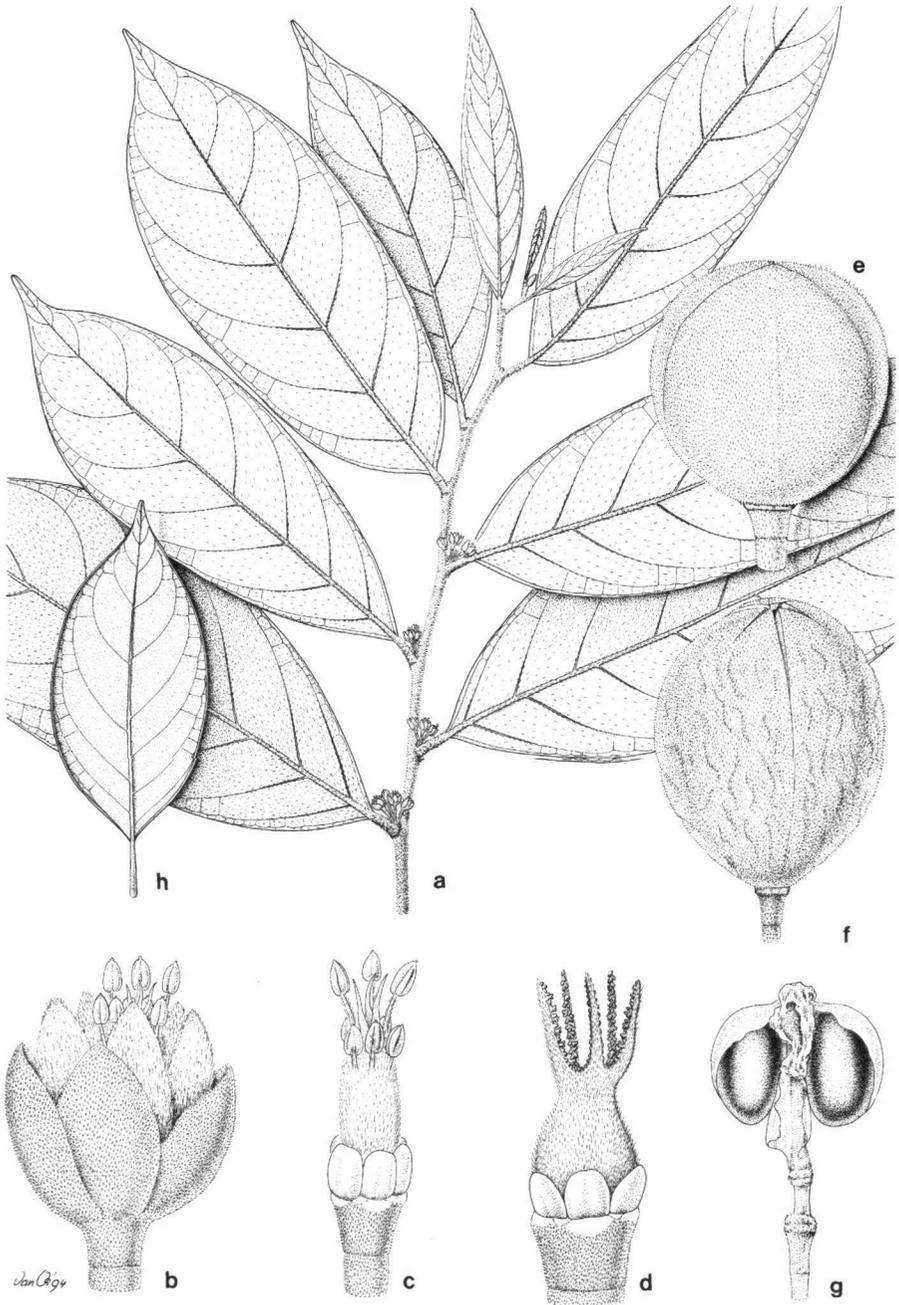
*Trigonopleura dubia* (Elmer) Merr., Philipp. J. Sc., Bot. 11 (1916) 77; Pax & K. Hoffm. in Engl., Pflanzenr. IV, 147, xiv Euph.-Add. 6 (1919) 42. — *Alsodeia dubia* Elmer (Violaceae), Leaflet Philipp. Bot. 8 (March 1915) 2875. — Type: *Elmer 13956* (holo PNH†; iso L, NSW), Philippines, Mindanao, Agusan Prov., Cabadbaran (Mt Urdaneta).

*Trigonopleura philippinensis* Merr., Philipp. J. Sc., Bot. 10 (July 1915) 275. — Type: *BS (Ramos) 17475* (holo PNH†; iso K, L), Philippines, Samar.

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

Tree, up to 25 m high, d.b.h. 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. *Leaves* descending; stipules obovate, c. 7 by 2.5 mm; 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, index 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 in diam., odourless, ascending; pistillate flowers not seen. *Pedicels* 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 in staminate flowers, cream white. *Disc* lobes 0.9–1.4 by 0.7–0.9 mm. *Stamens* in staminate flowers: androphore 4–5.5 mm long; filament 1–1.3 mm long, cream white; anther ± triangular, 0.8–1.1 by 0.7–0.9 mm, dull yellow. *Pistil* in pistillate flower not seen. *Fruit* 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; aril also adaxially closing; plumule and radicle not seen.

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



**Habitat & Ecology** — Found in primary Dipterocarp forest to logged-over forest, on shady to open places like streams and forest margins. Altitude 200–1250 m. Fl. Mar., Apr. (Sep.); fr. Mar.–July.

**Vernacular name** — Badabogan (Manobo lang.).

**Note** — Typical for *T. dubia*, just as 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 — Fig. 2h; Map 1

*Trigonopleura macrocarpa* Airy Shaw, Kew Bull. 36 (1981) 610. — Type: *S* (*Rosli & Galau*) 15747 (holo K; iso L), Borneo, Sarawak, Arboretum Semengoh Forest Reserve.

Tree, up to 30 m high, up to 1.5 m girth; flowering branches 2–2.5 mm thick, smooth, hirsute when very young. *Leaves*: stipules obovate, 2–2.5 by 0.6–0.7 mm; 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, index 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. *Flowers* c. 6.5 by 6 mm in diam., white, pistillate flowers not seen. *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 in staminate flowers. *Disc* lobes 1.2–1.3 by 0.5–1.3 mm. *Stamens* in staminate flowers: androphore c. 5.3 mm long; filament c. 0.8 mm long; anther ± triangular, c. 1 by 0.9 mm. *Pistil* in pistillate flower not seen. *Fruit* 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.

**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. Fl. Sep., fr. Nov.

**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

Fig. 2. — a. Habit of *Trigonopleura malayana* Hook. f., × 0.5. — b & c. Staminate flower of *T. dubia* (Elmer) Merr., with sepals and petals (b) and without, showing the disk lobes and the androphore with stamens (c), × 6. — d. Female flower of *T. malayana* without sepals and petals, showing disk lobes and gynoeceium, × 6; e–g: fruits of *T. malayana*, × 3; e. spirit-preserved fruit, not wrinkled; f. dried fruit, typically wrinkled; g. dehisced fruit, showing two seeds partly covered by an aril. — h. Lower surface of the smaller leaves of *T. macrocarpa* Airy Shaw with recurved margins, × 0.5 (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 in L).

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. — Fig. 2a, d–g; Map 2

*Trigonopleura malayana* Hook. f., Fl. Brit. India 5 (1887) 399; Hook. Ic. Pl. 18 (1888) t. 1753; Pax & K. Hoffm. in Engl., Pflanzenr. IV, 147, iii (1911) 95, f. 1b–d, 30; Ridl., Fl. Mal. Penin. 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. Add. Ser. 4 (1975) 201; Kew Bull. 36 (1981) 350. — Lectotype (proposed here): *Maingay KD 1452* (holo K), Malaya (The other two syntypes, *Scortechini* specimens, are sterile).

*Trigonopleura borneensis* Merr., Philipp. J. Sc., 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. (under Sterculiaceae), J. Roy. As. Soc. Str. Br. 82 (1920) 173; Fl. Mal. Penin. 1 (1922) 290. — Type: *Curtis 3745* (K, holo), Malaysia, Penang, Government Hill.

Tree, up to 27 m high; d.b.h. 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*: 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. *Sapwood* white to light brown; heartwood dark brown; cambium yellow. *Leaves*: stipules obovate, 2.5–9 by 0.8–3 mm; 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, index 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 in 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* obovate, 3–3.8 by 1.1–1.3 mm in staminate flowers, 3.8–5.8 by 1.2–3 mm in pistillate flowers, white. *Disc* lobes 0.7–1.4 by 0.3–1.2 mm. *Stamens* in staminate flowers: androphore 4–5.2 mm long; filament 0.5–0.8 mm long, white; anther ± triangular, 0.7–1 by 0.4–0.8 mm, yellow. *Pistil* in pistillate flower: 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. *Fruit* 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.

*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. *Fl.* Mar.–Oct.; *fr.* (Mar.–)May–Dec.

Wood anatomy — See Stern, Amer. J. Bot. 54 (1967) 665, 667, 671, fig. 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, Dusun-Kinabatangan); gambir hutan (Malay); kadaloy, kadnoi, kadoroi, kodoloi, kodoroi (Dusun-Kinabatangan); Sarawak: akil (Malay); enkunit, kelali (Kayan); kayu masam, kayu sedi, sedi, selait, sidek kayu (Iban); kratuok (Dayak).

Notes — This species is widespread on the Sunda Shelf (Map 2) and it is somewhat variable. In Peninsular Malaysia two forms can be seen: 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.

In Borneo the specimens can vary between (sub)glabrous (and then 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 *T. macrocarpa*; examples of very hairy specimens are: *Endert* 1960; *Guigonis* 306; *W. de Jong* 445; *Paymans* 78.

#### ACKNOWLEDGEMENTS

We are grateful to the organizations which helped to organize the fourth 'SE Asian regional training course on plant taxonomy', i.e., UNESCO/MAB, LIPI, Puslitbang Biologi, Herbarium Bogoriense, Rijksherbarium/Hortus Botanicus, and the Office for International Cooperation, Leiden University. We also like to thank the lecturers, Dedi Darnaedi, Kuswata Kartawinata, Sivarajan, Hubert Turner, Rugayah, Uway Warsita, Rochadi Abdulhadi, Harry Wiriadinata, and Rusdy Nasution.

The directors of A, BM, BO, F, G, K, L, MO, NSW, NY, P, UC, US, and Z are thanked for loans of their material or for enabling us to visit their institute.

We like to thank Pieter Baas, Piet Leenhouts, Marco Roos, and an anonymous referee for improvement of the manuscript. We are obliged to Jan van Os for the beautiful drawing. Max van Balgooy kindly identified specimens.

The maps were made with the map drawing program KORT (© Bertil Hansen, C) and the coordinates database COOR (© Peter van Welzen, L).

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## IDENTIFICATION LIST

Material of *Trigonopleura* studied: 1 = *T. dubia* (Elmer) Merr.; 2 = *T. macrocarpa* Airy Shaw; 3 = *T. malayana* Hook. f.

- A series 1745: 3; 2119: 3 — Afriastini 192: 3 — Agama 9954: 3 — Amdjah 64: 3.
- bb series 26456: 3; 28655: 3; 29633: 3; 29657: 3; 33991: 3; 34200: 3; 34468: 3; 34745: 3 — Boschproefstation 83.E.1.P.752: 3; 83.E.1.P.1031: 3 — BS series 17475: 1; 83916: 1; 84060: 1.
- CF series 1977: 3 — Curtis 1523: 3; 3670: 3; 3743: 3.
- Elmer 13956: 1 — Endert 1877: 3; 1878: 3; 1960: 3.
- FB series 23900: 1 — Forbes 3058: 3; 3143: 3.
- Grashoff 884: 3 — Guignonis 306: 3.
- Hose 676: 3.
- Jacobs 5392: 3; 5414: 3 — Jaheri 1155: 3; 1476: 3 — W. de Jong 445: 3.
- Keith 9042: 3 — KEP series 94455: 3; 104857: 3; 105025: 3 — KEP/FRI series 4488: 3; 5745: 3; 7901: 3; 7905: 3; 7985: 3; 8324: 3; 13303: 3; 16136: 3; 16937: 3 — King's collector 3610: 3; 3650: 3; 7587: 3; 10178: 3 — Kostermans 5753: 3; 6673: 3 — Kostermans & Anta 110: 3; 411: 3; 739: 3; 1179: 3; 1225: 3.
- Laumonier TFB 2057: 3; TFB 2061: 3.
- Maingay KD 1452: 3 — Maxwell 82-102: 3.
- Nooteboom 4477: 3 — Nooteboom & Chai 2176: 3.
- Paymans 78: 3 — Pennington 8001: 3 — Pickles 3424: 3 — PNH series 14357: 1; 14511: 1; 21602: 1; 41876: 1; 117730: 1 — Pusa 8494: 3.
- S series 15747: 2; 15822: 3; 16653: 3; 18916: 3; 23241: 3; 25378: 2; 25491: 2; 28955: 3; 29167: 3; 29575: 3; 31730: 3; 32256: 3; 41134: 3; 41267: 3; 43360: 3; 43467: 3; 46464: 3; 46802: 3 — SAN series 16940: 3; 17572: 3; 17752: 3; 17821: 3; 28467: 3; 35883: 3; 40608: 3; 41933: 3; 44679: 3; 50509: 3; 66019: 3; 73818: 3; 89570: 3; 90518: 3; 93696: 3; 96986: 3; 99696: 3; 113461: 3 — Scortechini 738: 3; 2056: 3 — Sinclair 10588: 3 — Soepadmo 107: 3.
- Teijsmann HB 8272: 3; 11035: 3; 11328: 3 — Thorenaar 83.E.1.P.752: 3.
- Wenzel 709: 1; 854: 1; 3536: 1.