PICRODENDRACEAE (formerly EUPHORBIACEAE s.l. subfam. OLDFIELDIOIDEAE)

(P.C. van Welzen, Leiden, The Netherlands & P.I. Forster, Indooroopilly, Australia)

Picrodendraceae Small, J. New York Bot. Gard. 18 (1917) 184. — Euphorbiaceae tribe Picrodendreae (Small) G.L.Webster, Taxon 24 (1975) 595; Ann. Missouri Bot. Gard. 81 (1994) 60; Radcl.-Sm., Gen. Euphorbiacearum (2001) 100. — Type: Picrodendron.

Euphorbiaceae-Phyllanthoideae-Phyllantheae-Dissiliariinae Pax & K.Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 281. — Type: Dissiliaria F.Muell.

Euphorbiaceae-Phyllanthoideae-Phyllantheae-Paivaeusinae Pax & K.Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 281. — Type: Paivaeusa Welw. (= Oldfieldia Benth.).

Euphorbiaceae-Phyllanthoideae-Phyllantheae-Petalostimatinae Pax & K.Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 281. — Type: Petalostigma F.Muell.

Euphorbiaceae-Phyllanthoideae-Phyllantheae-Toxicodendrinae Pax & K.Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 281. — Type: Toxicodendron Thunb. (= Hyaenanche Benth.).

Euphorbiaceae subfam. Oldfieldioideae Eg.Köhler & G.L.Webster, J. Arnold Arbor. 48 (1967) 48; G.L.Webster, Taxon 24 (1975) 595; Ann. Missouri Bot. Gard. 81 (1994) 81; Radcl.-Sm., Gen. Euphorbiacearum (2001) 81. — Type: Oldfieldia Benth.

(Sub)shrubs to trees, monoecious or dioecious. *Indumentum* of simple hairs. *Stipules* absent or present, persistent or caducous. *Leaves* alternate to opposite to verticillate, simple or palmate, petiolate. *Inflorescences* axillary fascicles, spikes, racemes, cymes and panicles, bracteate. *Flowers* unisexual, actinomorphic, pedicellate; sepals (3 or) 4–8 (or 12 or 13), imbricate, usually free; petals usually absent. *Staminate flowers*: disc absent to outside, in between and inside stamens; stamens 2–86, usually free; pistillode present or absent. *Pistillate flowers*: disc absent to usually annular; ovary 2–4(–5)-locular; ovules 2 per locule (except in *Scagea*); stigmas entire to rarely bifid or multifid, sometimes very broad. *Fruits* dehiscent capsules, rarely drupaceous. *Seeds* 1 (or 2) per locule, with or without caruncle; testa smooth; endosperm usually copious (rarely absent).

DISTRIBUTION

A family (or subfamily) with c. 100 species. Most species are found in the Southern Hemisphere, with many endemic genera and species in Australia, New Caledonia, Madagascar, Africa, Central and South America. In Malesia only four genera, three of which with a single species in New Guinea only; *Austrobuxus* (3 species) is the only one also found in West Malesia.

¹⁾ With contributions by P. Baas (wood anatomy) and R.W.J.M. van der Ham (pollen morphology).

Drawings by Esmée Winkel and Jan van Os.

TAXONOMY

The family was generally regarded as part of the Euphorbiaceae s.l. (Webster 1994; Rad-cliffe-Smith 2001), and classified as the subfamily Oldfieldioideae, including four tribes and several subtribes. Most typical for this otherwise indistinct family is the pollen (see below). *Croizatia* Steyerm. (originally belonging here in tribe Croizatieae; central and southern America) differed with 5 petals, an extrastaminal disc, divided stigmas, and lacking the pollen type (Levin 1992) and, based on molecular phylogenetic analysis (Wurdack et al. 2004), is currently placed in the Phyllanthaceae (Euphorbiaceae s.l. subfam. Phyllanthoideae). Also deviating is *Paradrypetes* Kuhlm. (tribe Podocalyceae subtribe Paradrypetinae; monotypic, Brazil), which probably belongs to the Rhizophoraceae, but agrees in wood anatomy and pollen details with *Podocalyx* Klotzsch (same tribe, subtribe Podocalycinae, monotypic in Amazonia; Levin 1992).

References: Levin, G.A., Systematics of Paradrypetes (Euphorbiaceae). Syst. Bot. 17 (1992) 74–83. — Radcliffe-Smith, A., Gen. Euphorbiacearum (2001) 125–129. — Webster, G.L., Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81 (1994) 67, 68. — Wurdack, K.J., P. Hoffmann, R. Samuel, A. de Bruijn, M. van der Bank & M.W. Chase, Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte Euphorbiaceae sensu lato) using plastid RBCL DNA sequences. Amer. J. Bot. 91 (2004) 1882–1900.

WOOD ANATOMY (P. Baas)

Wood anatomically only the genera *Austrobuxus* and *Petalostigma* are well documented. Hayden (1994) and Westra & Koek-Noorman (2004) also provide some information on the wood anatomy of *Choriceras*. The wood anatomy of *Kairothamnus* is unknown.

Because of their strong differences *Austrobuxus* and *Petalostigma* are here described separately.

Austrobuxus: Vessels almost exclusively solitary; perforations mainly simple but with few scalariform plates; vessel-ray pits with reduced borders. Fibres thick-walled and with distinctly bordered pits in both radial and tangential walls. Axial parenchyma mainly diffuse-in-aggregates and in short uniseriate bands. Rays 1–2-seriate, heterocellular. Prismatic crystals occasionally present in chambered axial parenchyma. Silica bodies absent.

Petalostigma: Vessels mainly in long radial multiples; perforations all simple; intervessel pits alternate, 4–7 μm; vessel-ray pits similar or with slightly reduced borders. Fibres thick-walled with simple to minutely bordered pits. Axial parenchyma mainly diffuse. Rays mainly uniseriate, but biseriate portions present in some species, heterocellular. Crystals absent, but silica bodies present in at least some species (*P. cf. pubescens*).

Choriceras shares with Petalostigma the extensive vessel multiples.

The great wood anatomical heterogeneity of this small satellite family of the Euphorbiaceae s.l. is noteworthy.

Literature: Bamber, R.K., Fibre types in the wood of Euphorbiaceae. Austral. J. Bot. 22 (1974) 629–634. — Hayden, W.J., Systematic anatomy of Euphorbiaceae subfamily Oldfieldioideae. I. Overview.

Ann. Missouri Bot. Gard. 81 (1994) 180–202. — Insidewood database 2002 onwards (http://insidewood.lib.ncsu.edu). — Metcalfe, C.R. & L. Chalk, Anatomy of the Dicotyledons, Oxford, Clarendon Press (1950). — Ogata, K. & A. Kalat, Wood anatomy of some trees, shrubs and climbers in Brunei Darussalam. Brunei Forestry Research Project. Special Publ. No. 3 (1997). — Westra, L.Y.Th. & J. Koek-Noorman, Wood Atlas of the Euphorbiaceae. IAWA J. Supplement 4 (2004).

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

Study of the pollen morphology of the Picrodendraceae was initiated, using light microscopy, by Erdtman (1952), Punt (1962) and Köhler (1965). Hayden et al. (1984) applied scanning electron microscopy of several genera to consider the relationships of *Picrodendron*, while Lobreau-Callen & Suarez Cervera (1994) used scanning and transmission electron microscopy of the pollen of 11 genera to investigate the taxonomic position of *Hymenocardia* in the Euphorbiaceae s.l. (this genus is now in the Phyllanthaceae). A comprehensive analysis including scanning and transmission data of nearly all genera was published by Levin & Simpson (1994) and Simpson & Levin (1994).

The pollen of all Picrodendraceae is shed as medium-sized monads (P by E = 22-50 by 22-50 µm). Pollen grain shape is suboblate to spheroidal (P/E = 0.81-1.00). The aperture system is either zonoaperturate: 6-7-colporate, 4-8-brevicolporate to -porate, or pantoaperturate: 5-7-, 10-40-porate. The exine is tectate and usually shows an irregularly structured infratectum. Sometimes, the infratectum is columellate (*Androstachys*) or much reduced (*Paradrypetes*, *Podocalyx*). The nexine is thick, irregular or absent. The tectum is mostly perforate, sometimes imperforate (*Paradrypetes*), and provided with echinae of c. 1-5.5 µm. The pollen of *Choriceras* and *Longetia* has a scabrate tectum. The poorly known pollen of *Sankowskya*, described as 'smooth' by Forster (2005), might be similar to that of *Choriceras* and *Longetia*.

According to Levin & Simpson (1994), four or more apertures per pollen grain may be considered as a synapomorphy of the family Picrodendraceae (excl. *Croizatia*, which has 3-colporate pollen). Pantoaperturate pollen is a synapomorphy of the clade (subtribe) Pseudanthinae (*Kairothamnus*, *Micranteum*, *Neoroepera*, *Pseudanthus*, *Scagea*, *Stachystemon*). A clade consisting of *Paradrypetes* and *Podocalyx* is supported by the occurrence of a much reduced infratectum.

References: Erdtman, G., Pollen morphology and plant taxonomy - Angiosperms (1952). Almquist & Wiksell, Stockholm. — Forster, P.I., Sankowskya, a new genus of Euphorbiaceae (Dissiliariinae) from the Australian wet tropics. Austrobaileya 4 (2005) 329–335. — Hayden, W.J., W.T. Gillis, D.E. Stone, C.R. Broome & G.L. Webster, Systematics and palynology of Picrodendron: further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65 (1984) 105–127. — Köhler, E., Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6 (1965) 26–120. — Levin, G.A. & M.G. Simpson, Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81 (1994) 203–238. — Lobreau-Callen, D. & M. Suarez Cervera, Pollen ultrastructure of Hymenocardia Wallich ex Lindley and comparison with other Euphorbiaceae. Rev. Palaeobot. Palynol. 81 (1994) 257–278. — Punt, W., Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7 (1962) 1–116. — Simpson, M.G. & G.A. Levin, Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Pl. Sci. 155 (1994) 313–341.

KEY TO THE GENERA

1a.	Leaves opposite; stipules absent
b.	Leaves spirally arranged; stipules or stipule scars present
2a.	Leaf blade margin crenate to serrate with 20-40 short teeth. Fruit lobes horned
	with stigma remnants
b.	Leaf blade margin entire. Fruits without appendices
3a.	Leaf blade apex caudate, lower surface glabrous. Stamens 10-14, filaments free
	Stigmas spade-like
b.	Leaf blade apex rounded to apiculate, lower surface sericeous. Stamens 28-68
	filaments united. Stigmas petal-like 4. Petalostigma

1. AUSTROBUXUS

Austrobuxus Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 444; Müll. Arg. in DC., Prodr. 15, 2 (1866) 1254;
Steenis, Blumea 12 (1964) 362; Airy Shaw, Kew Bull. 25 (1971) 506; Whitmore, Tree Fl. Malaya 2 (1973) 63; Airy Shaw, Kew Bull. 29 (1974) 303; Kew Bull., Addit. Ser. 4 (1975) 43; Kew Bull. 35 (1980) 597; 36 (1981) 258; McPherson & Tirel, Fl. Nouv.-Calédonie 14 (1987) 187; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 57; P.I. Forst., Austrobaileya 4 (1997) 620; Radcl.-Sm., Gen. Euphorbiacearum (2001) 90; S.S. Larsen in Chayam. & Welzen, Fl. Thailand 8 (2005) 105; Welzen & P.I. Forst., Nordic J. Bot. 28 (2010) 189. — Type: Austrobuxus nitidus Miq.

Buraeavia Baill., Adansonia 11 (1873) 83; Guillaumin, Fl. Anal. Synopt. Nouv.-Calédonie (1948) 181.
 Lectotype (Webster 1994): Buraeavia carunculata (Baill.) Baill. (= Austrobuxus carunculatus (Baill.) Airy Shaw).

Choriophyllum Benth., Hooker's Icon. Pl. 13 (1879) 62, t. 1280. — Type: Choriophyllum malayanum Benth. (= Austrobuxus nitidus Miq.).

Longetia auct. non Baill. ex Müll.Arg.: Ridl., Fl. Malay Penins. 3 (1924) 224; Corner, Wayside Trees Malaya 1 (1940) 260.

Shrubs to trees, dioecious; latex absent. *Indumentum* of simple hairs, most parts glabrescent; glandular and stinging hairs absent. Stipules absent (Malesia). Leaves simple, decussate; axillary buds usually covered by two relatively big scales, easily mistaken for stipules; petiole channelled above; blade symmetric, coriaceous, base attenuate to cuneate, margin entire to very laxly crenulate, flat to recurved, with very small glandular dots or teeth in shallow cavities, drying blackish; venation pinnate, generally indistinct, nerves looped and closed near margin, veins reticulate. Inflorescences axillary, imperfectly cymose, often thyrsoid, staminate ones with several flowers per node, pistillate ones generally with one flower or flowers in small groups per node; bracts hairy outside, glabrous to slightly hairy inside. Flowers actinomorphic; pedicel slightly hairy, glabrescent; sepals imbricate, glabrous to slightly hairy outside; petals absent. Staminate flowers pale green to yellowish to white, fragrant; pedicel cylindrical; sepals free, reflexed, the 2 outer ones smaller; stamens 4-9 (Malesia), around a raised receptacle, filaments glabrous; anthers elliptic, between basi- and dorsifixed, opening latro-extrorsely with longitudinal slits; pistillode absent, but receptacle raised and pistillode-like. Pistillate flowers: pedicel often elongating in fruit; sepals 4–8, ovate, tightly together in the young flower, apex rounded, outer ones very thick (and if present, inner ones thinner, with membranous upper margin); ovary 2-4-locular, 2 ovules per locule;

style absent, stigmas short, reniform to completely split, shortly papillate above. *Fruits* regmas, red, exo- and mesocarp detaching, endocarp woody, dehiscing into 2-valved cocci from base to apex, completely loculicidal, partly septicidal; persistent column very slender, basally with collar of carpel remnants, apically shortly T-shaped. *Seeds* obovoid, at most one developing per locule, the others abortive, shiny, caruncle yellowish to black when dry, orange to deep red when fresh, consisting of short to longer papillae.

Distribution — About 25 species, the majority endemic in New Caledonia, the rest in Australia and the West Pacific, three species in Malesia.

Note — *Austrobuxus* was synonymised for a long time with *Longetia* Baill. ex Müll. Arg. (the name *Longetia* is younger than *Austrobuxus*, but it was generally used as accepted name). McPherson & Tirel (1987) redefined the generic circumscriptions, both genera are separated based on different pollen types. *Longetia* is currently a monotypic genus of New Caledonia, while *Austrobuxus* is the species richest genus within the Picrodendraceae with also its main centre of distribution in New Caledonia.

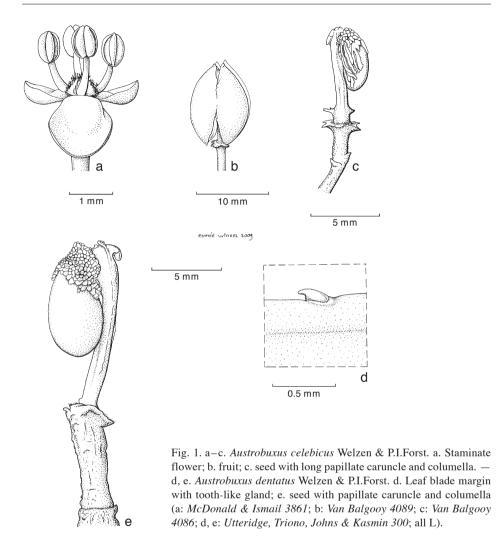
KEY TO THE SPECIES

- b. Leaf blade margins with black drying glandular teeth (check several leaves, teeth caducous, leaving glandular dot-like scars). New Guinea. 2. A. dentatus
- - b. Caruncle with up to 1.5 mm long, straight papillae. Ovary 2-4-locular. Fruits 10-22 by 9-16 mm. Leaves up to 16 cm long. Staminate flowers with (3 or) 4 or 5 sepals and (4 or) 5 stamens. Thailand, West Malesia 3. A. nitidus

1. Austrobuxus celebicus Welzen & P.I.Forst.

Austrobuxus celebicus Welzen & P.I.Forst., Nordic J. Bot. 28 (2010) 190, f. 1a-c, 3. — Type: E.F. de Vogel 6392 (holo L; iso L), Celebes, Sulawesi Selatan, north shore of Lake Towuti.

(Shrubs to) trees, up to 13 m high, dbh up to 30 cm; branchlets usually lenticellate when older, flattened when young, diameter of flowering ones 1.5–3 mm. *Indumentum* of brownish hairs. *Outer bark* nearly smooth to cracking and fissured vertically to flaky, brown to brownish grey to purplish grey; inner bark dark brown. *Leaves*: petiole 5–8 mm long, slightly hairy when young; blade elliptic (to somewhat obovate), 2.5–8 by 1–3.2 cm, length/width ratio 2.3–3.2, margin flat (to slightly recurved), with glandular dots, apex bluntly acute to acuminate, upper surface basally very slightly hairy when young, smooth, lower surface hairy when young, soon glabrous, smooth; venation indistinct, nerves 8–10 per side. *Inflorescences* single, basally cymose to upward imperfectly cymose, sericeous, staminate ones up to 2.4 cm long; bracts triangular, largest ones c. 2.1 by 1.2 mm wide. *Staminate flowers* c. 2.5 mm diam., buds greenish yellow; pedicel 3–3.8 mm long; sepals 4, ovate, 2 outer 1–1.2 by 1–1.2 mm, 2 inner 1.3–1.5 by c. 1.3



mm; stamens 4, filaments c. 1 mm long, anthers c. 0.7 by 0.6 mm, pale to golden yellow; receptacle somewhat hairy. *Pistillate flowers* not seen, data from fruits; pedicel 3–4 mm long; outer sepals 4 (or 5?), ovate, c. 1 by 1.2 mm, thick; ovary 2-locular; stigmas split, lobes up to 0.6 mm long, shortly papillate above. *Fruits* ellipsoid, 9–12 by 8–9 mm, wall thin, up to 1 mm thick; column 7–9 mm long. *Seeds* 5.5–6 by c. 3 by 1.5–2 mm, shiny dark brown when dry, caruncle black when dry, consisting of long, wavy papillae in a lax group, up to 5 mm long. — **Fig. 1a–c; Map 1.**

Distribution — *Malesia*: Endemic on Sulawesi.

Habitat & Ecology — Grasslands with short forest, heath forest; soil sandy, generally iron rich ultrabasic/serpentine. Altitude: 300–1700 m. Flowering: June to July; fruiting: July, August.

Note — Very likely an endemic species of ultrabasic soils.

2. Austrobuxus dentatus Welzen & P.I.Forst.

Austrobuxus dentatus Welzen & P.I.Forst., Nordic J. Bot. 28 (2010) 191, f. 1d, e, 3. — Type: Versteegh BW 266 (holo L; iso L), Netherlands New Guinea [= Indonesian Papua], Arfak Mountains, Anggi Lakes, Lake Anggi Gigi, Iray.

Shrubs to trees, up to 12 m high, dbh up to 15 cm; flowering branchlets 2-4.5 mm diam., somewhat wrinkled when dry, the youngest shoots somewhat flattened, smooth, the older ones rough. Outer bark cracked with reticulate grooves, brown; wood quite tough, without exudate nor smell; sapwood pink; heartwood pale straw-coloured. Leaves: petiole 3-8 mm long, slightly hairy when young, red; blade elliptic to obovate, 2.5-10 by 1-4.7 cm, length/width ratio 1.7-3.6, margin recurved, with teeth, these drying black, caducous, scar glandular dot-like, apex rounded to blunt, upper surface glabrous, smooth, dark green, lower surface slightly hairy when young, soon glabrous, smooth, light green; venation distinct on both sides especially the lower surface, nerves 8-11 per side. Staminate inflorescences and flowers unknown. Pistillate inflorescences single to few together, cymose, somewhat hairy, up to 1.7 cm long; largest bracts triangular, c. 1.5 by 1.5 mm, slightly hairy outside. Pistillate flowers unknown, data from fruits; pedicels up to 10 mm in fruit, slightly hairy; sepals 4, ovate, c. 1.6 by 2 mm, outside and especially the margin hairy; disc entire to lobed, hairy; ovary 2-4-locular, glabrous?; stigmas reniform when young to soon completely split. Fruits subglobose, 14-15 by 13-14 mm, yellow to (orange-)red to brownish red, glossy, wall generally thin, up to 1 mm thick; column 11–13 mm long. Seeds obovoid, c. 7 by 4.8 by 3 mm, red, shiny light brown when dry; caruncle yellow, black when dry, consisting of straight, moderately-long to long papillae, up to 2-5 mm long, drying yellowish (long) to brownish to blackish (short), in a rather lax group. — Fig. 1d, e; Map 1.

Distribution — *Malesia*: Endemic in New Guinea (Indonesian Papua).

Habitat & Ecology — Mixed heath forest, scrubby woodland with open places, primary forest, young secondary forest; soil: peaty clay, with limestone and sandstone boulders and outcrops. Altitude: 580–2100 m. Fruiting: February, April to June, August.

Vernacular names — Meptekeh (Dani); Seroema (Manikiong); Taoewa (Kapaukoe). Note — This species is only found at higher altitudes, the most western specimen was collected at the lowest altitude, all others are above 1700 m. Typical are the black drying, glandular teeth along the leaf blade margins, which are caducous and leave as scar a black dot similar to the glandular dots found in all other species and perhaps with still a glandular function. There is some variability. The two most eastern localities tend to have larger leaves and caruncle papillae that are up to 5 mm long and which dry yellowish; while the two central specimens have very small leaves, and much shorter papillae (2 mm) that dry black. The most western specimen is in between in leaf size, has > 2 mm long papillae, which dry brownish.

3. Austrobuxus nitidus Miq.

Austrobuxus nitidus Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 445; Airy Shaw, Kew Bull. 25 (1971) 506;
Whitmore, Tree Fl. Malaya 2 (1973) 63; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 43; Kew Bull. 36 (1981) 258; S.S.Larsen in Chayam. & Welzen, Fl. Thailand 8 (2005) 105, f. 23, pl. I: 2; Welzen & P.I.Forst., Nordic J. Bot. 28 (2010) 191, f. 2, 3. — Buxus nitidus (Miq.) Hallier f., Meded. Rijks-

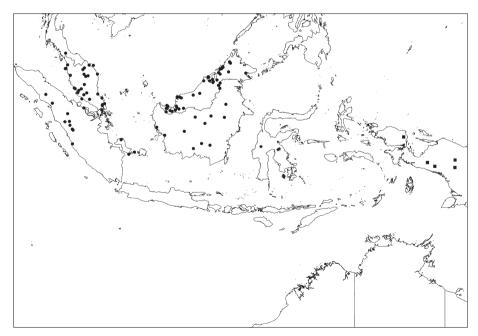
Herb. 37 (1918) 16. — Longetia nitida (Miq.) Steenis, Blumea 12 (1964) 362. — Austrobuxus nitidus Miq. var. nitidus: Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 43. — Type: Teijsmann HB 769 (holo U; iso L, U), West Coast Sumatra, prope Siboga.

Choriophyllum malayanum Benth., Hooker's Icon. Pl. 13 (1879) 62, t. 1280; Merr., J. Straits Branch Roy. Asiat. Soc., Spec. No. (1921) 333. — Longetia malayana (Benth.) Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 291; Ridl., Fl. Malay Penins. 3 (1924) 224; Corner, Wayside Trees Malaya 1 (1940) 260. — Syntypes: Beccari PB 3270 (Fl, n.v., K), Borneo, Sarawak; Beccari PB 3305 (Fl, n.v., K), Borneo, Sarawak; Beccari PB 3329 (Fl, n.v., K), Borneo, Sarawak, Beccari PB 3344 (Fl, n.v., K), Borneo, Sarawak; Griffith KD 5016 (K), Malay Peninsula; Maingay KD 1404 (K, L), Malaya, Penang; Maingay KD 1404/2 (K, L), Malaya, Penang; Maingay KD 2558A (K), Malaya, Malacca; Wallich Cat. 7975 (K), Singapore.

Choriophyllum montanum Ridl., J. Linn. Soc., Bot. 38 (1908) 322. — Longetia montana (Ridl.) Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 291; Ridl., Fl. Malay Penins. 3 (1924) 224. — Austrobuxus montanus (Ridl.) Airy Shaw, Kew Bull. 25 (1971) 507. — Austrobuxus nitidus Miq. var. montanus (Ridl.) Whitmore, Gard. Bull. Singapore 26 (1972) 51. — Type: L. Wray & H.C. Robinson 5424 (K; reported by Ridley as 5434), Malaya, Pahang, Gunong Tahan.

Austrobuxus nitidus Miq. var. macrocarpus Airy Shaw, Kew Bull. 25 (1971) 506; Kew Bull., Addit. Ser. 4 (1975) 43. — Type: KEP (R. Ismail) 104888 (holo K; iso KEP, n.v., L), Malaya, Selangor, Gunung Berembun, near Bukit Tangga.

(Shrubs to) trees, up to 30 m high, bole up to 6 m, dbh up to 50 cm; branchlets pale straw to greyish to greyish brown, flowering ones 2.5–4 mm diam., somewhat wrinkled when dry. *Indumentum* of brownish hairs. *Outer bark* smooth to rough to broadly fissured to flaky, greyish white to (dark) grey to greyish brown to dark brown, 1–2 mm



Map 1. Distribution of *Austrobuxus celebicus* Welzen & P.I.Forst. (\bigstar); *A. dentatus* Welzen & P.I.Forst. (\blacksquare) and *A. nitidus* Miq. (\blacksquare).

thick; inner bark pale yellow to pink to reddish brown to brown, fibrous, 5-10 mm thick; sapwood white to yellowish to pale brown, soft; heartwood pinkish brown to red, hard, dense. Leaves: petiole 4-14 mm long, slightly hairy when young, green to red; blade elliptic to obovate, 1.4-16 by 1-6 cm, length/width ratio 1.9-3.2, margin flat to recurved, with glandular dots, apex emarginate to rounded (to bluntly acuminate), upper surface slightly hairy when young, soon glabrous, smooth, dark green, glossy, lower surface hairy when young, soon glabrous, smooth, lighter green to glaucous to grey-green, shiny; venation generally indistinct to distinct on the lower surface, midrib green to brownish yellow beneath, nerves 6-9 per side. Inflorescences single to up to c. 3 together, cymose, but often thyrsoid, sericeous to subglabrous, staminate ones up to 5.5 cm long, pistillate ones up to 1 cm long, with basally several bracts; bracts triangular, largest ones 1–1.7 by 1–1.4 mm. Staminate flowers 3–4 mm diam.; pedicel 1.7-6 mm long; sepals (3 or) 4 or 5, ovate, the 2 outer ones 1.2-1.8 by 1-1.5 mm, the 2 or 3 inner ones 1.8-2.2 by 1.5-2.8 mm; stamens (4 or) 5, filaments 1.3-2.8 mm long, white; anthers 0.7–1.2 by 0.7–1 mm, pale to golden yellow; receptacle hairy, yellow to orange. Pistillate flowers 2.7-3.7 mm diam., green to red to greenish brown; pedicel 1.5-3.5 mm long, elongating up to 12 mm in fruit; sepals 4-8, ovate, 1-2 by 1.5-2.5 mm, apex rounded, 4 outer with 2 smaller, very thick, inner ones thinner, with membranous upper margin; ovary globose to ovoid, 1.2-3 by 1.5-2 mm, subglabrous to hairy, glabrescent, 2-4-locular; stigmas split in up to 1 mm long lobes, shortly papillate above. Fruits globose to obovoid, 10-22 by 9-16 mm, wall generally thin, up to 3 mm thick; column 10–17 mm long. Seeds obovoid, 8–10 by 5–6 by 3–4 mm, shiny dark brown when dry; caruncle black when dry, consisting of straight, short papillae, up to 1.5 mm long, in a tight group. — Fig. 2; Map 1.

Distribution — Peninsular Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo. Habitat & Ecology — Primary forest, secondary forest, *Agathis* forest, kerangas, fresh water seasonal swamp, primary and secondary peat swamp forest, riverine forest, montane mossy forest; sometimes along roads and sea shore; soil: acidic sand, peat, clay; bedrock: granite, igneous intrusives, sandstone. Altitude: sea level up to 2200 m. Flowering and fruiting whole year. Fruits eaten by monkeys (*Gianno 504*).

Uses — Sumatra: Fruit produces edible oil. Borneo (Sabah): Wood used for construction purposes (Bajau).

Vernacular names — Malay Peninsula: Dalet (Semelai). Sumatra: Haoendoloksapot; Kalek manoendjang; Tamasoe harangan; Tonggi tonggi. Borneo: Kalimantan: Kalek lilin, kasoe; Sabah: Oba suluk (Brunei); Oba sapan(g); Parapat; Susu-sudu (Bajau); Sarawak: Rabong, Ubah banih. English: Penang holly tree (Corner 1940).

Note — The two varieties, A. nitidus var. macrocarpum and var. montanum could not be distinguished, because of a continuous range in sizes of the leaf blades (var. montanum with smaller leaves) and fruits (var. macrocarpum with larger fruits). There was also no geocline in these sizes, though plants from higher altitude tend to have smaller leaf blades and smaller fruits. The plants in Thailand and the Malay Peninsula are generally somewhat more hairy when young and the bracts of the axillary buds are larger and more distinct.

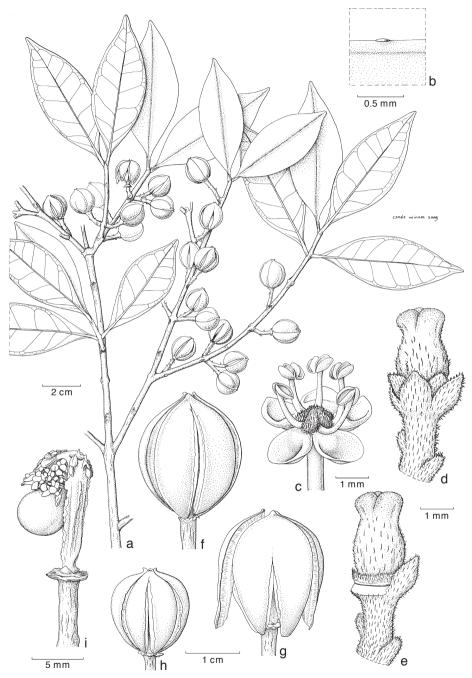


Fig. 2. Austrobuxus nitidus Miq. a. Habit; b. leaf margin with gland; c. staminate flower; d. pistillate flower; e. pistillate flower with part of sepals removed showing hairy disc; f. large fruit; g. large fruit dehiscing; h. small fruit; i. seed with papillate caruncle and columella (a, b, h: Shah 817; c: S (Anderson) 8571; d, e: Shah 1434; f, g: S (Brunig) 1063; h: Sidiyasa & Arifin 1095; all L).

2. CHORICERAS

Choriceras Baill., Adansonia 11 (1873) 119; Airy Shaw, Kew Bull. 14 (1961) 356; 16 (1963) 344;
35 (1980) 604; Kew Bull., Addit. Ser. 8 (1980) 46; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 58; P.I.Forst. & Welzen, Blumea 44 (1999) 100; Radcl.-Sm., Gen. Euphorbiacearum (2001) 94. — Type: Choriceras australiana Baill. [= Choriceras tricorne (Benth.) Airy Shaw].

Shrubs or trees, evergreen, monoecious; branchlets puberulous; stems and foliage without latex. *Indumentum* of simple, multicellular hairs; glandular and stinging hairs absent. *Stipules* entire, inconspicuous, caducous. *Leaves* opposite, petiolate, ovate to elliptic, coriaceous, margin (sub)entire or crenate to serrate, glands absent, penninerved. *Inflorescences* axillary, with bracteate, solitary flowers or fascicles of flowers. *Flowers* unisexual, actinomorphic, pedicellate, sepals in 2 whorls, free, imbricate, ± equal, petals and disc absent. *Staminate flowers* in dense multiflowered fascicles; sepals 2+2 or 3+3; stamens 4 or 6, filaments free, inserted on slightly raised receptacle, anthers dorsifixed, bilobate, thecae globose and longitudinally dehiscent. *Pistillate flowers* 1–3 together; sepals 3+3; ovary 3- or 4-locular, 2 ovules per locule; style absent; stigmas simple, not split. *Fruit* capsular, trilobate, smooth, dehiscing septicidally into 3 or 4 bivalved cocci; lobes horned with stigma remnants. *Seeds* ovoid; testa crustaceous; albumen fleshy; caruncle absent; cotyledons broad, flat.

Distribution — Two species in Australia; in Malesia: one extending into New Guinea. Classification — Webster (1994) and Radcliffe-Smith (2001) classified this genus within subfamily *Oldfieldioideae* in tribe *Caletieae* subtribe *Dissiliariinae*.

1. Choriceras tricorne (Benth.) Airy Shaw

Choriceras tricorne (Benth.) Airy Shaw, Kew Bull. 14 (1961) 356; 35 (1980) 604; Kew Bull., Addit. Ser. 8 (1980) 46; P.I.Forst. & Welzen, Blumea 44 (1999) 100, f. 1. — Dissilaria tricornis Benth., Fl. Australia 6 (1873) 91; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 292. — Lectotype (Airy Shaw 1980): A. Cunningham 265 (K), Australia, Northern Territory, Port Essington.

Choriceras australiana Baill., Adansonia 11 (1873) 119. — Type: Leguillou s.n. (P), Australia, Northern Territory, Raffles Bay.

Shrubs to small trees, up to 7 m high, often multistemmed. *Indumentum* of transluscent to yellow-ferruginous, simple hairs, glabrescent unless stated otherwise. *Outer bark* grey to brown, rough to flaky; inner bark streaky dark pink to red; cambium furrowed; sapwood pale amber, rather hard; heartwood dark pink. *Stipules* subulate, 1–1.8 by c. 0.3 mm, densely pubescent. *Leaves*: petioles 2–7 by 0.8–1 mm, (sub)glabrous to densely pubescent; blade elliptic, 1–9 by 0.45–3.2 cm, length/width ratio 2.2–2.8, base cuneate to truncate, margin crenate to serrate with 20–40 short teeth, apex obtuse to acute, strongly discoloured, upper surface dark glossy green, glabrous or with scattered hairs on the midrib; lower surface pale green, subglabrous; venation of 6–8 nerves per side, veins reticulate, indistinct. *Inflorescences* up to 10 mm long. *Staminate flowers* 2–3 mm diam., cream-yellow; pedicels 2.6–9 mm, glabrous; sepals orbicular to elliptic, 1–1.6 by 0.7–0.9 mm, glabrous; stamens 4 or 6, filaments 1.2–2 mm long, basally sparsely to densely hairy, anthers globose, 0.4–0.6 by 0.3–0.5 mm. *Pistillate flowers* 2.4–4.5 mm diam.; pedicels 1.5–2 mm long, with scattered hairs; sepals ovate to

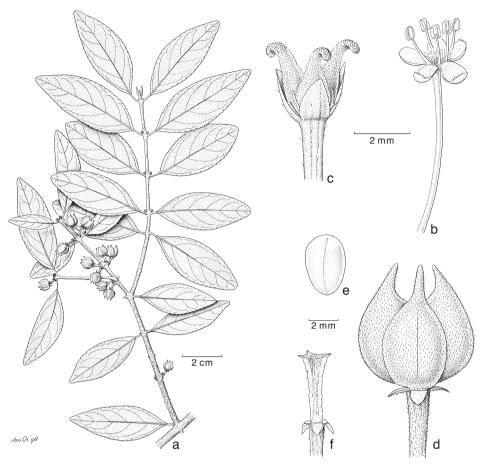


Fig. 3. Choriceras tricorne (Benth.) Airy Shaw. a. Habit; b. staminate flower; c. pistillate flower; d. fruit; e. seed; f. columella after dehiscence (a, d: NGF (Henty & Katik) 38771; b, c: Brass 8391; e, f: Paijmans 319; all L).

elliptic, 1.5-1.8 by 1-1.3 mm, glabrous or with scattered hairs; ovary usually 3-locular, subglobose, 1-1.5 by 2-2.5 mm diam., glabrous; stigmas 1.5-2.5 mm long, strongly recurved, papillose. *Fruits* globose, 4-7 by 5-11 mm diam., green-grey. *Seeds* ovoid, 3.5-4.8 by 2.5-3 by 2-3 mm thick, smooth, pale brown. — **Fig. 3.**

Distribution — North Australia (Northern Territory and Queensland); in *Malesia*: New Guinea (SE Papua in Indonesia and Western Province in Papua New Guinea).

Habitat & Ecology — Heath land, savannah with *Acacia*, *Eucalyptus*, and *Melaleuca*, open forest, vine thickets, and margin of rainforest; usually on sandy soils, also on reddish loam. Altitude: sea level up to 400 m. Flowering and fruiting throughout the year after heavy rain.

3. KAIROTHAMNUS

Kairothamnus Airy Shaw, Kew Bull. 34 (1980) 596; Kew Bull., Addit. Ser. 8 (1980) 121; Stuppy,
Syst. Morph. Anat. Samen biovul. Euphorb. (1995) 170; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 59; Radcl.-Sm., Gen. Euphorbiacearum (2001) 96. — Type: Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw.

Shrubs to trees, only plants with one sex observed, but probably monoecious (Radcliffe-Smith 2001). Indumentum mainly absent but simple hairs on ovary/fruit and staminate 'disc'. Stipules early caducous, minute. Leaves alternate, simple; petiole short, completely slightly pulvinate, transversely cracked when dry; blade with entire margin, caudate, penninerved. Inflorescences axillary fascicles, either with groups of staminate flowers or 1 or 2 pistillate flowers; bracts minute. Flowers pedicellate, actinomorphic, petals lacking, cream to white. Staminate flowers: sepals 4, free, imbricate, in 2 sizes; disc (or receptacle) flat, covering receptacle with holes for stamens, hairy; stamens 10-14, free, anthers between basi- and dorsifixed, 2-thecate, thecae parallel, opening latro-extrorse with lengthwise slits; pistillode very small, pyramidal, up to 0.2 mm high. Pistillate flowers: pedicel elongating in fruit; sepals in 2 differently shaped whorls of 3, imbricate; disc lobes 3, somewhat club-shaped, opposite outer sepals, glabrous; ovary 3-locular, densely sericeous; 2 ovules per locule; style absent, stigmas erect, spade-like, adaxial surface stigmatic. Fruits capsular, dehiscing septicidally and (partly) loculicidally, brown; pedicel elongating up to 7.7 cm, thickening towards apex; wall woody when dry, less than 1 mm thick, glabrescent outside, glabrous inside, exocarp separating from meso- and endocarp via fibrous layer; columella slender, T-shaped, with fibrous covering. Seeds bean-like but triangular in transverse section, exotesta shiny, smooth, without fleshy layer or appendages.

Distribution — Monotypic, endemic in Papua New Guinea, Morobe Province (Lae and Morobe Subprovince).

Classification — Webster (1994) and Radcliffe-Smith (2001) place *Kairothamnus* in the subfam. Oldfieoldioideae (= fam. Picrodendraceae), tribe Caletieae, subtribe Pseudanthinae. This equals the seed anatomical *Micrantheum* group of Stuppy (1995). However, the leaves are reminiscent of the genus *Phyllanthus* (see species epithet) and the cracks in the petiole of dried specimens resemble *Cleistanthus* (both genera in the Phyllanthaceae or, formerly, the Euphorbiaceae subfam. Phyllanthoideae). However, the seed resembles that of *Austrobuxus* (Oldfieldioideae).

1. Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw

Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw, Kew Bull. 34 (1980) 596; Kew Bull., Addit.
Ser. 8 (1980) 21, pl. 1, f. 1. — Austrobuxus phyllanthoides Airy Shaw, Kew Bull. 29 (1974) 303.
— Type: NGF (R.J. Johns) 47324 (holo K; iso L), Papua New Guinea, Morobe District, Morobe Subdistrict, Paiawa Valley, 7°35' S, 147°15' E.

Shrubs to medium-sized trees, up to 15 m high, bole up to 5 m high, dbh up to 20 cm; branches drooping; flowering branches 0.8–1.3 mm thick, epidermis of older branchlets with longitudinal slits around pustular lenticels. *Bark* 6–8 mm thick; outer bark smooth to vertically fissured, peeling off in flakes, grey to grey-brown; middle bark

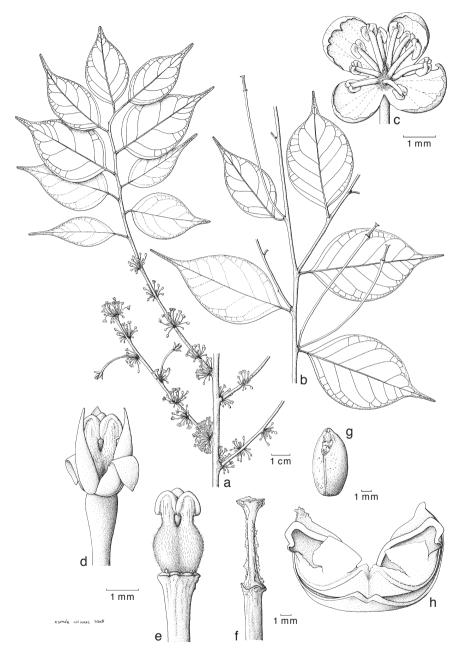


Fig. 4. *Kairothamnus phyllanthoides* (Airy Shaw) Airy Shaw. a. Habit with staminate flowers; b. habit with three dehisced fruits; c. pistillate flower with hairy, disc-like part of receptacle; d. pistillate flower with erect and reflected sepals; e. pistillate flower with sepals removed, note small disc gland at base of ovary; f. columella; g. seed; h. mericarp, completely dehisced septicidally and only partly longitudinally (a, c–e: *NGF* (*Streimann*) 24462, K; b, f: *LAE* (*Foreman*) 52046, L; g, h: *NGF* (*Streimann*) 45108, L).

green; inner bark greenish deep red to deep red; wood hard and heavy, straw-coloured. Stipules triangular, 0.5–1.2 by 0.4–0.6 mm, symmetric to asymmetric. Leaves: petiole channelled above, 3-8 mm long; blade ovate, 3.3-8.7 by 1.2-4.9 cm, length/width ratio 1.7-2.2, symmetric, papyraceous, base broadly cuneate; margin somewhat revolute, apex caudate, tip rounded and mucronulate, both surfaces smooth, though often pustules present, yellowish green to dark green and generally glossy above, light green and duller beneath; venation slightly raised on both sides when dry, nerves 5-7 per side till apex, looped and closed near margin, veins and veinlets reticulate. *Inflorescences*: bracts c. 0.7 by 0.5 mm, apex erose. Staminate flowers c. 5 mm diam., very fragrant; pedicel 8-9.5 mm long, capillary, cylindrical; sepals: 2 smaller ovate, c. 1.8 by 1.5 mm, margin entire, 2 larger obovate, c. 2.7 by 2 mm, apex very broadly rounded and serrate; filaments 1–1.5 mm long, thick, cylindrical; anthers c. 0.6 by 0.5 mm. *Pistillate* flowers 4.5-5 mm diam.; pedicel c. 1.5 cm long, cylindrical, broadening towards apex; sepals 6, in two whorls of 3, outer whorl elliptic, c. 5 by 1 mm, acute, apex recurved, inner spathulate, c. 4 by 2 mm, subcucullate, margin membranous, apex acute, black; disc lobes c. 0.3 mm high; ovary ovoid, c. 1.5 by 1.5 mm, stigmas with c. 0.5 mm high stipe and c. 1.3 by 1.1 mm blade-like part. Fruits (seen dehisced) ovoid to subglobose, up to 13 by 13 mm, green when young; pedicel elongating up to 7.7 cm; columella 7–8 mm long. Seeds elliptic, 8.4-8.5 by 4-4.2 by 3.5-3.8 mm. — Fig. 4.

Distribution — See under genus.

Habitat & Ecology — Along river banks in late secondary forest; soil: once recorded from ultrabasic soil. Altitude: sea level up to 70(-200) m. Flowering: April, May, August; fruiting: April, May, June, August.

4. PETALOSTIGMA

Petalostigma F.Muell., Hooker's J. Bot. Kew Gard. Misc. 9 (1875) 16; Pax & K.Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 281; Airy Shaw, Kew Bull. 31 (1976) 366; 35 (1980) 661; Kew Bull., Addit. Ser. 8 (1980) 178; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 58; P.I.Forst. & Welzen, Blumea 44 (1999) 105; Radcl.-Sm., Gen. Euphorbiacearum (2001) 95. — Type: Petalostigma quadriloculare F.Muell.

Shrubs or trees, evergreen, dioecious; stems and foliage without conspicuous latex. *Bark* greyish black, tessellated. *Indumentum* of simple hairs, not glandular, stinging hairs absent. *Stipules* entire, inconspicuous, caducous. *Leaves* spirally arranged, simple, petiolate, elobate, margin entire, glands absent, penninerved. *Inflorescences* axillary, bracteate fascicles or very short racemes with groups of flowers. *Flowers* actinomorphic; petals and disc absent. *Staminate flowers* pedicellate; sepals 4, free, imbricate, cucullate, ± equal; stamens 18–86, filaments connate and attached to a slightly raised receptacle; anthers dorsifixed, bilobate, thecae oblong, longitudinally dehiscent; pistilode absent. *Pistillate flowers* sessile to pedicellate; sepals 6–8, imbricate, free; ovary 3- or 4-locular, ovules 2 per locule, style short, stigmas simple, flabellate (petal-like). *Fruits* capsular, quadri- or trilobate, tardily dehiscing septicidally into bivalved cocci; sarcocarp fleshy, orange to red. *Seeds* ellipsoid to flattened ellipsoid to ovoid; testa crustaceous; albumen fleshy; caruncles entire, non-arilloid; cotyledons broad, flat.

Distribution — Five species from Australia, one also in Malesia: New Guinea.

Habitat & Ecology — Trees in open woodland and open forest dominated by Eucalypts. Altitude: 50–900 m. Flowering and fruiting after seasonal storm rains.

Classification — Webster (1994) and Radcliffe-Smith (2001) classified this genus within subfam. Oldfieldioideae in tribe Caletieae subtribe Petalostigmatinae.

1. Petalostigma pubescens Domin

Petalostigma pubescens Domin, Biblioth. Bot. 89 (1928) 871; Airy Shaw, Kew Bull. 31 (1976) 368;
35 (1980) 663; Kew Bull., Addit. Ser. 8 (1980) 178; P.I.Forst. & Welzen, Blumea 44 (1999) 105,
f. 3. — Lectotype (Airy Shaw 1976): Mitchell 483/615, young fruiting specimen (K), Australia, 'Subtropical New Holland' (Queensland, W of Brisbane).

Petalostigma quadriloculare F.Muell. var. pubescens Müll.Arg., Flora 47 (1864) 481. — Type: F. Mueller s.n., 1885-7 (K), Australia, Northern Territory, Arnhem Land.

Petalostigma quadriloculare F.Muell. var. genuina Müll.Arg. in DC., Prodr. 15, 2 (1866) 273, nom. illeg. — Type: F. Mueller s.n., 1855-7 (K), Australia, Northern Territory, Arnhem Land.

Petalostigma quadriloculare F.Muell. var. nigrum Ewart & O.B.Davies, Fl. N. Territory (1917) 166, t. 17. — Syntypes: Campbell 17 (MEL), Australia, N of 15 degrees; G.F. Hill 387 (MEL), Australia, Northern Territory, 70 miles N of Camp IV; G.F. Hill 908 (MEL), Australia, Northern Territory, Borroloola.

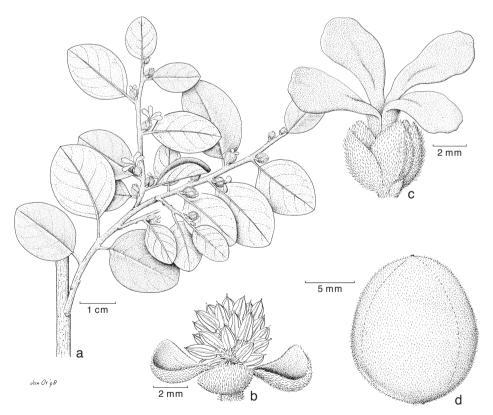


Fig. 5. Petalostigma pubescens Domin. a. Habit; b. staminate flower; c. pistillate flower with four large petaloid stigmas; d. fruit (a, b: Hyland 9148; c: Hubbard 4640; d: Hyland 8026; all L).

Petalostigma nummularium Airy Shaw, Kew Bull. 31 (1976) 373; 35 (1980) 663. — Type: C.R. Dunlop 2290 (holo K; iso BRI, DNA), Australia, Northern Territory, W of Frewena.

Petalostigma australianum auct. non Baill.: Baill., Adansonia 7 (1867) 356, t. 2, pro parte ('Crescit in Australia ... Leichhardt', t. 2).

Shrubs to small trees, up to 7 m high, usually single-stemmed. *Indumentum* of yellow-ferruginous hairs, mainly glabrescent. Bark roughly fissured, black-grey. Stipules linear-lanceolate, 4-6 by 0.3-0.8 mm, with dense hairs. Leaves: petioles 2.5-10 mm long, densely hairy; blade elliptic, orbicular or ovate, 10-65 by 7-45 mm, strongly discoloured, base cuneate, rounded or truncate, apex rounded to apiculate, upper surface dark glossy green, not granular, with sparse hairs when young; lower surface cream to cream-brown or ferruginous-brown, densely sericeous; venation with 5-7 pairs of nerves, veins ± obscure, reticulate. Flowers cream. Staminate flowers 5–12 mm diam.; pedicels 1–2 mm long, with sparse hairs; sepals 4, orbicular, broadly ovate to obovate, cucullate, 3.5-6 by 2.5-5 mm, sparsely hairy outside; stamens 28-68, connate into a column of 1.5–2 mm high, filaments 0.8–1.2 mm long, connate for most of their length, anthers oblong, 1.5-2 by 0.5-1 mm, usually with sparse hairs on apex of connective although occasionally glabrous. Pistillate flowers 5-8 mm diam.; pedicels 1.5-2.5 mm long, densely hairy; sepals 8, ovate to elliptic-ovate, 3.5-5.5 by 1.5-3 mm, densely hairy outside; ovary ovoid, 3.5-4 by c. 3 mm diam., with dense antrorse hairs; stigmas 4, elliptic-oblong, 5-6.5 by 1.4-2.5 mm, with sparse hairs on top and densely hairy on back. Fruit globose to subglobose, 11–22 by 15–20 mm diam., orange-yellow to orange. Seed ellipsoid, 6–9 by 3–4.5 by 3–4 mm thick, smooth to slightly rugose, glossy redbrown; caruncle \pm reniform, 1.5–2.5 by 1.8–2.5 mm, yellow to yellow-red. — Fig. 5.

Distribution — N and E Australia (Western Australia, Northern Territory, Queensland, New South Wales); in *Malesia*: Papua New Guinea (Western Province).

Habitat & Ecology — Open woodland and open forest dominated by eucalypts, also in coastal sand-dune; on various soils. Altitude: 20–900 m.