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**An enumeration of Sabah Passifloraceae,
with a revised key to *Adenia* species**

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Summary. An annotated enumeration of the five wild species of Passifloraceae in Sabah (four in *Adenia*, one in *Passiflora*) is presented. Introduced and naturalised species of *Passiflora* are mentioned. *Adenia heterophylla* (Blume) Koord. is new for Sabah, as well as *Adenia macrocarpa* (Blume) Koord. forma *microcarpa* (Hallier f.) W.J. de Wilde, a new form.

Since the revision of *Adenia* (De Wilde, 1971) and the treatment of the family Passifloraceae for Flora Malesiana (De Wilde, 1972a), and the revisions of Old World *Passiflora* (De Wilde, 1972b; Green, 1972), this family has received little taxonomic attention, except recently by De Wilde & Duyfjes (2010). Modern studies, mainly morphological and phylogenetic, have been conducted by Krosnick & Freudenstein (2005), and Krosnick *et al.* (2006, 2009). Passifloraceae with *c.* 10 genera worldwide comprises in Malesia three genera, viz. *Paropsia* Thouars (trees, one species in Peninsular Malaysia) and two genera of climbers, *Passiflora* L. (including the East Malesian genus *Hollrungia* K. Schum.) and *Adenia* Forssk. These latter two genera have their main occurrence outside Australasia: *Passiflora* has its centre in America, *c.* 350 species, and none in Africa; *Adenia* has its centre in Africa (and Madagascar), *c.* 90 species, and none in America.

More recent collections included three gatherings of *Adenia heterophylla*, which is new for Sabah. For Passifloraceae, Sabah and vicinity appear to be a relative hotspot of diversity in SE Asia, with seven taxa, excluding the widely naturalised *Passiflora foetida*. Passifloraceae are characterised by flowers with a hypanthium, a saucer- or cup-shaped lowest part of the flower, on the rim of which the sepals (sometimes largely connate) and petals (corolla) are inserted, and also the corona, variously shaped by threads or folds, except for *Adenia*, which has 5 disc-glands, and where the corona is absent or consists of fine hairs only. The ovary is superior, placed on an androgynophore. Two genera of

Passifloraceae occur in Borneo: *Passiflora* with large and showy flowers and *Adenia* with small, somewhat tubular, greenish creamy flowers.

Tendrils

The climbing *Passifloraceae* are tendril-climbers. They bear tendrils essentially in all leaf axils and are, as such, recognisable in the sterile state. The tendrils are prehensile tendrils, spiralling after attachment. Tendrils can be of cauline or foliar origin, and those of *Passifloraceae* are derived from the axillary inflorescences, and hence of cauline origin (Harden *et al.*, 2007). In S.E. Asia, climbers with dispersed leaves and spiralling tendrils at the nodes belong only to three families: (1) Cucurbitaceae with the tendril never truly axillary but always at some angle with the leaf-petiole; stipules absent, (2) *Passifloraceae* with the tendril situated in the leaf axil; stipules small, and (3) Vitaceae with the tendril situated opposite the leaf; stipules large.

Some odd taxa with dispersed leaves outside these three families may have resembling cauline tendrils, but not at every leafy stem-node and mostly only coiling, not spiralling, e.g., *Erythralum* (Olacaceae), *Lophopyxis* (Lophopyxidaceae = Celastraceae), *Gouania* (Rhamnaceae), and possibly some others, to be found in the list of climbers with hooks or tendrils as given by Van Balgooy (1997, p. 15).

Heteroblasty and Heterophylly

1. Heteroblasty. In juvenile forms the leaf blades may be quite different in shape and in presence or position of the leaf glands, as compared to the adult stage. In adult *Adenia cordifolia*, for instance, the basal glands of the cordate, ovate blades are situated in two distinct, separate, hollowed auricles lateral at the top of the petiole, whereas in the juvenile stage these auricles are absent, and the blade of a peculiar lunate or 3-lobed shape with mostly peltate base, with or without one or two very small glands. Similar heteroblasty is found in *A. macrophylla*, and possibly is prevalent in the third species found in Sabah, *A. heterophylla*. The striking difference in leaf shape of the juvenile form, with axillary tendrils with adherent discs at the apices, creeping up while clinging to trunks of big trees, and that of the adult leaves is depicted for *A. cordifolia* in Fig. 1.

A comparison of look-alike juvenile forms of the other *Adenia* species, and species of genera in other families (e.g. *Alsomitra* (Blume) Spach in Cucurbitaceae, *Piper* L. in Piperaceae), all with a similar creeping way to reach height in the forest, would be interesting.

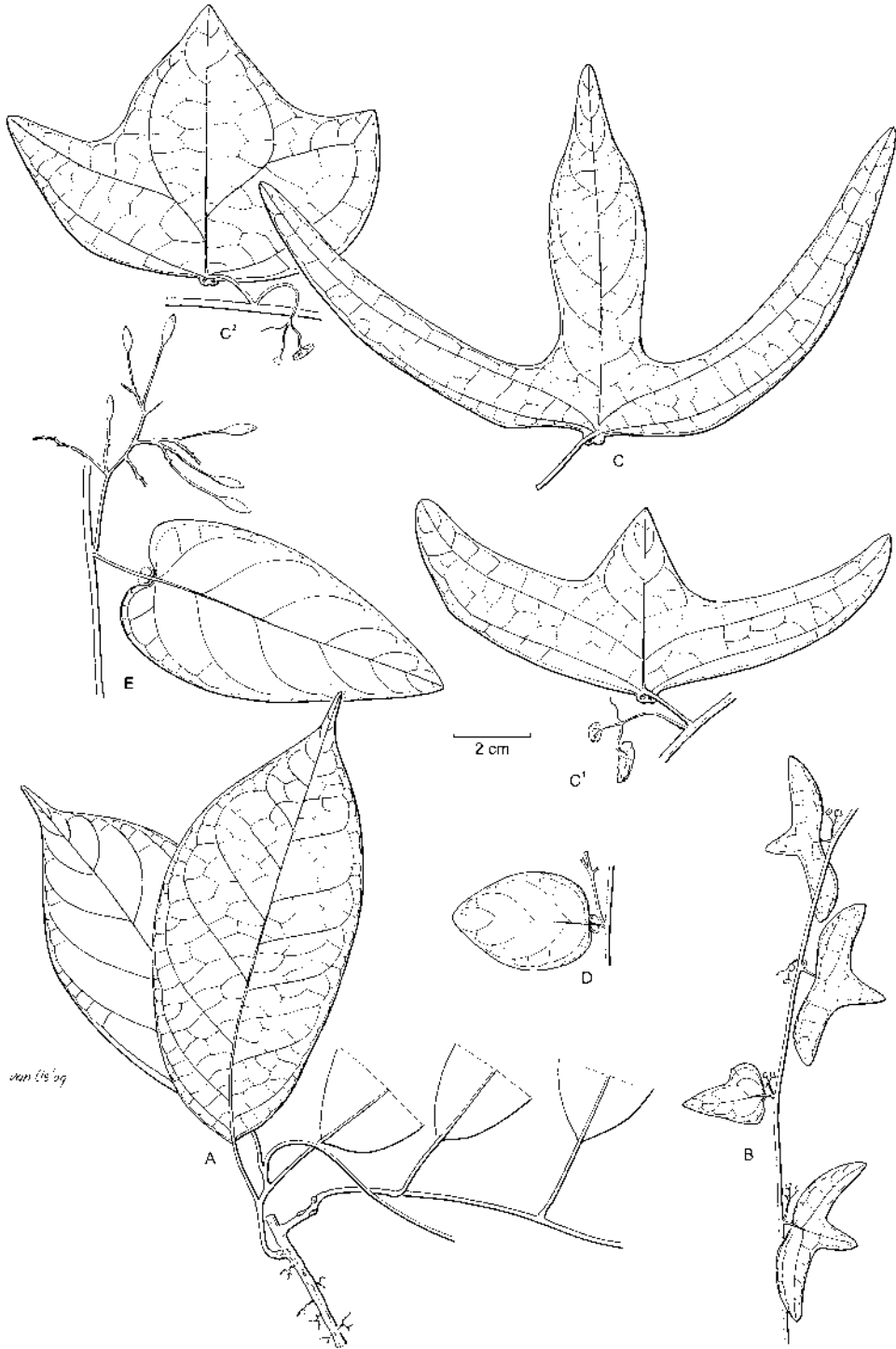


Fig. 1. *Adenia cordifolia* (Blume) Engl. — Heteroblasty. **A.** Perennial herb on the forest bottom. **B.** Upward-creeping shoot on tree trunk. **C–C2.** Various shaped leaves of upward-creeping shoots. **D–E.** Leaves of adult stage. **A:** Chew CWL 1011. **B:** Brooke 8168. **C:** Seah S 36. **C1–C2:** Clemens 30075. **D:** Korthals s.n. **E:** Van Niel 3998.

2. Heterophylly. It is well-known that in many climbing plants the adult leaf blades may be variable in shape, either unlobed or variously (deeply) lobed. In SE Asian *Adenia* this phenomenon is most obvious in *A. heterophylla*, also to be seen in the recent collections from Sabah. In contrast, the adult leaf blades of *A. cordifolia*, *A. macrophylla*, and *A. kinabaluensis* can be more or less variable of shape, but they are never lobed.

KEY TO THE GENERA

Flowers small, hypanthium narrow, elongate, perianth *c.* 0.5 cm diameter or less; unisexual (plants dioecious); anthers basifixed. Fruit opening into 3 valves ***Adenia***
 Flowers large, hypanthium broad, saucer-shaped, perianth 2–3 cm diameter; hermaphroditic; anthers versatile. Fruit ultimately decaying, not opening with valves
 ***Passiflora***

Enumeration of Taxa

Adenia Forssk.

Adenia Forssk., Fl. Aegypt.-Arab. (1775) 77; W.J. de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 50; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 417.

All of the Sabah species belong to sect. *Erythrocarpus* (M. Roem.) W.J. de Wilde. The flowers of *Adenia* (unisexual) are small, and a key to male flowering specimens, using rather technical characters, is provided by De Wilde (1972a). The present key emphasises leaf and fruit characters, presented in view of the new form, forma *microcarpa* in *A. macrophylla* var. *macrophylla*, which separates on fruit size.

KEY TO *ADENIA* SPECIES (fruiting specimens)

1. Leaf blade either unlobed or lobed, suborbicular to lanceolate in outline, 5–25 cm long, base cordate to acute. Gland-bearing auricles shallowly concave, more-or-less adnate to the blade, sometimes \pm peltately connate 2
- Leaf blade always unlobed, ovate to oblong in outline, 2.5–10(–17) cm long, base deeply cordate to subtruncate. Gland-bearing auricles hemi-globular, deeply concave, \pm separate from the blade, not peltately connate 4
2. Fruit (narrowly) ellipsoid; dry pericarp coriaceous. Leaf blade either unlobed or lobed ***2. A. heterophylla*** subsp. ***heterophylla*** (with 2 varieties)
- Fruit subglobose or ovoid-ellipsoid; dry pericarp woody. Leaf blade unlobed 3

3. Leaf blade ovate(-elliptic) in outline, base cordate to broadly rounded, apex 0.5–1.5 cm acuminate; sub 3–5-plinerved; dark brown at both surfaces on drying. Glands at blade base large, extending beyond the auricles onto the blade. Fruits globose; dry valves c. 3 mm thick **3. *A. kinabaluensis***
 Leaf blade suborbicular, (ob)ovate to oblong-lanceolate in outline, base acute-acuminate to rounded, apex obtuse to acute, to 1 cm acuminate; palmately nerved or sub (3–)5-plinerved- to -pinninerved; on drying green to dark brown above, pale brownish or greenish to whitish beneath. Glands at blade base restricted to the auricles. Fruits globose or short ovoid-ellipsoid; dry valves 0.5–3 mm thick
 **4. *A. macrophylla*** (with 2 varieties)
4. Fruit fusiform, ± 3(–6)-angular; dry valves firm-coriaceous, 1–1.5 mm thick
 **1. *A. cordifolia***
 Fruit globose, not angular; dry valves ± woody, (1–)1.5–2.5 mm thick. — Philippines (Sulu Islands, Basilan Island, Mindanao)
 **2. *A. crassa*** (not in Sabah, but may be expected)

1. *Adenia cordifolia* (Blume) Engl., Bot. Jahrb. 14 (1891) 376; W.J.de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 232, f. 34, 36; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 430, f. 4. — Type: *Blume s.n.* (lecto L, barcode L0010330, here designated), Java. (Fig. 1, 5B)

This species is widely distributed in West Malaysia and is common in Sabah.

[***Adenia crassa*** Merr., Philipp. J. Sci, C 10 (1915) 331; W.J. de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 235, f. 34; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 431. — Type: *Reillo* BS 15419, Basilan (iso K).

This species has not been recorded in Borneo, but it is quite common and endemic to adjoining Philippine area: W Mindanao, Basilan Is, and the Sulu Islands. It resembles *A. cordifolia*, but differs in the stouter 3–5-palmately-nerved leaf blades, and thicker fruit valves.]

2. *Adenia heterophylla* (Blume) Koord. subsp. ***heterophylla*** — *Adenia heterophylla* (Blume) Koord., Exkurs. Fl. Java 2 (1912) 637. — *Modecca heterophylla* Blume, Bijdr. 15 (1826) 940. — Type: *Blume s.n.* (holo L, barcode L0010354; iso L, 2 sheets).

KEY TO THE VARIETIES

Leaf blade submembranous or coriaceous, orbicular to lanceolate(-linear) in outline, unlobed to deeply 5-lobed, base cordate to acute, margin entire or dentate; nerves

palmate to pinnate. Gland-bearing auricles well marked off from the blade, glands ± limited to the auricles **a. var. *heterophylla***
Leaf blade strongly coriaceous, (ovate-)oblong in outline, unlobed, base rounded to subacute, margin entire; nerves pinnate. Gland-bearing auricles broadly adnate to the blade, the glands extended on the blade **b. var. *celebica***

a. var. *heterophylla* W.J.de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 216, f. 35; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 426.

Adenia heterophylla, as conceived by De Wilde (1971) is very variable and widespread in SE Asia, with four regional subspecies. The subsp. *heterophylla* occurs in the area from Indochina through West and East Malesia to NE Australia, but was until its latest revision (De Wilde, 1971, 1972a) not known from Borneo. Several collections, only from Sabah, have become known since then. The var. *heterophylla* is extremely variable in blade shape and, also in the Sabah collections, the (adult) leaf blades can be very dissimilar (Fig. 2).

SPECIMENS EXAMINED—Quota Belud: *Shea & Minjulu* SAN 76301 (L, SAN); Tambunan: *Beaman et al.* 7496 (L, SAN); 7808 (Mt Kinabalu, 750 m, ultramafic; L, SAN); Kudat, Pulau Malawali: *Beaman et al.* SAN 145744 (150 m, on ultramafic; L, SAN).

b. var. *celebica* (Koord.) W.J. de Wilde. — *Adenia heterophylla* (Blume) Koord. subsp. *heterophylla* var. *celebica* (Koord.) W.J. de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 220, f. 35; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 427. — *Adenia celebica* Koord., Syst. Verz. (Koord.-Schum.) 3 (1914) 90. — Type: *Koorders 16607*, Sulawesi, Manado (holo BO).

The variety *celebica* is distributed in Sulawesi and Seram and it is known from Sabah by only one rather old collection, *Anon. (J. Brooker?) 43* (E). The status of this taxon in Sabah needs further study.

3. *Adenia kinabaluensis* W.J. de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 225, f. 35; Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 429. — Type: *J. & M.S. Clemens 30074*, Tenompok (holo NY; iso BO, HBG, K, L). (Fig. 5A, C)

This species is endemic to Mt Kinabalu area; all known collections are from Ranau District, at (1000–)1500–1800 m altitude.

SPECIMENS EXAMINED—*Carr* SFN 27204 (L, SING); *J. & M.S. Clemens* 2826, (? 2883), 28104, 29421, 30074 (type), 5127(7) (all: L); *De Wilde & Duyffjes* 21987 (L), SAN

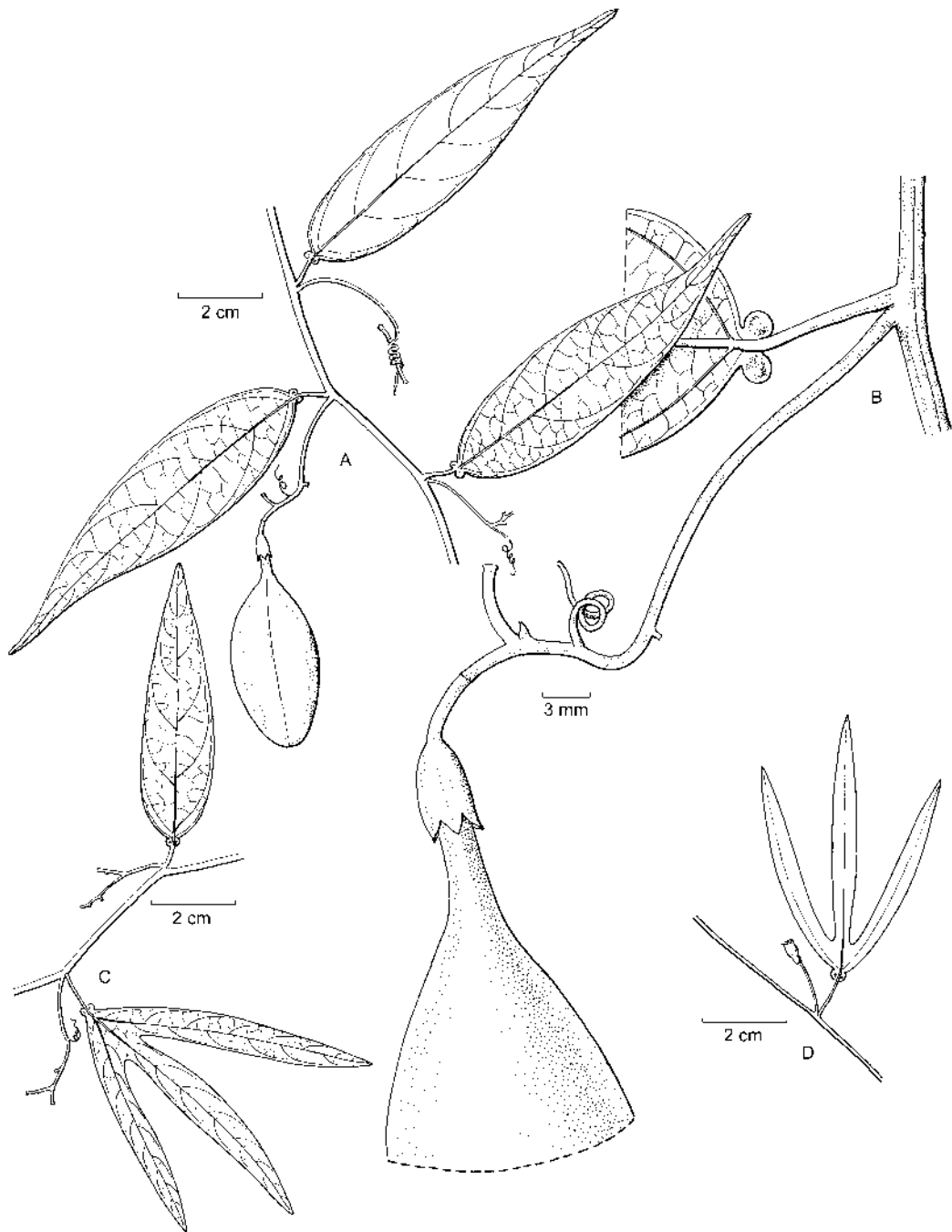


Fig. 2. *Adenia heterophylla* (Blume) Koord. subsp. *heterophylla*. **A–D.** Various parts of adult, fruiting branch with entire and lobed leaves. All from Sugau *et al.* SAN 145744.

139461, SAN 139466 (all: L, SAN); *De Wilde et al.* SAN 144543 (L, SAN); *Wood & Kapis Siseron* SAN 17015 (L, SAN); *Wood & Wyatt Smith* SAN A4496 (L, SAN).

4. *Adenia macrophylla* (Blume) Koord., Exkurs. Fl. Java 2 (1912) 637; W.J.de Wilde, Meded. Landbouwhogeschool Wageningen 71, 18 (1971) 226, f. 34; Fl. Males., Ser. 1, Spermat. 7 (1972a) 427. — *Modecca macrophylla* Blume, Bijdr. 15 (1826) 939. — Type: *Blume s.n.*, Java, G. Salak (lecto L, barcode L0010383, here designated; isolecto L, 3 sheets).

KEY TO THE VARIETIES

Leaf blade suborbicular to lanceolate in outline, palmately- to pinninerved. Fruit (2–)3–6(–6.5) cm long; gynophore *c.* 10 mm long **a. var. *macrophylla***
Leaf blade suborbicular to ovate in outline, 3–5-(sub)-plinerved. Fruit 2–3 cm long; gynophore *c.* 10 mm long
..... **b. var. *smilacina*** (not known from Sabah, but may be expected)

a. var. *macrophylla*

Two forms can be distinguished on fruit size.

KEY TO THE FORMS

Fruit excluding gynophore 3 cm long or more forma ***macrophylla***
Fruit excluding gynophore less than 3 cm long forma ***microcarpa***

forma ***macrophylla***

The forma *macrophylla* is distributed in Sumatra, Peninsular Malaysia, West and Central Java, and all over Borneo.

A seed and a seedling from the same seed sample are shown in Fig. 3. As can be seen, the cotyledons much enlarge with germination, and the first foliage leaves are still destitute of an axillary tendril.

forma ***microcarpa*** (Hallier f.) W.J. de Wilde, *stat. nov.* — *Adenia borneensis* Hallier f. var. *microcarpa* Hallier f., Meded. Rijks-Herb. 42 (1922) 16. — Type: *De Vriese 43*, West Borneo (lecto L, here designated; isolecto BO).

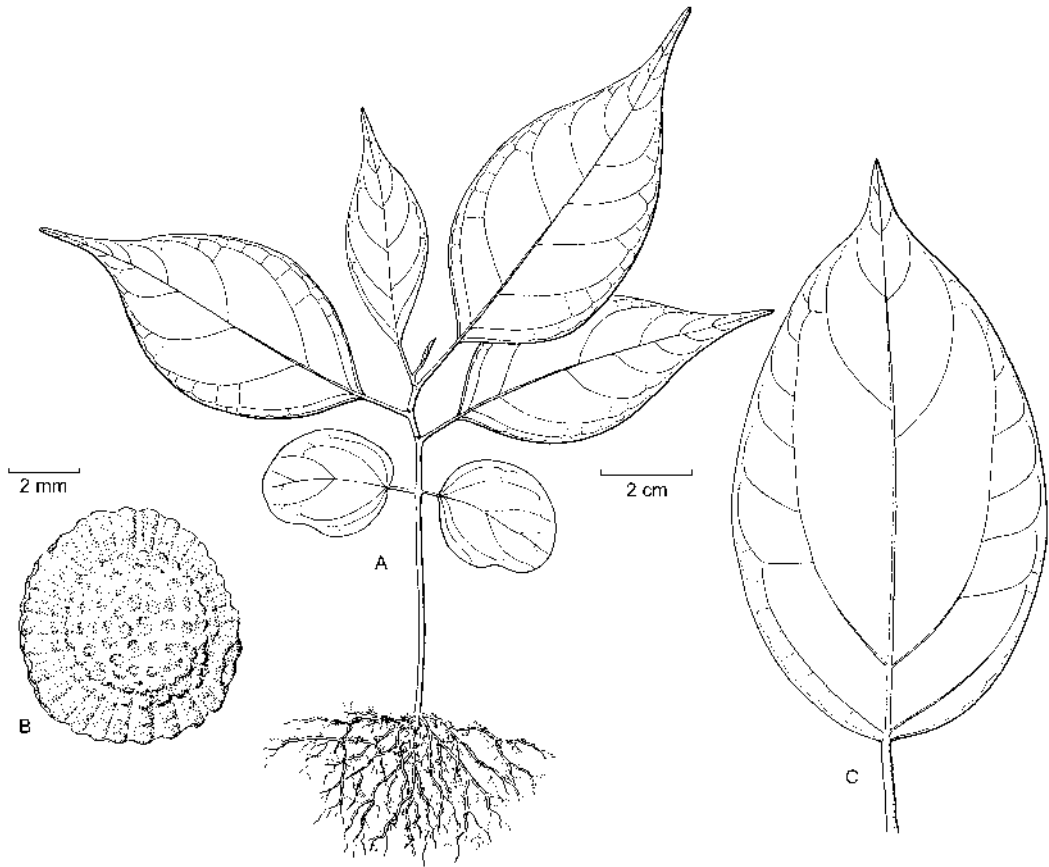


Fig. 3. *Adenia macrophylla* (Blume) Koord. var. *macrophylla*. **A.** Seedling, note opposite cotyledons. **B.** Seed. **A:** *Mogea & De Wilde 4371*. **B:** Cultivated from *Mogea & De Wilde 4371*.

The forma *microcarpa*, with fruits 2–3 cm long, is known from Sabah by one collection: *Sigun SAN 127324*, 25-IX-2009, Beaufort, Bt. Bendira. Furthermore the forma is distributed in West Kalimantan, and Sarawak.

b. var. *smilacina* (Hallier f) W.J.de Wilde. — *Adenia borneensis* Hallier f. var. *smilacina* (Hallier f.) W.J.de Wilde, *Meded. Landbouwhogeschool Wageningen* 71, 18 (1971) 230, f. 34; *Fl. Males. Ser. 1, Spermat.* 7, 2 (1972a) 429, f. 34. — *A. smilacina* Hallier f., *Meded. Rijks-Herb.* 42 (1922) 17. — Type: *Amdjah 379*, NE Borneo (holo L; iso BO, K).

This variety is distributed in Brunei, Sarawak, and in NE Kalimantan (G. Labang), close to the border with Sabah, where it is known from low altitudes. Its leaves resemble those of *A. kinabaluensis*, a montane species.

***Passiflora* L.**

Passiflora L., Sp. Pl. 2 (1753) 955; W.J. de Wilde, Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 407; Blumea 20 (1972b) 229.

KEY TO THE WILD AND NATURALISED SPECIES

1. Bracts and bracteoles inconspicuous, involucre wanting 2
Bracts and bracteoles conspicuous, forming an involucre 3
2. Flowers 1–1.5 cm diam., apetalous. Fruits ripening purple-black, globose, 1–1.3 cm diam **4. *P. suberosa***
Flowers larger, 2–3(–3.5) cm diam., with petals. Fruits ripening (bluish-)green, globose to ellipsoid, 1.5–2 cm diam **3. *P. perakensis***
3. Involucral bracts deeply dissected **2. *P. foetida***
Involucral bracts entire **1. *P. edulis***

1. *Passiflora edulis* Sims, Bot. Mag. 45 (1818) t. 1989; W.J. de Wilde, Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 410. — Type (Killip 1938): “from a plant cultivated in Europe, probably originally from Brasil”.

Passiflora edulis, Passion Fruit, Purple Granadilla, is cultivated for its edible juicy fruits. It easily escapes and may locally establish in the surrounding indigenous vegetation.

2. *Passiflora foetida* L., Sp. Pl. 2 (1753) 959; W.J. de Wilde, Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 410. — Type: *Herb. Linn. No. 1070.24*, “Habitat in Dominica, Martinicana, Curassao” (lecto LINN, designated by Killip (1938) 481, fide C.E. Jarvis, *Order Out of Chaos* (2007) 726). (Fig. 5D)

Many not always clearly defined varieties have been described for this originally American but now widely distributed weedy species. For the Malesian material one should accept the varietal name, *P. foetida* L. var. *hispida* (Triana & Planch.) Killip.

3. *Passiflora perakensis* Hallier f., Meded. Rijks-Herb. 42 (1922) 5; W.J. de Wilde, Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 414; Blumea (1972b) 242. — Type: *Scortechini 2192*, Perak (holo L). (Fig. 4.)

This species is distributed in southern Thailand, Sumatra, Peninsular Malaysia and Sabah.



Fig. 5. A, C. *Adenia kinabaluensis* W.J.de Wilde. B. *Adenia cordifolia* (Blume) Engl. D. *Passiflora foetida* L.

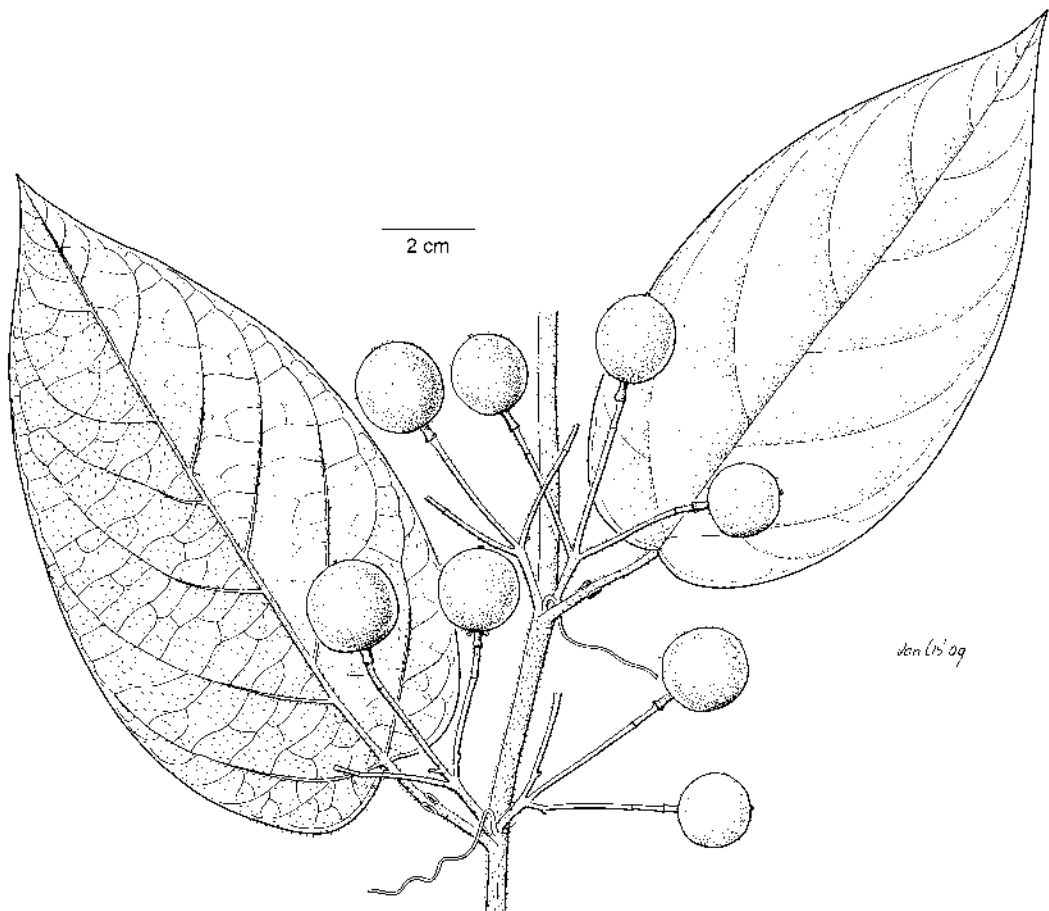


Fig. 4. *Passiflora perakensis* Hallier f., detail of fruiting branch (Sugau JBS 63).

At the time of the latest revision (De Wilde 1972b) it was known from Sabah by one collection only, but at present quite a number of additional specimens from Sabah are known. Some of the Sabah specimens are broad-leaved and more densely hairy as compared to the specimens from Sumatra and Peninsular Malaysia.

Passiflora perakensis resembles *P. siamica* Craib, a species from India (Assam), China (Yunnan), Myanmar, Laos, Vietnam, central and northern Thailand. The latter differs, e.g., in having narrower leaves and (5–)6–8 stamens, while *P. perakensis* has broader leaves and 5 stamens.

SPECIMENS EXAMINED (all in fruit) — **Sipitang:** *Madani & Lassan* SAN 134023 (L, SAN); **Tambunan:** *Beaman et al.* 7184 (hairy form; L, SAN); *De Wilde & Duyffjes* 21957

(L); *Gambating* SAN 60825 (broad-leaved, densely hairy; L, SAN); *George et al.* SAN 122690 (L, SAN); *Joseph & Tuyuk* SAN 130189 (L, SAN); *Joseph, Lideh, et al.* SAN 110054 (L, SAN); *Krispinus* SAN 121714 (differing in strongly hairy leaves; L, SAN); *Sugau* JBS 63 (L, SAN); Keningau: *Aban & Nicholas* SAN 65383 (L, SAN).

4. *Passiflora suberosa* L., Sp. Pl. 2 (1753) 958; W.J. de Wilde Fl. Males. Ser. 1, Spermat. 7, 2 (1972a) 411. — Type: *Herb. Linn. No.* 1070.21, “Habitat in Dominica, Antillis” (lecto LINN, Wijnands in *Bot. Commelins* (1983) 171, fide C.E. Jarvis, *Order Out of Chaos* (2007) 727).

Originally from South America, at present a widespread weedy species, but not yet recorded for Borneo, where it can be expected, including Sabah.

OTHER INTRODUCED SPECIES. A limited number of species introduced from America are occasionally cultivated in gardens, either as ornamental plants or for the fruits. The most frequently found are *Passiflora quadrangularis* L. ((Giant) Granadilla, Marquisa) with large edible fruit, and *P. laurifolia* L. (Yellow Granadilla). See further De Wilde (1972a).

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**A synopsis of *Rothmannia* (Rubiaceae) in the Philippines,
with four new combinations and a new species**

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Summary. Four new combinations are made for Philippine *Rothmannia*: *R. graciliflora* (Merr.) J.T. Pereira & Ridsdale, *R. lagunensis* (Merr.) J.T. Pereira & Ridsdale, *R. merrillii* (Elmer) J.T. Pereira & Ridsdale, and *R. negrosensis* (Merr.) J.T. Pereira & Ridsdale. A new species, *R. leytensis* J.T. Pereira & Ridsdale is also described.

Rothmannia Thunb. was named after Dr Georgius Rothman (1739–1778), a Swedish physician and botanist in 1776. It is typified by *Rothmannia capensis* from Cape, South Africa. In 1781, this species was transferred to the genus *Gardenia*, under the name *G. rothmannia* L.f., by Linnaeus in the *Supplementum Plantarum Systematis Vegetabilium*. Many other conceptual changes have since occurred, notably with a number of other *Gardenieae* entities variously mixed up with *Gardenia* s.l. or *Randia* s.l., including taxa best placed within or close to the *Rothmannia* group.

The taxonomic history of this alliance of genera, and that of *Rothmannia* in particular, is complex (Pereira, Lim & Wong, in prep.). Whether or not *Rothmannia* s.l. is best considered an heterogeneous pantropical assemblage as in the case of *Randia* s.l., or if it is a large complex genus with incipient specialisation in different directions, requires more insight (see also concepts considered by Fagerlind 1943, Bremekamp 1957, Keay 1958; Wong 1984, 1989; Bridson & Verdcourt 1988), particularly from molecular phylogenetic work (Pereira 2008). Nevertheless nearly all members of the *Rothmannia* group, particularly in Asia, are easy to recognise by a characteristic vegetative character: the sympodially

developing branch unit of two nodes occurring very close together, in which one member of a leaf pair is vestigial and the other leaf pair normally developed, so that trifoliate leaf clusters result. This feature, together with terminal flowers either solitary or in small cymes that are later displaced to one side during sympodial branch development, and berry-like, indehiscent fruits of medium to large size (2–5 cm or more across) that are 2-loculate with axile placentation and many seeds immersed in a pulp-like tissue, sets the group apart from other genera formerly confused with either *Gardenia* or *Randia* s.l.

Rothmannia strictly applies to a coherent group comprising the African type species and a number of other species in Africa that also have right-contorted corolla lobes. However, morphological and palynological studies have found difficulty in placing the other African members with left-contorted corolla lobes truly apart from Asian members of the *Rothmannia* group (Pereira, 2008). In brief, although the taxonomic limits of *Rothmannia* are still being investigated, it is still the most practical grouping for an entire suite of Asian taxa.

***Rothmannia* s.l. in the Philippines**

Unlike elsewhere in Asia (e.g., Bremekamp 1957, Wong 1984, Coode et al. 1996, Shui et al. 2003), the recognition of *Rothmannia* has not yet been adopted for a number of relevant Philippine taxa. In fact, the baseline account for a great many Philippine plant groups is the *Enumeration of Philippine Flowering Plants* by Merrill (1923), and likewise, a number of names placed under *Gardenia* do not apply to that genus as recently revised by Wong & Low (2011).

Here we transfer four names under *Gardenia* or *Randia* to *Rothmannia*, where they are more correctly placed. In addition, a new species is also described.

KEY TO PHILIPPINE *ROTHMANNIA*

1. Calyx glabrous to scantily puberulous, the hairs if present, very minute and scattered (detectable only with ×10 magnification) on the surface 2
 Calyx conspicuously (sparsely to densely pubescent) hairy on the surface, hairs *c.* 0.5 mm long, visible to the unaided eye 3

2. Leaf apex acuminate, acumen to 1 cm long; tertiary venation a much-branched network between secondary veins. Corolla throat glabrous inside; lobes 5, slender, 1–1.5 × 0.25–0.3 cm; tube pubescent at the upper half of the outer surface. Style and stigma included but reaching just below the corolla mouth and the level of or above the anthers **2. *R. lagunensis***

- Leaf apex acute to obtuse, acumen to 0.3 cm long only; tertiary venation visible as simple connections between secondary veins to almost invisible. Corolla throat hairy inside; lobe typically 6–8, rarely 5, larger 2–4.5 × 0.5–1.5 cm; tube glabrous on the outer surface. Style and stigma included but reaching less than 2/3 way along the corolla tube and well below the level of the anthers **3. *R. merrillii***
3. Inflorescences laxly arranged, with 2–3 distinct branching orders. Corolla tube short, below 2.5 cm long **1. *R. graciliflora***
 Inflorescences compact, with 1–2 distinct branching orders. Corolla tube longer, 6–9 cm long 4
4. Leaves tertiary venation visible as simple connections between secondary veins. Flowers 2–3 per cyme. Corolla lobes typically 6–8, rarely 5, large, 2.7–4.5 × (1.5–)1.8–2.5 cm; throat with hairy zone covering part or all the tube from the corolla mouth downwards **4. *R. negrosensis***
 Leaves tertiary venation a much-branched network between secondary veins. Flowers 4–9 per cyme. Corolla lobes 5, smaller, 1.2–2.5 × 0.4–0.9 cm; throat glabrous **5. *R. leytenis***

Four new combinations in *Rothmannia*

1. *Rothmannia graciliflora* (Merr.) J.T. Pereira & Ridsdale, comb. nov.

Randia graciliflora Merr., Philipp. J. Sci., C 10 (1915) 109; Merr., Enum. Philip. Fl. Pl. 3 (1923) 527. LECTOTYPE (here designated): *Miranda* F.B. 17988, Philippines, Mindanao, Misamis, Mt Malindang (January–February 1913 FLO) (US!) (isolectotypes L! P! SING! NY!).

Gardenia negrosensis sensu Merr., Philip. Fl. Pl. 3 (1923) 527 pro parte quoad *Ramos & Edaño* B.S. 36787; non Merr. (1915).

Tree, to 18 m high. Twigs pubescent when young, becoming glabrescent when old. Branch leaves typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves. Stipules triangular, 3 × 5 mm long, 4 × 7 mm wide, sparsely pubescent outside; apex acuminate, 0.5–1 mm long. Young leaves on shoot tips pubescent on both sides. Mature leaves with petiole 0.1 × 0.4 cm long, 1 × 1.5 mm thick, pubescent; lamina elliptic, obovate to oblanceolate, 12 × 16(–24) cm long, 3.5 × 7(–9) cm wide, upper surface sparsely pubescent when young, becoming glabrescent when mature, lower surface sparsely pubescent; leaf base cuneate, symmetric to unequal; leaf apex acuminate, acumen 0.4 × 1 cm long; chartaceous when dry; midrib on upper side flat,

glabrous to sparsely pubescent, on lower side raised, pubescent; secondary veins 7 × 10(–13) pairs, on upper side flat, glabrous to glabrescent, on lower side raised, pubescent; tertiary venation visible as a much-branched network between pairs of secondary veins. **Inflorescences:** peduncle 0.3 × 1 cm long, 1 × 2 mm thick, pubescent; habit laxly arranged, with 2 × 3 distinct branching orders, rachis 1.2 × 2.5 cm long, primary branches along the rachis 2–3 pairs, 0.5 × 1 cm long; bracts ovate, 1.5 × 2.5 mm long, 1.5 × 2 mm wide, pubescent. Flowers 11 × 25 per cyme; pedicels subobsolete to 1 mm long, *c.* 1 mm thick; calyx tube 3.5 × 4 mm long, 2 × 3 mm wide, sparsely pubescent at the limb but densely pubescent at the hypanthium, hairs suberect, surface visible; calyx limb cup-shaped; calyx lobes 5, narrowly triangular, 0.5 × 2 mm long, sparsely pubescent; corolla hypocrateriform, the tube 1.8 × 2.4 cm long, bulging at the upper half, 2 × 2.5 mm wide at the throat, 1 × 1.5 mm wide at the base; non-speckled inside, outer surface pubescent, inner surface glabrous; corolla lobes 5, narrowly elliptic, 0.6 × 0.9 cm long, 0.15 × 0.2 cm wide, outside sparsely pubescent on the uncovered half of the lobes, inside glabrous; anthers 5 × 6, fully included within the tube (inserted at the upper $\frac{1}{3}$), 6 × 7 mm long; style and stigma 6 × 10 mm long, included but reaching less than $\frac{2}{3}$ along the corolla tube, and well below the anthers, style smooth, glabrous. **Immature fruits** globose, 2 × 2.8 cm long, 2 × 2.5 cm wide, glabrescent to glabrous, drying smooth; fruit wall *c.* 1 mm thick; peduncle 0.5 × 1.5 cm long, 0.2 × 0.3 mm thick. Seeds not seen.

NOTES. In the original publication of Merrill in the *Philipp. J. Sci.*, C 10 (1915) 109, there is only one specimen cited which is the type specimen for the species. However, the holotype specimen which was in PNH (as Merrill had worked there), was destroyed, hence, one of the isotypes is designated the lectotype (Article 9, paragraph 9.2 of the International Code of Botanical Nomenclature, Vienna Code 2006).

DISTRIBUTION. Thus far only known from 5 collections, recorded from the southern part of the Philippines (Mindanao and Basilan).

SPECIMENS EXAMINED—PHILIPPINES. MINDANAO: Zamboanga, *Villamil* 21884 A (May–June 1914 FRU) (K!), *Babaran* 26139 (July 1916 FRU) (K! P!); Malangas, *Ramos & Edano* 36787 (October–November 1919 FRU) (L!), Misamis, Mt. Malindang, *Miranda* 17988 (January–February 1913 FLO) (lectotype US!) (isolectotypes L! P! SING!). Basilan, *Tecson & Rouve* 25804 (May 1916 FRU) (K!).

2. *Rothmannia lagunensis* (Merr.) J.T. Pereira & Ridsdale, **comb. nov.**

Gardenia lagunensis Merr., *Philipp. J. Sci.*, C 10 (1915) 110; *Enum. Philip. Fl. Pl.* 3 (1923) 530. NEOTYPE (here designated): *Ramos* Bur. Sci. 14934, Philippines, Luzon, San Antonio Province, Laguna (June 1912) (L!).

Tree, to *c.* 25 m high, to 35 cm diameter. Bark smooth, grey-black; inner bark light brown. Twigs pubescent when young, becoming glabrescent to glabrous when old. Branch leaves typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves. Stipules ovate, 2 × 3 mm long, 3 × 5 mm wide, glabrous outside; apex acute, to 1 mm long. Young **leaves** on shoot tips pubescent on both sides. Mature leaves with petiole 0.5 × 1.1 cm long, 1 × 1.5 mm thick, glabrous to scantily puberulous; lamina oblanceolate, lanceolate to elliptic, 6 × 12(–13.5) cm long, 2 × 6 cm wide, upper surface glabrous, lower surface scantily pubescent becoming glabrous; leaf base cuneate, attenuate, equal to unequal; leaf apex acuminate, acumen to 1 cm long; thin-coriaceous when dry; midrib on upper side flat, scantily puberulous to pubescent, on lower side raised, glabrous; secondary veins 5 × 6(–7) pairs, on upper side flat, glabrous, on lower side slightly raised, scantily puberulous to pubescent; tertiary venation visible as a much-branched network between pairs of secondary veins. **Inflorescences** (bud): peduncle subsessile to 0.5 cm long, 1 × 1.5 mm thick, glabrous; habit compact, unbranched or with 1(–2) distinct branching orders, rachis 0.2 × 0.5 cm long, primary branches along the rachis 1 pair, 0.2 × 0.5 cm long; bracts ovate, 1.5 × 2 mm long, 1.5 × 2 mm wide, glabrous, hairy along the margin. Flowers in buds 1 × 3(–5) per cyme; pedicels subobsolete to 1 mm long, 1 × 1.5 mm thick; calyx tube 4 × 6 mm long, 3.5 × 4.5 mm wide, scantily puberulous to pubescent, hairs appressed, surface visible; calyx limb cup-shaped; calyx lobes 5, triangular, 1 × 1.5 mm long, scantily puberulous; corolla hypocrateriform, the tube 7 × 8 cm long, *c.* 3 mm wide at the throat, *c.* 1.5 mm wide at the base; non-speckled inside, outer surface scantily puberulous at the upper half, inner surface glabrous; corolla lobes 5, oblong, 1 × 1.5 cm long, 0.25 × 0.3 cm wide, glabrous or with minute hairs sparsely distributed at the margin or fringes of the lobes outside, glabrous inside; anthers 5, fully included within the tube or only with tips slightly protruding (inserted at the upper 1/3), 12 × 14 mm long; style and stigma 75 × 85 mm long, included but reaching just below the corolla mouth and the level of or above of the anthers, style smooth, glabrous. **Fruits** globose to ellipsoid, 2.5 × 3.5(–5) cm long, 2.5 × 4 cm wide, glabrous, drying typically smooth; fruit wall *c.* 1 mm thick; peduncle 0.4 × 0.5 cm long, 2 × 3 mm thick. Seeds slightly to much flattened and broadly ovate or suborbicular to narrowly triangular, 8 × 10 mm × 6–7 mm.

NOTES. Merrill (in the *Philipp. J. Sci.*, C 10 (1915) 110) had designated the collection C.F. Baker 3176 as the type specimen of the basionym, *Gardenia lagunensis*. However, the holotype of this collection which was deposited in PNH had been destroyed during the Second World War. Attempts were made to locate isotypes from the herbaria at POM and NY, where C.F. Baker's collections were normally deposited (Stafleu & Cowan, 1976), but were futile. The search continued to other herbaria in the United States, e.g., UC and A, but was again futile. Based on Article 9, paragraph 9.6 of the International Code of Botanical Nomenclature, Vienna Code (2006), a neotype was designated.

DISTRIBUTION. Known only from Luzon island of the Philippines.

HABITAT. Recorded in Mixed Dipterocarp forest, to 300 m.

SPECIMENS EXAMINED—PHILIPPINES. LUZON: Linutan, *Loher* 1481 A (sine datum FLO) (K!), Montalban, *Loher* 1482 A (sine datum FLO) (K!); Camarines Sur, *Alambra* F.B. 28093 (July 1920 FLO) (K!); Quezon National Park, 25 km E of Lucena, 200–300 m, *Soejarto* et al. 7828 (12 July 1992 FRU) (L!); Tayabas, *Bawan* F.B. 24936 (December 1915 FRU) (P!); Laguna, *Conicosa F.B. 29461* (August 1923 FRU) (A!), *Ramos* 1401 (February 1913 FRU) (L! SING!); Rizal, *Ramos* 2635 (May 1907 FRU) (BO! L!); Mt Susong-Dalaga, *Ramos & Edano* Bur. Sci. 29392 (August, 1917 FRU) (K!); San Antonio, *Ramos* Bur. Sci. 14934 (June 1912 FRU) (neotype L!), *Ramos* Bur. Sci. 23845 (October 1915 FRU) (A!); Angat, *Ramos* Bur. Sci. 22297 (December 1914 FLO) (A! L! PNH! SING!).

3. *Rothmannia merrillii* (Elmer) J.T. Pereira & Ridsdale, **comb. nov.**

Gardenia merrillii Elmer, Leafl. Philipp. Bot. 1 (1906) 5; Leafl. Philipp. Bot. 4 (1912) 1330; Gibbs, Journ. Linn. Soc. Bot. 42 (1914) 94; Merr., Enum. Philip. Fl. Pl. 3 (1923) 530; Merr., Philipp. J. Sci. 29 (1926) 421, pro parte excl. Celebes specimens; Merr., Bibl. En. Born. Pl., J. Straits Branch Roy. Asiat. Soc., Sp. No. (1921) 564 pro parte quoad *Gibbs* 4340, *Foxworthy* 600; Masamune, En. Phan. Born. (1942) 682. LECTOTYPE (here designated): *Merrill* 669, Philippines, Island of Calomian, Culion (February 1903 FLO) (lectotype US!) (isolectotypes A! SING! NY!).

Randia keithii C.E.C. Fisch., Bull. Misc. Inform. Kew (1932) 180; Masamune, En. Phan. Born. (1942) 708. *Rothmannia keithii* (C.E. Fischer) Bremek., Proc. K. Ned. Akad. van Wet.-P 60 (1957) 6. TYPE: *Keith* 1215, North Borneo, Sandakan, 500 ft [152 m] (20 February 1929 FLO) (holotype K!).

Treelet to small tree, to 6(–12) m high, to 10 cm diameter. Bark smooth to finely fissured, grey-black to dark brown; inner bark brownish to greenish yellow. Sapwood whitish to white-orange. Twigs glabrous. Branch leaves typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves. Stipules shortly ovate-triangular, 1 × 3 mm long, 3–5(–6) mm wide, glabrous to sometimes scantily pubescent outside; apex cuspidate, 0.5 × 1 mm long. Young **leaves** on shoot tips scantily pubescent, especially on the lower surface. Mature leaves with petiole (0.1–)0.3 × 1.3 cm long, 1 × 1.5 mm thick, glabrous to scantily puberulous; lamina narrowly to broadly elliptic, elliptic-oblong, oblanceolate to obovate, 5 × 20 cm long, (1.5–)4–8(–10) cm wide, upper surface glabrous, lower surface typically glabrous, sometimes sparsely puberulous; leaf base attenuate, cuneate to sometimes unequal; leaf apex acute to obtuse, acumen to 0.3 cm

long; thin to thick-coriaceous when dry; midrib on upper side flat, glabrous, on lower side raised, glabrous to occasionally scantily puberulous; secondary veins $5 \times 8(-9)$ pairs, on upper side flat, glabrous, on lower side raised, glabrous to occasionally puberulous; tertiary venation visible as simple connections between pairs of secondary veins to almost invisible.

Inflorescences: peduncle 0.15×0.5 cm long, 2×3 mm thick, glabrous to sparsely puberulous; habit compact, unbranched to with 1(-2) distinct branching orders, rachis $0.1-0.5$ cm long, primary branches along the rachis 1(-2) pairs, $0.1-0.5$ cm long; bracts ovate, 1×2.5 mm long, 1×2 mm wide, glabrous to sparsely puberulous. Flowers $1 \times 5(-9)$ per cyme; pedicels subobsolete to 1 mm long, *c.* 1 mm thick; calyx tube $4 \times 6(-10)$ mm long, 3×6 mm wide, glabrous to scantily puberulous, hairs appressed, surface visible; calyx cup-shaped; calyx lobes $(5-6) \times 8(-10)$, short-triangular, 0.5×2.5 mm long, glabrous to sparsely puberulous; corolla hypocrateriform, white, the tube $3.5 \times 7.5(-12)$ cm long, 5×9 mm wide at the throat, 2×3 mm wide at the base; non-speckled inside, outer surface glabrous, inner surface with hairy zone covering part or all of the tube from the corolla mouth downwards; corolla lobes $(5-6) \times 8$, lanceolate, oblong-elliptic to obovate, 2×4.5 cm long, $0.5 \times 1(-1.5)$ cm wide, outside glabrous or with minute hairs sparsely distributed at the margin or fringes of the lobes, inside glabrous; anthers 6×10 , fully included within the tube (inserted at the upper $1/3$), 6×10 mm long; style and stigma 10×34 mm long, included but reaching less than $2/3$ way along the corolla tube and well below the level of the anthers, style smooth, glabrous. **Fruits** globose, $2.5 \times 4.5(-5)$ cm long, $2.5 \times 4.5(-5)$ cm wide, glabrous, drying smooth to wrinkled; fruit wall 1×2 mm thick; peduncle sessile to 0.3 cm long, 2×4 mm thick. Seeds slightly to much flattened and broadly ovate or suborbicular to narrowly triangular, $10-11$ mm \times $8-10$ mm.

NOTES. In 1906, Elmer published the basionym, *Gardenia merrillii* in *Leaflet Philipp. Bot.* 1, pg. 5 and cited two specimens, *Merrill* 669 from Culion, collected in February 1903 and *Garcia* FB 1226 from Mindoro, collected in January 1903. As there was no clear type designated, one of the two syntypes is designated lectotype. Because most of Merrill's material that was mainly deposited at the Philippine National Herbarium (PNH) was probably destroyed during the Second World War (Van Steenis-Kruseman, 1950), one of the duplicates of *Merrill* 669 is chosen for the lectotype specimen (Article 9, paragraph 9.2 of the International Code of Botanical Nomenclature, Vienna Code 2006).

This species is very variable in terms of leaf size; corolla tube length; hairiness on the nerves (glabrous to pubescent), peduncle (glabrous to pubescent), bracteoles (glabrous to pubescent), domatia (glabrous to pubescent) and number of flowers per cyme. The Sabah specimens tend to have fewer flowers, usually 1, rarely 3 per cyme. However, the Philippine specimens vary from solitary flowered to 3-5-flowered. The flowers are commonly arranged as 3-5 flowers per cyme, to a maximum of 9 flowers. Furthermore, the corolla tube length typically varies from 3.5 cm to 7.5 cm long, however, in one specimen collected by Ridsdale, from Palanan, N.E. Luzon (ISU 93): the corolla tube is extremely long 10-12 cm long.

VERNACULAR NAMES. Sabah: *kelimpong* (Kudat); *sarakat* (Dusun-Rungus); *cempaka putih* (Malay). Philippines: *rosal-gobat* (Mindoro); *Bagaai*, *niogniog* (Bisaya).

DISTRIBUTION. Endemic to the Philippines and Borneo (Sabah).

HABITAT. Primary to secondary forests, including *kerangas* forest, sandstone hills, coastal forest and on ultrabasic substrate, and calcareous outcrops, to 850 m alt.

SPECIMENS EXAMINED—PHILIPPINES. No locality. *Marche* B 119 (10 January 1885 FLO) (P!); *Vidal* 1447 (sine datum FRU) (L!). **LUZON:** Tayabas Lucena, *Merrill* 2888 (June 1903 FLO) (BM! K!); Isabela Prov., Palanan, Diguyo, 50 m, *Ridsdale*, *Dejan & Baquiran* ISU 93 (22 April 1991 FLO) (L! SAN!). **CAGAYAN PROV.:** *Bernardo* F.B. 27085 (October 1917 FRU) (A! K!). **MINDORO:** No locality. *Merritt* F.B. 8568 (January 1908 FRU) (SING!); Pinamalayan, *Ramos* Bur. Sci. 40890 (June 1922 FRU) (L!); Bongabon & Pinamalayan, *Maliwanag* 221 (5 February–5 April 1941 FLO) (PNH!); Baco, *Merrill* 1195 (January 1903 FLO) (K!), *Merrill* 1226 (January 1903 FLO) (A! K! SING! NY!), Baco river, *Mcgregor* 137 (April to May 1905 FLO) (K!); Paluan, *Ramos* Bur. Sci. 39474 (April 1921 FRU) (SING!); Mansalay, *Paniza* PNH 9426 (18 April 1948 FRU) (A!), Mansalay, Bo, Manual, *Sulit* PNH 17140 (30 December 1952 FLO) (L!); N slope of Mt Alinyaban, 5 km SW of Puerto Galera, *Burley* 128 (24 April 1987 FLO) (K!), Puerto Galera Bay, *Santos* 5165 (16 April 1952 FLO) (L!), Mt Yagaw, 350 m, *Sulit & Conklin* PNH 16774 (28 November 1952 FRU) (L! PNH!). Golo Island, *Merrill* PNH 11540 (August 1922 FLO/FRU) (A! L! SING!). **PALAWAN:** No locality. *Agama* PNH 21618 (May 1914 FRU) (P!); *Curran* 3517 (January 1906 ST) (L!); *Escritor* Bur. Sci. 21571 (August 1913 ST) (P!); Aborlan, Sagpangan, along river, *Celestino & J. Ramos* PNH 23090 (16 May 1955 FLO) (L! PNH!); about 4 km off Aborlan-Inagawan main road, 50–100 m, *Soejarto* et al. 6608 (15 April 1989 FLO) (L!); Iraan Mountains, *Sulit* PNH 12549 (May–June 1950 FLO) (L!), Km 112, Pinagbatuan, *Mendoza & Espiritu* PNH 91187 (27 August 1964 FLO) (PNH!, SAN!); St. Paul's Bay, Cabayungan Village, 40 m, *Podzorski* SMHI 2081 (10 May 1984 FLO) (KEP! PNH! SAN!); Puerto Princesa, c. 36 km north of the city, 40 m, *sine coll.* SMHI 1063 (11 May 1984 FRU) (L!); Mt Pulgar, *Elmer* 13126 (April 1911 FRU) (L!); Irawan River valley head, 150 m *Ridsdale* SMHI 84 (15 March 1984 FLO) (L!), *Ridsdale* SMHI 98, (16 March 1984 FLO) (KEP! PNH! SAN!); Mt Beaufort, 150–170 m, *Ridsdale* SMHI 1689 (15 May 1984 FRU) (L!); N of Tagburos, c. km 17, N of Puerto Princessa, low forest on ultrabasic, *Ridsdale* 1096 (27 October 1985 FRU) (L!); *Vidal* 1447 (sine datum FRU) (L!), Babuyan, *Edano* 266 (16 March 1947 ST) (SING!), Km 36, Puerto Princessa to Roxas, 10 m, *Dransfield* SMHI 1237 (12 May 1984 FLO/FRU) (KEP! K! L! SAN!); Narra, Victoria Peaks, Trident Mining Company concession area, partially damaged steep-slope forest on ultrabasic soils, 300–450 m, *Ridsdale* SMHI 1809 (22 May 1984 FLO) (L!), 520 m, *Podzorski* SMHI 2091 (18 May 1984 FRU) (L!), 490–590 m, *Ridsdale* SMHI 1704 (17 May 1984 FRU) (L!); Mt Victoria, 850 m, *sine coll.* SMHI 1704A (17 May 1984 FRU) (L!); Bato-Bato, 10 km south of Narra, on side road from the main trunk Narra-Aboabo, 100 m,

Soejarto & Fernando 7384 (26 January 1991 FRU) (L!); Taytay: Lake Manguao, valley stream, *Ridsdale* SMHI 378 (9 April 1984 FLO/FRU) (L!); Ibangley, *Sagcal, Romero et al.* PPI 364 (31 January 1991 FLO) (L!); Bataraza, Sumbiling, Sitio Gamayon, Bulanjao Range, 50 m, *Soejarto & Madulid* 9052 (22 March 1995 FLO) (L!); Quezon Sitio Bongalon, *Cordero & Espiritu* PNH 91599 (13 May 1964 FRU) (L!); Busuanga Island, *Lopez* Bur. Sci. 41371 (September 1922 FRU) (L!), *Ramos* Bur. Sci. 41254 (September 1922 FLO) (L!); Culion Island, *Merrill* 612 (December 1902 FRU) (SING!), *Merrill* 669 (February 1903 FLO) (lectotype US!; isolectotypes A! NY! SING!); Bayas Island: *Copeland* 112 (January 1904 FRU) (P!). Sibuyan Island, Romblon, Magdiwang, Silum, Sitio Kulasian, *Reynoso, Fuentes & Rivers* PPI 14116 (20 February 1994 FRU) (L!). **PANAY:** *McGregor* Bur. Sci. 32195 (May–August 1918 FRU) (A!), *McGregor* Bur. Sci. 32392 (May–August 1918 ST) (SING!), *McGregor* Bur. Sci. 32584 (May–August 1918 FLO) (BO! SING!); Semirara Island, *Alcasid* PNH 6421 (March 1940 FLO) (A!); Buenavista, *Taleon* PNH 33906 (7 April 1955 FLO) (SAN! PNH!); Southwestern range of Mt Baloy, Laggit, c. 3 km SE of Lublub, 250–300 m, *Varadarajan, Reyoso, Fernando & Mosing* 1552 (8 August 1987 FRU) (K! L!). **NEGROS:** Canlaon National Park, Mt Canlaon, Wasay trail, *Stone et al.* PPI 6307 (23 March 1992 FLO) (L!); Mt Katugasan, *Edano* PNH 21784 (March 1954 FLO) (K! PNH! SING!). Guimaras Island, Buenavista, *Sulit* PNH 11787 (3 March 1950 FLO/FRU) (L! PNH! SING!). Paragua Island: 1500 ft, San Antonio Bay, dry slopes, *Merrill* 839 (February 1903 FLO) (K!). **BORNEO. SABAH.** No locality: *Governor Creagh* s.n. (August 1895 FLO) (K!). **Kudat:** *Boden-Kloss* SFN 19296 (16 September 1927 FRU) (SING!); near Kudat, *Meijer* SAN 19935 (10 September 1959 FLO) (L!, SAN!), *Meijer* SAN 19936 (10 September 1959 FRU) (SAN!); behind STM Telecom Station, *Kamaruddin & Sukup* KMS 2193 (11 March 1988 FRU) (SAN!); Bak bak, 200 ft [61 m], *Brand* SAN 30924 (17 July 1962 FRU) (SAN!); Loro F.R., 400 ft [122 m], *Tai* SAN 51081 (18 May 1965 FRU) (K!); Balambangan Island, W from base camp, 1.5 km from base camp, *Dolois et al.* SP 18462 (24 May 2003 FLO) (SNP!); Malawali Island: 50 ft, *Diwol & Awang* SAN 89971 (25 March 1979 FRU) (SAN!), 30 ft [9 m], *Fox* SAN 69505 (24 February 1970 FRU) (SAN!), Tanjong, *Sugau et al.* SAN 145703 (8 August 2002 FRU) (SAN!); Labuan F.R.: *Austin* A 1245 (29 February 1948 FLO) (KEP!, SING!), 50 m, *Diwol* SAN 135356 (8 September 1998 FLO/FRU) (K, L, KEP, SAN!), 50 ft [15 m], *Maidin* SH 7328 (7 June 1937 FRU) (KEP! L! SING!); Lajong F.R.: *Majawat* SAN 132063 (28 October 1991 FRU) (L! SAN! SAR!), *Leopold, Pius, Tangah & Soinin* SAN 145151 (16 October 2002 FLO/FRU) (SAN!). **Pitas:** Kg Payas, *George & Amin* SAN 121258 (12 May 1987 FRU) (KEP! SAN!). **Kota Kinabalu:** 200 ft [61 m], *Saikeh* SAN 67153 (10 February 1971 FRU) (SAN!); Bukit Padang, *Meijer* SAN 23827 (15 February 1961 FLO) (SAN!); Gaya Island: *Haviland* 1438 (August 1892 FLO) (K!), 200 ft [61 m], *Aban* SAN 42017 (26 July 1966 FRU) (SAN!), 100 ft [31 m], *Ampuria* SAN 41307 (4 March 1964 FRU) (SAN!), *Berhaman, Meijer & Madani* SAN 134601 (30 June 1992 FRU) (SAN!), 300 ft [91 m], *Kanis & Kuripin* SAN 56117 (16 February 1966 FRU) (KEP! SAN!), south west, 100 ft [31 m], *Stone, Anderson & Leopold* SAN 86850 (15 April 1977 FRU) (KEP! SAN! SAR!), 150ft [46 m], *Wyatt-Smith* KEP 80296 (4 August 1954 FLO) (KEP! L!); Taman

Tunku Abdul Rahman, beach vegetation, *Pereira & Postar* JTP 698 (4 March 2000 FRU) (SAN!); 250 ft [72 m], *Mujin* SAN 33575 (8 April 1963 FRU) (SAN!), trail to highest point, *Rimi* et al. SP 7288 (23 March 1995 FRU) (SAN! SNP!), trail to Police Beach, *Dolois* et al. SP 9417 (20 May 1999 FRU) (SNP!), Police Beach trail to base camp, *Dolois* et al. SP 9508 (21 July 1999 FRU) (SAN! SNP!); Trail to Padang Point, *Rimi* et al. SP 7802 (25 June 1998 FRU) (SNP!); Manukan Island: *Rimi* et al. SP 7840 (24 June 1998 FLO) (SNP!), *Wong & Jamili* s.n. (1994 FLO/FRU) (SAN! SAR! SING!). **Beaufort:** Siaunggau Forest Reserve, *Diwol & Karim* SAN 78155 (31 May 1974 FRU) (SAN! SAR! SING!). **Kota Belud:** 500 m, *Gibbs* 4340 (16 May 1913 FLO) (K!), *Henderson* SFN 38959 (8 April 1950 FLO/FRU) (L! SING!). **Sandakan:** *Creagh* s.n. (August 1895 FLO) (K!), 100 m, *Foxworthy* 600 (January–March 1916 FLO) (PNH!), *Keith* 1215, 500 ft [152 m] (20 February 1929 FLO) (K!); COF's compound, 300 ft [91 m], cultivated, *Keith* S.H. 8862 (4 March 1938 FRU) (KEP! L! SING!), near catchment area, *Orolfo* 831 (3 May 1926 FRU) (SING!); 26 ft [8 m], *Ramos* 1195 (24 September 1920 FRU) (PNH!), *Wood* 741 (February–March 1920 FRU) (P!); behind Cheng Ming School, 300 ft., *Pereira* SAN 41096 (12 April 1964 FRU) (K! SAN!); Buli Sim Sim, 800 ft [244 m], *Keith* A 1506 (21 February 1948 FRU) (BKF! KEP! P! SING!); SW of Trig Buli Sim Sim, 500 ft [152 m], *Pereira* SAN 41052 (28 November 1963 FRU) (SAN!), 0.5 mile SW of Trig Buli Sim-Sim, 400 ft [122 m], *Pereira* SAN 41073 (8 December 1963 FRU) (SAN!); Sibuga Road, 200 ft [61 m], *Abu Bakar* SAN 27750 (15 November 1961 ST) (SAN!); Kebun China: *Ampon, Talip & Chow* SAN 68479 (25 November 1969 FRU) (SAN!), *Singh* SAN 34719 (25 April 1962 FRU) (SAN!), low undulating country, *Singh* SAN 39256 (13 August 1963 FRU) (SAN!); Batu Sapi, 90 ft [27 m], *Sayu* SAN 38822 (30 September 1963 FRU) (SAN!); Leila F.R.: *Charington* SAN 23664 (3 January 1961 FRU) (K, KEP! L, SAN! SAR!), 300 ft [91 m], *James* SAN 32552 (10 November 1962 FRU) (SAN! SAR!), *Kapis* SAN 34688 (10 March 1962 FRU) (KEP! L! SAN! SAR! SING!), *Kumin* SAN 58837 (12 November 1968 FRU) (SAN!), *Ogata* 10646 (4 August 1968 FRU) (L!), 91 ft [28 m], *Patrick & Jali* SAN 62547 (15 March 1968 FLO) (SAN! SING!), 100 ft [31 m], *Saikeh* SAN 65559 (14 May 1969 FRU) (SAN!), 350 ft [107 m], *Sam* SAN 28831 (28 February 1962 FLO) (KEP! SAN! SAR! SING!), 75 ft [23 m], *Sayu* SAN 38887 (10 August 1963 FRU) (SAN! SING!), water catchment area, *Stone* 6688 (17 March 1967 FLO) (KLU! L!); Jalan Kulam, 90 ft [27 m], *Kumin* SAN 73587 (12 August 1971 FRU) (SAN! SAR!), *Patrick* SAN 70208 (24 August 1970 FRU) (SAN! SAR!); Taman Datuk Chong Thien Vun, *Amin* SAN 95147 (22 April 1982 FRU) (KEP! SAN! SAR!), *Meijer* SAN 141282 (10 November 1994 FRU) (SAN!); Kabili-Sepilok F.R.: 0–70 m, *Kessler* SAN 118033 (23 February 1989 FLO) (SAN! L!), *Ridsdale* 2029 (21 May 1989 FRU) (L!); RP292–2, Plot 2×1, *Pereira & Diwol* JTP 398 (8 January 1997 ST) (SAN!), 30 m, *Pereira & Postar* JTP 581 (10 February 1999 FRU) (SAN!), *Pereira* et al. JTP 848 (May 2002 FRU) (SAN!); 150 m, *Wong & Puff* WKM 2109 (11 April 1993 FRU) (SAN!); Mile 13, Labuk Rd., 50 ft [15 m], *Fox* SAN 70682 (29 July 1970 FRU) (SAN!); Seguntor, 300 ft [91 m], *Postar* et al. SAN 141146 (9 September 2004 FRU) (SAN!). **Labuk Sugut:** Bonggaya, Bukit Obar, 100–190 m, *Sugau* et al. JBS 266 (23 September 1997 FRU) (L! SAN!); Beluran, near Kg Baba, ridge, 620 m, *Postar* et al. SAN 145528 (19

August 2004 FRU) (SAN!); Tawai F.R., Tawai Hill, 150–1310 m, *Sukup* SA 1946 (24 August–2 September 1991 FRU) (UKMB!), *Leopold & Goh* et al. SAN 133845 (26 October 1999 FRU) (SAN!).

4. *Rothmannia negrosensis* (Merr.) J.T. Pereira & Ridsdale, comb. nov.

Gardenia negrosensis Merr., Philipp. J. Sci., C 10 (1915) 111–112, pro parte quoad *Celestino* Bur. Sci. 7333, Merr., Enum. Philip. Fl. Pl. 3 (1923) 530, pro parte quoad *Ramos & Edaño* Bur. Sci. 31358 & *Cardona* FB 23868, excl. *Ramos & Edaño* Bur. Sci. 36787 (= *Rothmannia graciliflora*), *Sandique* FB 26596 *Wenzel* 641 (= *R. leytensis*). NEOTYPE (here designated): *Celestino* Bur. Sci. 7333, Philippines Negros, Cadiz (February–March 1909 FLO) (L!).

Treelet to small tree, 5 × 12 m high. Twigs sparsely velvety hairy, becoming glabrescent when old. Branch leaves typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves. Stipules broadly ovate-triangular, 2 × 4 mm long, 5 × 8 mm wide, sparsely to densely pubescent outside; apex acute to cuspidate, *c.* 1 mm long. Young leaves on shoot tips pubescent to velvety hairy on both sides. Mature leaves with petiole 0.5 × 1.3 cm long, 2 × 3 mm thick, velvety hairy to glabrescent; lamina broadly elliptic to ovate, to sometimes lanceolate, (11.5–)14 × 22 cm long, (4–)6 × 10 cm wide, upper surface glabrous, lower surface puberulous to velvety hairy; leaf base cuneate, subrounded to unequal; leaf apex acute to short-acuminate, acumen to *c.* 0.3 cm long; thin-coriaceous to chartaceous when dry; midrib on upper side flat, glabrous, on lower side raised, velvety hairy; secondary veins 7 × 13 pairs, on upper side flat, glabrous, on lower side slightly raised, velvety hairy; tertiary venation visible as simple connections between pairs of secondary veins. **Inflorescences:** peduncle 0.2 × 0.3 cm long, 2.5 × 4 mm thick, velvety hairy to tomentose; habit compact, with only 1 distinct branching order, rachis 0.2 × 0.5 cm long, primary branches along the rachis 1 pair, 0.2 × 0.5 cm long; bracts broadly ovate, 3 × 4 mm long, 3 × 5 mm wide, pubescent. Flowers 2 × 3 per cyme; pedicels subobsolete to 1 mm long, *c.* 1 mm thick; calyx tube 5 × 7 mm long, 3 × 6 mm wide, sparsely pubescent to velvety hairy, hairs appressed, surface visible outside; calyx limb cup-shaped to conical; calyx lobes 5 × 6, short-triangular, 0.5 × 1 mm long, pubescent to velvety hairy; corolla hypocrateriform, the tube 6 × 9 cm long, 6 × 10 mm wide at the throat, 2.5 × 3 mm wide at the base; non-speckled inside, outer surface glabrescent to scantily pubescent, inner surface with hairy zone covering part or all of the tube from the corolla mouth downwards; corolla lobes (5–)6 × 8, broadly ovate, 2.7 × 4.5 cm long, (1.5–)1.8 × 2.5 cm wide, outside scantily puberulous on the uncovered half of the lobes, inside glabrous; anthers (5–)6–8, fully included within the tube (inserted at the upper $\frac{1}{3}$), 9 × 12 mm long; style and stigma *c.* 60 × 90 mm long, included but reaching just below the corolla mouth and the level of or above the anthers, style smooth, glabrous, stigma 2-lobed.

Fruits globose, 5.5 × 6 cm long, 2.5 × 6 cm wide, glabrous, drying smooth; fruit wall *c.* 1 mm thick; peduncle to 0.2 cm long, *c.* 4 mm thick. Seeds slightly to much flattened and broadly ovate or suborbicular to narrowly triangular, 10–11 mm × 7–9 mm.

NOTES. Merrill (1915) in *Philipp. J. Sci.*, C 10: 111, designated *Everett* FB 7255, collected from Negros, Philippines as the type of the basionym, *Gardenia negrosensis*. However, the holotype of this specimen was not located and is presumed destroyed in the Philippine National Herbarium during the Second World War (Van Steenis-Kruseman, 1950). The isotypes, if any, were also not located after search at the various relevant herbaria where Merrill's collections have been distributed, i.e., A, K, L, P, NY, SING, U, and US. Besides the type indicated by Merrill, he had also listed other specimens in the original description. One of the specimen, *Celestino* Bur. Sci. 7333 collected from Cadiz, Negros, around Feb–Mar 1909 and kept in Leiden, was available for study. Based on Article 9, paragraph 9.6 of the International Code of Botanical Nomenclature, Vienna Code (2006), *Celestina* Bur. Sci 7333 (L) is designated neotype.

This species is very similar to *R. merrillii*. However, *R. negrosensis* is consistently hairier than *R. merrillii* in a number of parts: the lower leaf surface (lamina) and its veins, inflorescence peduncle, bracts and calyx are velvety hairy to pubescent compared to *R. merrillii*, which is typically glabrous to scantily puberulous or only sparsely pubescent. The degree of hairiness in the inflorescences, calyces and leaves compared to *R. merrillii* have been pointed out by Merrill (1915). The outer surface of the corolla tube is typically glabrescent to scantily puberulous, but in *R. merrillii* is always glabrous. Another main distinguishing character of *R. negrosensis* is found in the corolla lobes, which are broader (typically 1.8–2.5 cm wide, but rarely less than 1.8 cm wide) than those of *R. merrillii* (typically 0.5–1 cm, rarely to 1.5 cm wide). In the original description of *Gardenia negrosensis*, the fruits were described as “subglobose to ovoid, up to 2.5 cm in diameter”. However, it is uncertain if this fruit measurement referred to a mature fruit. The only fruiting specimen (with mature fruits) available for study has a larger diameter than was described in the original publication, i.e., 6 cm diameter.

DISTRIBUTION. Thus far only found in the Philippines (Negros, Mindoro and Palawan islands).

HABITAT. Recorded in lowland to hill forests, to 850 m alt.

SPECIMENS EXAMINED—PHILIPPINES. NEGROS: *Cordona* 23868 (February–April 1915 FLO) (A! SING!); Capiz Prov., Jamindan, *Ramos & Edano* Ramos 31358 (April–May 1918 FLO) (L!). Cadiz, *Celestino* 7333 (February–March 1909 FLO) (neotype L!). **MINDORO:** Calintaaan, Poypoy, Sitio Sapaton, Mt Iglit-Baco National Park, 850 m, *Barbon, Garcia* PPI 22603 (26 August 1996 FRU) (L!); Mt Halcon, *Edano* PNH 3512 (January–February 1948 FLO) (L! SING!), Mt Halcon, *Ramos & Edano* Ramos

40730 (March 1922 FLO) (A!); San Teodoro, Sibuang Camp, *Ridsdale* 857 (12 February 1985 FRU) (L!). Sibuyan Island, Capiz Prov., Mt Guinting-Guinting (Magallanes), *Elmer* 12246 (April 1910 FLO) (L!), Mt Guinting-Guinting, 300 m, *Madulid* 6897 (16 June 1987 FRU) (L!). **PALAWAN:** St. Paul's Bay, Caboyugan village, W side of the road, 50 m, *Ridsdale* SMHI 1649 (7 May 1984 FRU) (K! L!).

A New Species of *Rothmannia* from the Philippines

Rothmannia leytensis J.T. Pereira & Ridsdale, **sp. nov.** (Fig. 1)

TYPE: *Wenzel* 641, Philippines, Leyte (8 March 1914 FLO) (holotype A! isotype BM!).

This new species closely resembles *Rothmannia negrosensis* (Merr.) J.T. Pereira & Ridsdale, from which it differs by having leaves with tertiary venation developing a much-branched network between secondary veins; more flowers per cyme (i.e. 4–9); a glabrous corolla throat and smaller corolla lobes.

Gardenia negrosensis sensu Merr., Enum. Philip. Fl. Pl. 3 (1923) 530, pro parte quoad *Wenzel* 741, 641; *Sandique* 26596; non Merr. (1915).

Tree. Twigs velvety hairy when young, becoming sparsely pubescent to glabrescent when old. Branch leaves typically in groups of 3's, each trifoliate group based on a distal node with only one leaf normally developed (the other vestigial or very much reduced in size), and the proximal node with a pair of normal leaves. Stipules ovate-triangular, 5 × 7 mm long, 5 × 7 mm wide, sparsely pubescent to tomentose; apex acute to acuminate, *c.* 1 mm long. Young **leaves** on shoot tips velvety hairy on both sides. Mature leaves with petiole 0.1 × 0.6 cm long, 2 × 3 mm thick, pubescent to tomentose outside; lamina elliptic to obovate, 10 × 18 cm long, 4.5 × 8 cm wide, upper surface glabrous to glabrescent, lower surface sparsely pubescent; leaf base cuneate to symmetric; leaf apex acute to acuminate, acumen to 0.5 cm long; thin-coriaceous when dry; midrib on upper side flat to slightly raised, glabrous, on lower side raised, pubescent; secondary veins 7 × 10 pairs, on upper side flat to slightly sunken, glabrous, on lower side raised, pubescent; tertiary venation visible as a much-branched network between pairs of secondary veins. **Inflorescences:** peduncle 0.2 × 0.4 cm long, 2 × 3 mm thick, velvety hairy to tomentose; habit compact, with 1 × 2 distinct branching orders, rachis 0.5 × 1 cm long, primary branches along the rachis 1 × 2 pairs, 0.4 × 0.6 cm long; bracts ovate, 2 × 3 mm long, 2 × 2.5 mm long, densely pubescent. Flowers 4 × 9 per cyme; pedicels to *c.* 1 mm long, to *c.* 1 mm thick; calyx tube 5 × 7 mm long, 3 × 4.5 mm wide, densely tomentose, hairs appressed to suberect, surface visible; calyx limb cup-shaped; calyx lobes 5, triangular, 1 × 2.5 mm long, tomentose; corolla hypocrateriform, the tube 6–8.2 cm long, 4 × 5 mm wide at the throat, 1 × 2 mm wide at the base; non-speckled inside, outer surface sparsely pubescent, inner surface glabrous; corolla lobes 5,

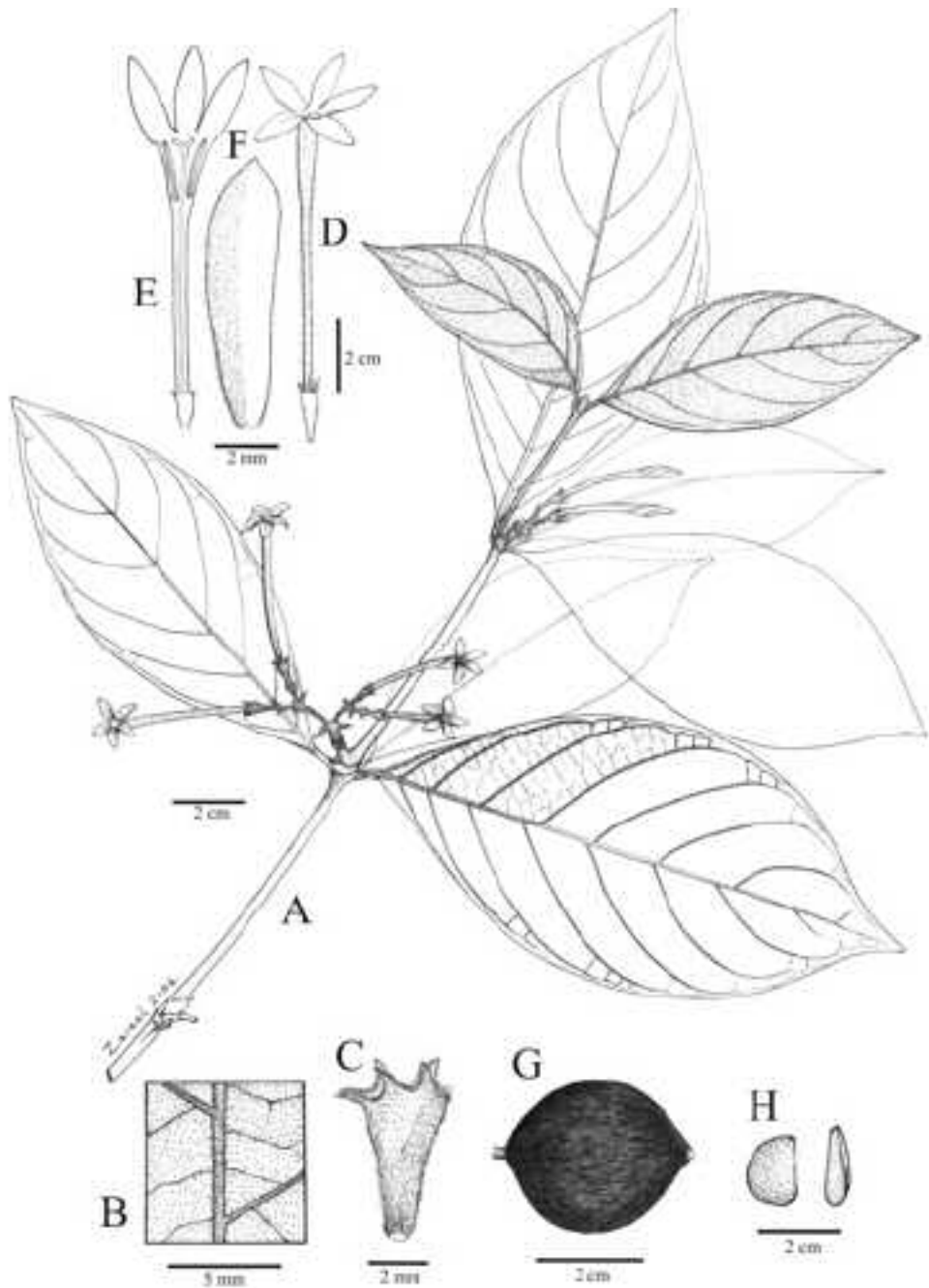


Fig. 1. *Rothmannia leytensis*. **A.** leafy branch with inflorescences. **B.** close-up of the lower leaf surface. **C.** outer surface of calyx tube. **D.** outer structure of flower. **E.** longitudinal section of flower. **F.** outer surface of corolla lobes. **G.** Fruit. **H.** seeds. **A–B** from *Sandique* 26596 (K), **C–F** from *Wenzel* 641 (BM), **G–H** from *Edano* 41727 (A & L).

elliptic to oblong, 1.2 × 2.5 cm long, 0.4 × 0.9 cm wide, outside pubescent on the uncovered half of the lobes, inside glabrous; anthers 5, fully included within the tube or only with tips slightly protruding (inserted at the upper $\frac{1}{3}$), 11 × 14 mm long; style and stigma 60 × 85 mm long, included but reaching just below the corolla mouth and the level of or above the anthers, style smooth, glabrous. **Fruits** globose, 3 × 4 cm long, 3 × 4 cm wide, sparsely pubescent when young, becoming glabrous when mature, drying smooth; fruit wall *c.* 1 mm thick; peduncle 0.3 × 0.5 cm long, 3 × 4 mm thick. Seeds slightly to much flattened and broadly ovate or suborbicular, 9–11 mm × 7–8 mm.

NOTES. Vegetatively, this species is very closely allied to another species of *Rothmannia* in Borneo, but is distinguishable by its relatively shorter peduncle and longer style and stigma complex.

DISTRIBUTION. Endemic to the Philippines (Leyte).

SPECIMENS EXAMINED—PHILIPPINES: No locality. *Wenzel* 741 (30 May 1914 FRU) (BM!). **LEYTE:** *Wenzel* 641 (8 March 1914 FLO) (holotype A! isotype BM!); Mt Abucayan, *Edano* 41727 (February 1923 FRU) (A! L! SING!), *Sandique* 26596 (March 1917 FLO) (K!).

Endemic Species

With so little known about taxonomic relationships within *Rothmannia* s.l., and about the Philippine taxa in particular, it would be highly premature to attempt to form any biogeographical analysis. However, it is not surprising, given how the evolution of biological lineages respond to isolation (Wong 2011), that four out of five Philippine *Rothmannia* species are endemic to just one or very few islands in that archipelago. Of the several species, *R. merrillii* is the most widespread, distributed in the Philippines (East and South Luzon, Mindoro, Palawan, Negros, Panay and the smaller islands such as Sibuyan, Guimaras, Calamian group, Golo and Semirara) and also in Sabah (commonly in the north and northeastern part and also western part, up to Beaufort).

It is also not certain if departures from standard morphological traits are of special significance. For example, the corolla in Malesian *Rothmannia* is typically 5-merous, but in two Philippine taxa, *R. merrillii* and *R. negrosensis*, an increased number of (6–8) lobes is often encountered in the corolla.

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The morphology and exine ornamentation of fresh pollen from four dipterocarp species in Sabah

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Summary. The pollen morphology and fine exine ornamentation of the dipterocarps *Parashorea tomentella* (Symington) Meijer, *Shorea multiflora* (Burck) Symington, *Shorea xanthophylla* Symington and *Shorea leprosula* Miq. were investigated from individuals growing in Sepilok Forest Reserve, Sabah. Fresh pollen was extracted from flowers collected in the canopy and analyzed using a combination of light microscopy and Scanning Electron Microscopy (SEM). The size of pollen grains was estimated from their polar axis length and equatorial diameter, and systematic descriptions were developed from the SEM images. The four species had contrasting polar axis lengths and equatorial diameter dimensions that varied in the range 11.7–38.0 μm and 11.5–32.7 μm , respectively. The pollen was monad, tricolpate and predominately spheroidal but the morphology varied among the species. *Parashorea tomentella* had narrow colpi and wide irregular muri. *Shorea multiflora* and *S. xanthophylla* had colpi covered by a colpus membrane with a microreticulate ornamentation. Pollen of *S. leprosula* were prolate spheroidal, subspheroidal or subprolate, lobate in polar view, with two obvious colpi and a microreticulate ornamentation. For these four species, pollen volume was significantly correlated to flower size. We conclude that with more research, pollen morphology could be a diagnostic tool for distinguishing among dipterocarp species in different sections of a genus (e.g. sections *Mutica* and *Richetioides* of *Shorea*) and between genera (*Shorea* and *Parashorea*). However, in our study, the two species of *Shorea* section *Richetioides* could not be distinguished on the basis of morphological differences.

Angiosperms exhibit a great diversity in pollen exine ornamentation and morphology. These traits can be used as a diagnostic tool for identifying plant families and species in studies of reproductive biology, palaeoecology and forensic science (Cruden & Lyon, 1985). Pollen identification is also a valuable technique for confirming the identity of pollen carried by flower visitors, and may contribute to investigations of pollination ecology and pollinator dynamics. The aim of this paper is to document previously undescribed information and images on pollen morphology and fine ornamentation of four dipterocarp species as an aid to our research on their reproductive ecology and pollination biology (Maycock *et al.*, 2008).

There are few published descriptions of the pollen of the Dipterocarpaceae. Investigations were reviewed by Ashton (1988) but the most comprehensive studies that include systematic descriptions and high resolution images are by Maury *et al.* (1975) and Talip (2008). Maury *et al.* (1975) documented pollen descriptions for nine species from six genera of Dipterocarpaceae and summarised existing information on another 26 species, while Talip (2008) examined the pollen morphology of 32 species of Malaysian dipterocarps. However, these studies were both based on pollen gathered from herbarium specimens, and there are concerns that drying may distort their shape and outline (Price & Ayers, 2008). Price and Ayers (2008) reported that the shape of pollen may change from oblate spheroidal to subprolate as a result of drying time and temperature, and recommended that either FAA-preserved material collected in the field, or fresh pollen, should be used for morphological studies.

The value of previous pollen descriptions have not been fully realised in research on dipterocarp reproductive biology and pollination ecology. To our knowledge, there are no studies of dipterocarp pollinators that have determined pollen loads using high resolution images. These images are important for robust identifications of pollen and pollinator, particularly when the pollen load contains a mixture of species, and for quantifying pollen load. There are also very few images and systematic descriptions of the pollen of dipterocarps in Sabah, and very little association between existing material and dipterocarp pollination ecology.

The aims of this study were (a) to describe pollen morphology based on freshly collected pollen of four dipterocarp species that are the subject of an on-going study of pollination biology, (b) to identify the extent of variation in pollen morphology between the four species, (c) to present clear high resolution images of the pollen as a reference for future taxonomic and ecological research, and (d) to determine the interspecific differences in pollen size between these four species and relate these differences to flower size.

Materials and Methods

The species studied were *Parashorea tomentella* (Symington) Meijer, *Shorea multiflora* (Burck) Symington, *Shorea xanthophylla* Symington and *Shorea leprosula* Miq. The fresh

flowers of *P. tomentella* are larger (mean calyx diameter 4.2 mm) than those of *S. leprosula* (mean calyx diameter 2.2 mm), and *S. multiflora* and *S. xanthophylla* (mean calyx diameter 1.3 mm and 1.2 mm, respectively). Previous research has indicated that the pollen from the Asiatic sub-family of the Dipterocarpaceae (Dipterocarpoideae) is monad, tricolpate and predominately spherical, while colpi are generally elongate and narrow, and covered with a thin colpus membrane. The exine consists of a thin endexine layer and a stronger ectexine layer (Maury *et al.*, 1975).

Pollen was collected during a minor dipterocarp flowering event in the Kabili-Sepilok Forest Reserve, in Sabah, Malaysia (5°10' N, 117°56' E) between May and July 2007. Pollen was sampled from fresh flowers that were collected during anthesis using mixed rope techniques. Inflorescences were removed by hand and placed in sealed bags. Flowers were dissected using a dissecting microscope and the pollen was carefully removed using drops of 70% ethanol. All ethanol residues were collected on a glass slide and the slide was analysed systematically; any clusters of pollen were carefully dispersed using a fine needle. Only fresh pollen was used for analysis and imaging. The analysis of pollen followed techniques described by Dafni (1992) and Shivanna (2003). Initial investigations of pollen morphology were conducted using light microscopy (LM) and a digital microscope imaging device (DMID), using the software SemAfore (JEOL, Sweden). The polar axis length and equatorial diameter of 50 individual pollen grains of each species were measured using the DMID.

For scanning electron microscopy (SEM), pollen grains were fixed in 70% ethanol and dehydrated in 100% ethanol, then transferred to hexamethyldisilazane for five minutes and allowed to air dry. Dehydrated pollen grains were then mounted onto metal stubs using double-sided adhesive tabs, sputter coated with gold using a EMitech K550 Sputter Coater (Quorum Technologies Ltd, UK), and examined using a JEOL 35CF Scanning Electron Microscope (JEOL, Japan) at an accelerating voltage of 10 kV and at different degrees of magnification. Dehydration and the vacuum created in the SEM chamber can cause pollen grains to distort (Hesse *et al.*, 2009). Therefore SEM images were compared with images obtained using the DMID in order to verify that the systematic descriptions of morphology and fine ornamentation were not biased by these distortions. Images were manipulated using the software Adobe Photoshop CS2 (Adobe, USA) and then compiled into an electronic reference library. Morphological descriptions of the pollen were created based on the SEM images, light microscopy and Punt *et al.* (2007). The following abbreviations are used for the pollen descriptions: P/E = Polar axis/Equatorial diameter, P = Polar axis, E = Equatorial diameter, PLL = Plica length, PLW = Plica width, CL = Colpus length, CW = Colpus width, L = Lumina length, M = Murus diameter.

The Kruskal-Wallis χ^2 was used to test for differences among species in polar axis length and equatorial diameter. We determined the volume of the pollen for each species using the formula $\pi PE^2/6$ (Harder, 1998). We also estimated pollen volume using mean polar length

and equatorial diameter data from Talip (2008) for eight species that occur within the Sepilok Forest Reserve. From previous studies (Maury *et al.*, 1975; Talip, 2008), it is apparent that there is significant inter-specific variation in pollen size and this is thought to be related to flower size and nutrient supply to the developing bud (Müller, 1979 cited in Talip, 2008), so we used linear models to investigate the relationship between flower size and pollen volume for our data and those of Talip (2008).

Results and Discussion

Systematic descriptions of pollen

Parashorea tomentella

The pollen was the largest of the four species (Fig. 1, P/E: $26.6 \pm 0.4 \times 25.9 \pm 0.4 \mu\text{m}$, $n = 50$). Individual grains were spheroidal, subspheroidal, oblate spheroidal or prolate

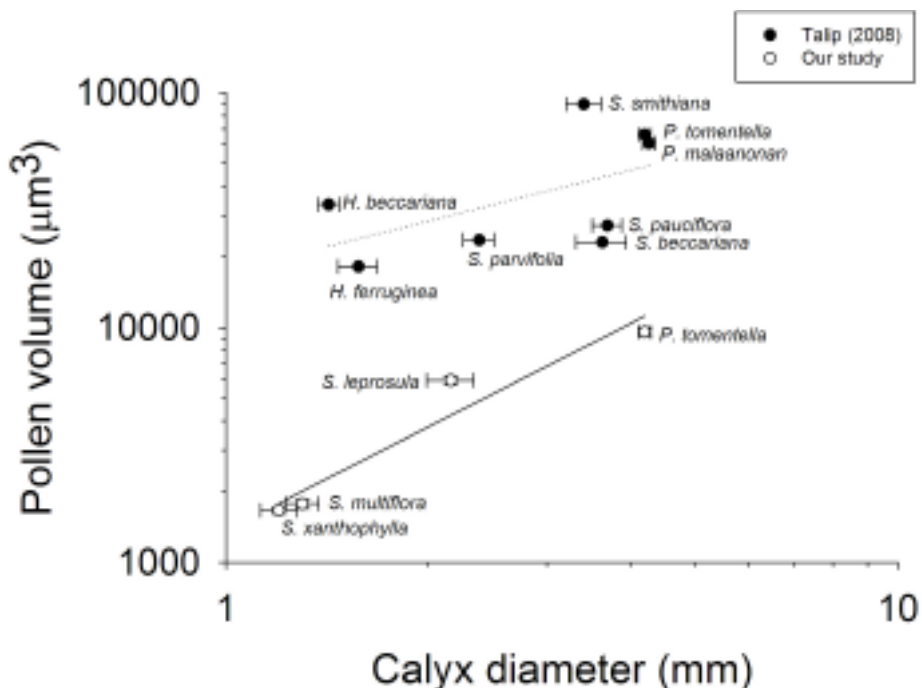


Fig. 1. Relationship between flower size, defined as the calyx diameter of the open flower, and pollen volume for the four species of dipterocarp sampled in Sepilok Forest Reserve, Sabah, Malaysia, and eight of the species examined by Talip (2008). The lines indicate the linear models for these data; the solid line indicates a significant relationship ($p < 0.05$) and a dotted line a non-significant relationship. The apparent difference in pollen volume between the two provenances of *P. tomentella* is discussed in the text.

spheroidal ($P/E = 0.98 \pm 0.02$), tricolpate, with narrow long colpi (CW: $1.6 \mu\text{m} \pm 0.5$, $n = 4$ colpi on four pollen grains, CL: $20.9 \mu\text{m} \pm 1.0 \mu\text{m}$, $n = 4$ colpi on three pollen grains). From LM images, we observed that one colpus was deeper and wider than the other two. SEM images suggested that one colpus culminated in an ectoaperture on one polar field (Fig. 2a & 2b). Light microscopy suggested that there was a thickening of the intine layer or a delimiting of the mesocolpium. The exine was microreticulate (Fig. 2c) with crotonoid patterning and wide muri (M: $0.62 \pm 0.03 \mu\text{m}$, $n = 10$ muri on one pollen grain). Segments of the muri were triangular and rectangular. The shape and dimensions of the lumina ranged from narrow and elongate to irregular and spherical (L: $1.03 \pm 0.12 \mu\text{m}$, $n = 10$ lumina on one pollen grain).

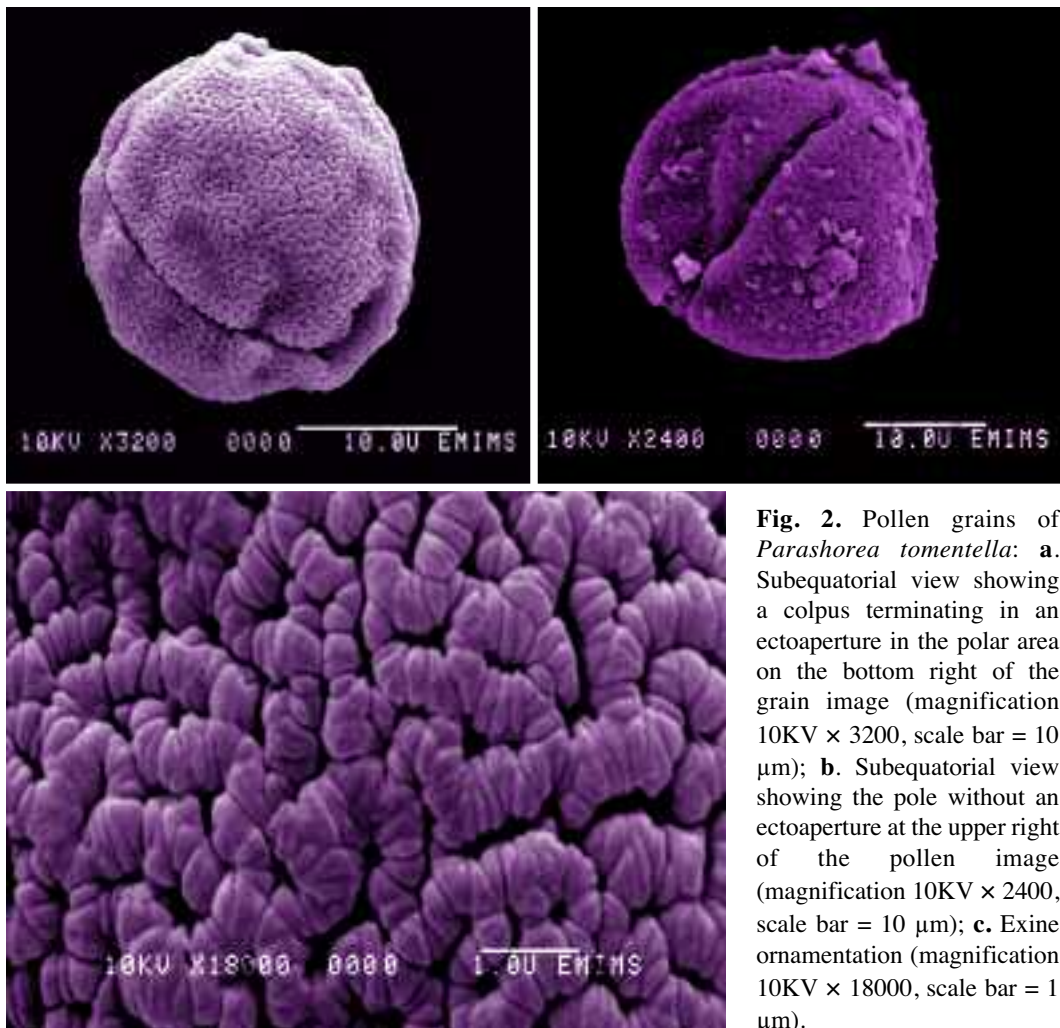


Fig. 2. Pollen grains of *Parashorea tomentella*: **a.** Subequatorial view showing a colpus terminating in an ectoaperture in the polar area on the bottom right of the grain image (magnification 10KV \times 3200, scale bar = 10 μm); **b.** Subequatorial view showing the pole without an ectoaperture at the upper right of the pollen image (magnification 10KV \times 2400, scale bar = 10 μm); **c.** Exine ornamentation (magnification 10KV \times 18000, scale bar = 1 μm).

Shorea multiflora

The pollen grains were small (P/E: $16.0 \pm 0.3 \mu\text{m} \times 14.4 \pm 0.2$, $n = 50$). Individual grains were spheroidal, subspheroidal or oblate spheroidal (P/E = 0.91 ± 0.02), tricolpate with three ectocolpi that were covered in a colpus membrane (Fig. 3a & 3b). The colpi were moderately long (CL: $10.1 \pm 0.4 \mu\text{m}$, $n = 2$ colpi on two pollen grains) but narrow (CW: $2.6 \pm 0.8 \mu\text{m}$, $n = 6$ colpi on four pollen grains). The polar fields were broad and the distances between the apices of the colpi were approximately equal (average $5.7 \mu\text{m} \pm 0.1$, $n = 3$). Light microscope images suggested that the endexine layer was thicker to support the exine between the colpi. The exine ornamentation was microreticulate, with a compact croton pattern. The raised muri (M: $0.23 \pm 0.01 \mu\text{m}$, $n = 10$ muri on one pollen grain) were scored into segments, primarily triangular but also rectangular (Fig. 3c). The microreticulate lumina were spherical to elliptical (L: $0.14 \pm 0.01 \mu\text{m}$, $n = 10$ lumina on one pollen grain) and isodiametric.

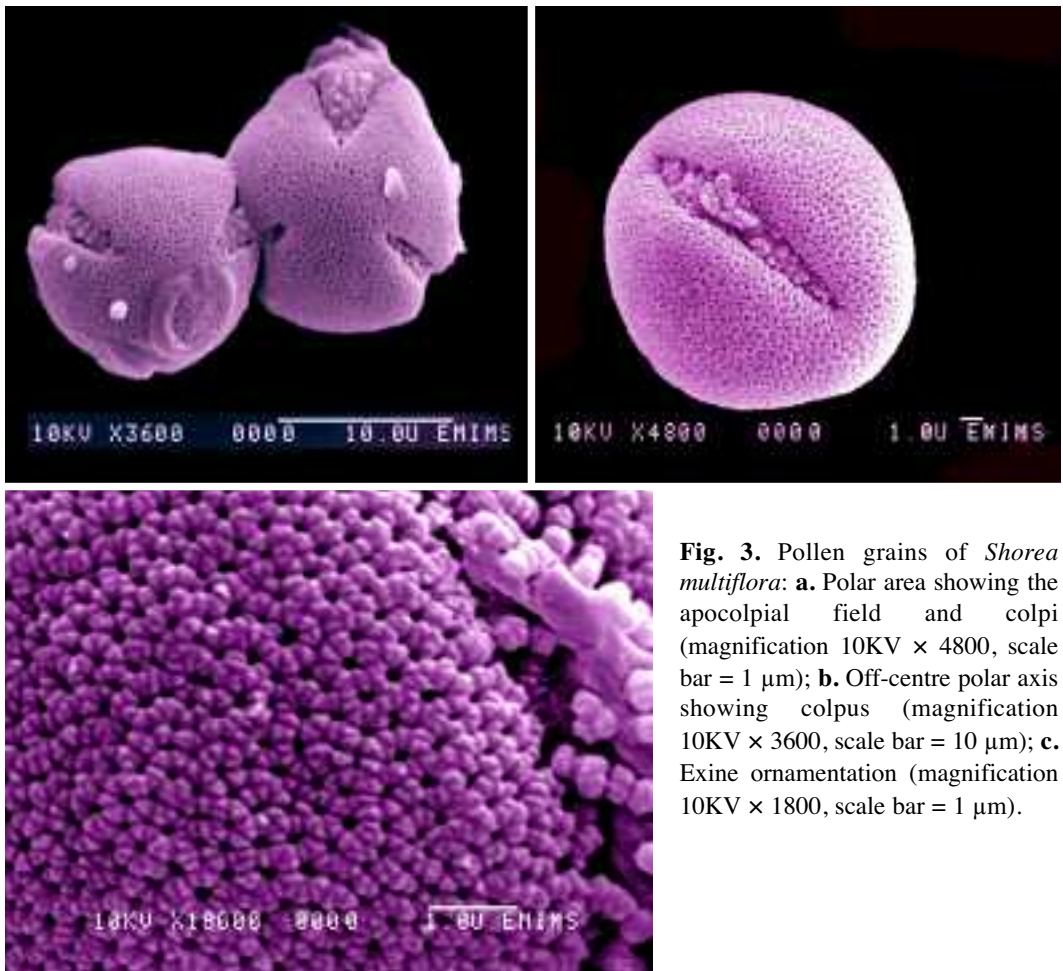


Fig. 3. Pollen grains of *Shorea multiflora*: **a.** Polar area showing the apocolpial field and colpi (magnification 10KV \times 4800, scale bar = 1 μm); **b.** Off-centre polar axis showing colpus (magnification 10KV \times 3600, scale bar = 10 μm); **c.** Exine ornamentation (magnification 10KV \times 1800, scale bar = 1 μm).

Shorea xanthophylla

The structure, size and shape of *S. xanthophylla* pollen were similar to those of *S. multiflora*. The pollen grains were small (P/E: $14.7 \pm 0.2 \times 14.6 \pm 0.2 \mu\text{m}$, $n = 50$), spheroidal, subspheroidal or oblate spheroidal (P/E = 1.00 ± 0.02) and tricolpate (Fig. 4a & 4b). The three colpi were narrower than *S. multiflora* (CW: $1.1 \pm 0.3 \mu\text{m}$, $n = 3$ colpi on two pollen grains) and covered with a colpus membrane. The orientation of the pollen grain in the SEM image prevented us from recording multiple colpi lengths (CL: $9.1 \mu\text{m}$, $n = 1$ colpus). The apices of the colpi were approximately equal in dimension (average $4.2 \mu\text{m} \pm 2.5$, $n = 3$ apices on one pollen grain). The exine ornamentation was microreticulate, with a compact croton pattern. The raised muri (M: $0.24 \pm 0.01 \mu\text{m}$, $n = 10$ muri on one pollen grain) were also scored into segments that were primarily triangular but also rectangular (Fig. 4c). Lumina were spherical to elliptical, and approximately isodiametric, although there was substantial variation in lumen size (L: $0.16 \pm 0.01 \mu\text{m}$, $n = 10$ lumina on one pollen grain).

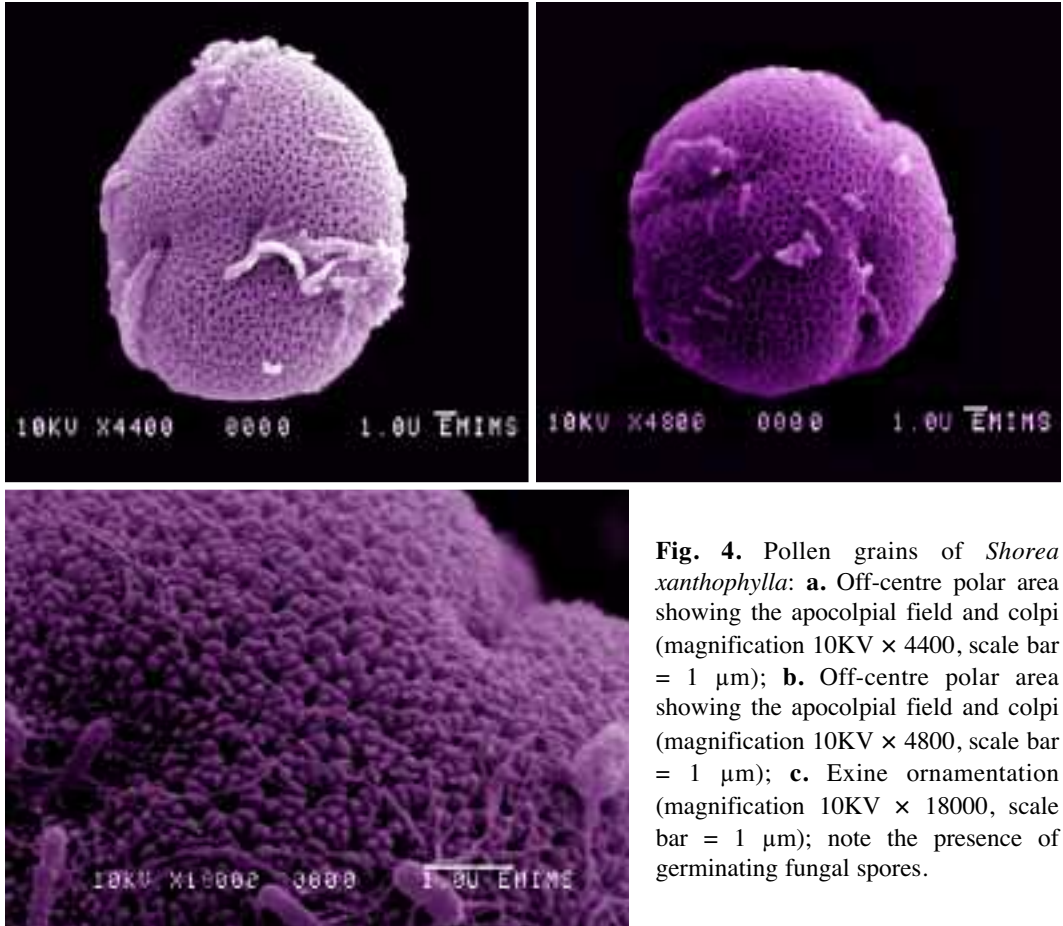


Fig. 4. Pollen grains of *Shorea xanthophylla*: **a.** Off-centre polar area showing the apocolpial field and colpi (magnification 10KV \times 4400, scale bar = $1 \mu\text{m}$); **b.** Off-centre polar area showing the apocolpial field and colpi (magnification 10KV \times 4800, scale bar = $1 \mu\text{m}$); **c.** Exine ornamentation (magnification 10KV \times 18000, scale bar = $1 \mu\text{m}$); note the presence of germinating fungal spores.

Shorea leprosula

The pollen grains were medium in size ($P/E: 24.0 \pm 0.4 \times 21.5 \pm 0.4 \mu\text{m}$, $n = 50$) and subspheroidal, prolate spheroidal and subprolate ($P/E = 1.12 \pm 0.02$). They had a lobate, triangular outline in polar view with a curved distal face (Fig. 5a). They were subspheroidal to rectangular in equatorial view (Fig. 5b). The pollen grains were tricolpate, with two obvious wide colpi (CW: $6.0 \pm 0.8 \mu\text{m}$, $n = 6$ colpi on three pollen grains) and a probable short shallow colpus on the curved distal face (observed with LM). The colpi were relatively long (CL: 8.1 ± 0.54 , $n = 6$ colpi on three pollen grains). Exine ornamentation was microreticulate with croton patterning. The muri were undulating and narrow (M: $0.35 \pm 0.02 \mu\text{m}$, $n = 10$ on one pollen grain) and scored into triangular, irregular and spherical segments (Fig. 5c). Lumina were broad (L: $0.56 \pm 0.04 \mu\text{m}$, $n = 10$ on one pollen grain) elongate, spherical or elliptical.

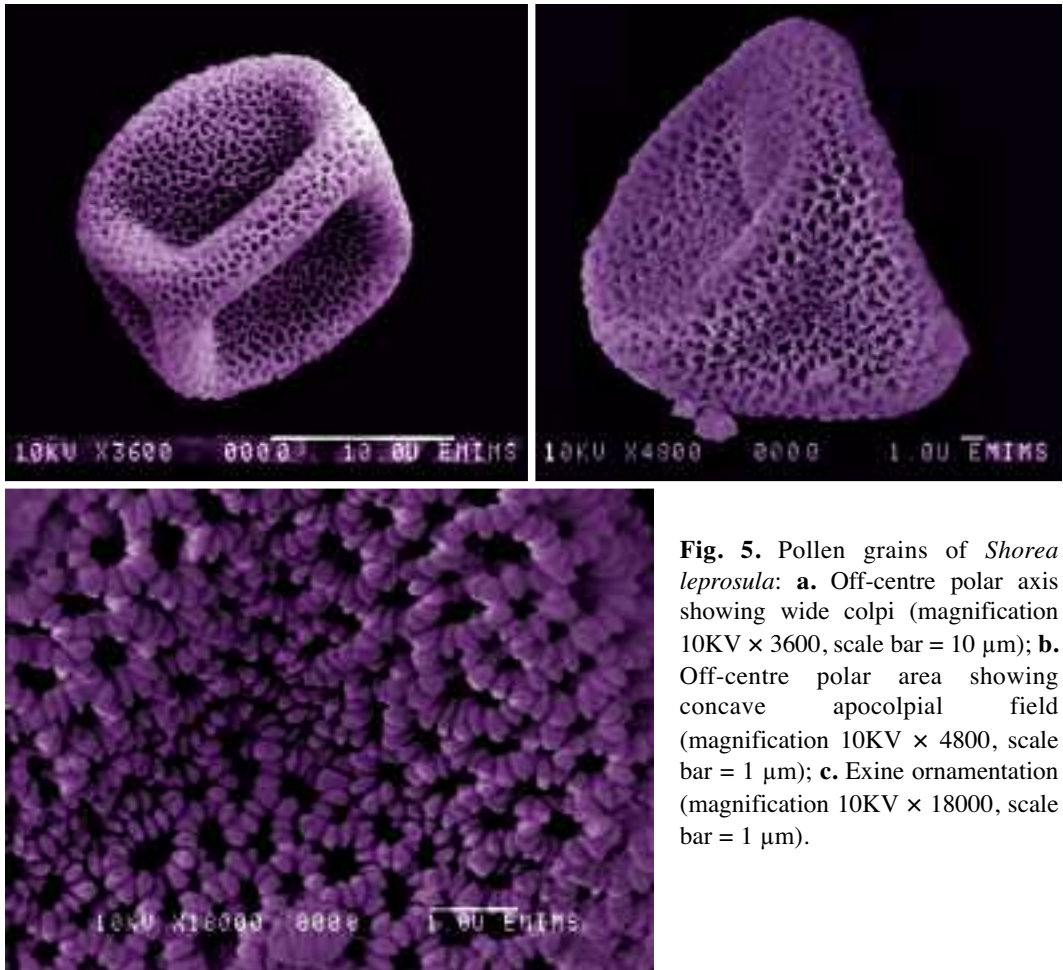


Fig. 5. Pollen grains of *Shorea leprosula*: **a.** Off-centre polar axis showing wide colpi (magnification 10KV \times 3600, scale bar = 10 μm); **b.** Off-centre polar area showing concave apocolpial field (magnification 10KV \times 4800, scale bar = 1 μm); **c.** Exine ornamentation (magnification 10KV \times 18000, scale bar = 1 μm).

The size and morphology of Dipterocarpaceae pollen

The basic tricolpate structure of Dipterocarpoideae pollen observed in this study concurs with previous descriptions and the images presented by Maury *et al.* (1975) and Talip (2008). Only two of the species we sampled at Sepilok Forest Reserve, *P. tomentella* and *S. leprosula*, have been examined in previous studies. Our description of *P. tomentella* is similar to that of Talip (2008), with the exception that she described values of mean polar length (P) and equatorial diameter (E) that were substantially greater than those we found: 55.75 μm (P) and 40.75 μm (E), respectively, compared to values of 26 μm (P) and 24 μm (E), respectively, for our samples. Talip's (2008) larger P and E measurements also lead to a larger P/E ratio, which implies a different shape class (prolate) whereas we found that *P. tomentella* pollen grains were mostly spheroidal. This disparity might be caused by inherent intraspecific variation in pollen size and shape, or it could have arisen because of different methodologies: Talip (2008) used pollen from herbarium specimens collected in 1960, whereas our study is based on fresh material. In addition, the use of acetolysis for preparation of pollen samples prior to examination by Talip (2008) may have increased pollen size relative to our pollen samples that were not acetolysed (Hesse & Waha, 1989). Alternatively size differences could be an artifact arising from measurement error: Talip's (2008) image (Fig. 1 (g)) of *P. tomentella* displays a 10 μm scale bar from which we estimate that equatorial diameter (E) should have been reported as about 23 μm and not the value of 40.75 μm actually quoted by Talip (2008). This re-assessment makes the values of equatorial diameter of *P. tomentella* pollen almost identical in Talip's (2008) study (23 μm) and ours (24 μm).

Ultimately, the cause of this discrepancy between the SEM images and the mean dimensions reported by Talip (2008) remains unknown, and further research is required to resolve the issue.

We found no previous description of the pollen of *S. multiflora* or *S. xanthophylla*. The basic outline, tricolpate structure, and microreticulate crotonoid patterning were similar for the two species. There was a significant difference in polar axis length between them (Kruskal-Wallis $\chi^2 = 13.9$, $df = 1$, $p < 0.001$), but no significant difference in equatorial diameter (Kruskal-Wallis $\chi^2 = 0.822$, $df = 1$, $p = 0.365$). The exine ornamentation was microreticulate crotonoid in both species. Similarly, the average size of the muri and lumina differed by only 0.01 μm and 0.02 μm , respectively. These similarities were anticipated because these species share similar floral and anther characteristics and belong to the same section *Richetioides* of *Shorea* and are therefore closely related.

We found only one published description of *S. leprosula* (Maury *et al.*, 1975), which detailed the shape as spherical and tricolpate, and with a circular equatorial outline. By contrast, we found pollen grains of *S. leprosula* to be subspheroidal in equatorial view and lobate triangular in polar view (Fig. 5). Maury *et al.* (1975) do not present an SEM image of *S. leprosula* pollen, but their LM images support their description and contrast with our

SEM images. In principle, the lobed shape of *S. leprosula* pollen grains in the SEM images of our study might have resulted from dehydration or collapse during sample preparation (Price & Ayers, 2008). Although we observed a similar lobed shape in images derived from LM, mature pollen grains change shape and volume after removal from the anther (Payne, 1972; Hesse, 2000) and these changes may account for the divergence in pollen morphology of *S. leprosula* between our study and Maury *et al.* (1975). Notwithstanding this caveat, it remains a possibility that pollen grains of *S. leprosula* display intraspecific variation in shape that would merit further study.

There are perceptible differences between the pollen morphology of *Parashorea tomentella* and the three *Shorea* species. There are also notable differences in outline and shape class between *S. leprosula* of section *Mutica* and the two species (*S. multiflora* & *S. xanthophylla*) of section *Richetioides*. However, in the absence of a broader survey of pollen morphology among the sections of *Shorea* and the genera of the Dipterocarpaceae, it is not possible to infer whether pollen identification based on shape and outline would be possible. Conversely, the pattern and dimensions of exine ornamentation were distinct among the four species in this study, except in the case of the two species of *Shorea* section *Richetioides*, and these traits might be used for distinguishing among these taxa. A broader review of dipterocarp pollen morphology (Maury *et al.*, 1975) found that pollen from related dipterocarp taxa shared similarities in exine ornamentation. We conclude that, despite the consistencies in pollen morphology amongst closely related species, pollen shape, size and exine ornamentation do not differ consistently among the genera of dipterocarps or the sections within the large genus *Shorea*. However, the association between the similarities in pollen morphology and relatedness suggests that pollen morphology may be phylogenetically constrained in the Dipterocarpaceae (Talip, 2008).

Pollen volume was relatively invariable within a species (CVs 9.8–12.2 %), but mean polar axis length differed among the species (Kruskal-Wallis $\chi^2 = 156$, $df = 3$, $P = < 0.001$). This difference in pollen volume was positively correlated to flower size ($R^2 = 0.92$, $P = 0.029$; Fig. 1). Similarly, although the relationship between pollen volume and flower size was not significant for the species examined by Talip (2008), the trend was positive but offset above the fitted line for the species we studied (Fig. 1). Müller (1979) also found a correspondence between pollen dimensions and flower size for the Dipterocarpaceae. A relationship between flower size and pollen size may be associated with a positive correlation between flower size and stigma depth and/or style length (Cruden, 2009; Ortega Olivencia *et al.*, 1997), although further work is required to examine these relationships within the Dipterocarpaceae.

CONCLUSIONS

The four species we examined could be grouped on the basis of exine ornamentation, which would allow us to distinguish between them except in the case of the two closely-related

species *S. multiflora* and *S. xanthophylla*. Our descriptions of the pollen size of *P. tomentella* and the shape and morphology of *S. leprosula* differ from previously published accounts, and we recommend that further research should be conducted to determine the cause of these differences. Finally, we found that pollen volume was positively correlated with flower size, across the four species we sampled, which corresponds to relationships inferred from larger data-sets. This relationship may have functional significance for dipterocarp reproductive biology and would be a worthy topic of future research.

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