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A TAXONOMIC REVISION OF PARANEPHELIUM (SAPINDACEAE)

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CONTENTS

SUMMARY

Paranephelium Miq. (Sapindaceae) is a small genus from Southeast Asia and West Malesia. In this revision four species are described, one of which is new.

INTRODUCTION

Paranephelium is a small genus in the Sapindaceae. It is placed in the pantropical tribe of the Cupanieae. Within this tribe, it is well delimited and recognisable by the fact that a true terminal leaflet is nearly always present. Furthermore, the seed is quite remarkable, resembling exactly the seed of the horsechestnut (*Aesculus*, Hippocastanaceae). This character it has in common with the closely allied genus *Amesiodendron*.

At the start of this investigation, the search for characters to separate species caused quite a problem. The flowers show no significant differences, in contrast with the fruits, in which a wide range of (wall) types can be distinguished. The monographer, Radlkofer (1931–33), based his whole system of the family primarily on fruits. Similarly, the eight species he distinguished in *Paranephelium* were mainly

based on different fruit wall types. This is particularly astonishing, when finding that, years before, he himself wrote the following about *Paranephelium* (1879: 80): 'Nach Analogie dessen, was die *Euphoria*- und *Xerospermum*-Arten zeigen, ist es sehr wohl möglich, dass die an der jungen Frucht ziemlich spitzen Fortsätze später sich verflachen.' (It is quite possible, that, like the *Euphoria*- and *Xerospermum*-species show, the sharp processes of the young fruits flatten later on.) I can fully agree with him in this matter. Unfortunately, he changed his mind later on. In his key of *Paranephelium*, Radlkofer (1933: 1322) used mainly the size and shape of the processes on the fruit wall to distinguish the species, even though he had mostly only immature fruits at his disposal.

Of the eight species Radlkofer described, I have kept three, based on vegetative characters. Besides, another still undescribed species appeared to occur in Borneo, collected in more recent time.

For this revision, I studied material from the herbaria CAL, FI, K, L, M, P, and SING.

I wish to express many thanks to my tutor, Dr. P.W. Leenhouts, for his patient and experienced guidance of my work.

PARANEPHELIUM

Paranephelium Miq., Sumatra (1861) 509; Radlk., Engl. Pflanzenr. 98 (1933) 1321–1326; non *Paranephelius* Poeppig & Endl., Nov. Gen. Sp. 3 (1843) 42, t. 248 (Compositae; see ICBN 75.1). – Type: *P. xestophyllum* Miq.

Mildea Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 88, nom. illeg.; non Griseb., Cat. Pl. Cub. (1866) 63 (Piperaceae). – Type: *M. xestophyllum* Miq. (= *P. xestophyllum*).

Scyphopetalum Hiern in Hook. f., Fl. Brit. India 1 (1875) 675. – Type: *S. ramiflorum* Hiern (= *P. xestophyllum*).

Small to medium-sized trees, sometimes shrubs. *Indumentum* on buds, young shoots and inflorescences, often still present on twigs (especially at branching points), axial parts of leaves and infructescences, yellow puberulous to tomentose, glabrescent; hairs solitary, simple; no glandular scales. *Twigs* terete, sometimes 5-grooved, corresponding with the lobed pith, smooth to verrucose with fine fissures, light yellow or grey brown to blackish redbrown, often with many small orbicular lenticels up to 1.5 mm in diam.; buds often two in the leaf-axil, mostly only the lower one developing. *Leaves* spirally arranged, impari- or sometimes paripinnate, 1–6-jugate, the leaflets accrescent in size towards the top, not stipulate, glabrous to hairy; petiole terete, at the base triangular thickened, wrinkled (until cracked) and hollowed above, not winged, finely ribbed to smooth, with few to many small lenticels; petiolules cylindrical to conical, variably grooved, at the base thickened, the petiolule of the terminal leaflet somewhat longer than those of the lateral leaflets, variably wrinkled. *Leaflets* (sub)opposite, mostly widest about, sometimes above the middle, especially so in the terminal leaflet or (rarely) the uppermost pair of leaflets, seldom beneath the middle (in the lowermost pair), thick papery ro coriaceous; margin entire to dentate; apex emarginate or rounded to caudate. *Nervation* open, midrib and nerves

raised to sunken above, beneath prominent; nerves either ending blindly, or when the margin is dentate each second one ending in a tooth. *Inflorescences* axillary, ramiflorous or (mostly pseudo)terminal, erect, thyrsoid, large, stout, woody and solitary to small, delicate, flexible and clustered together; the main axis with few branches, mainly at the base, to unbranched; branches oblique-erect, set with many dense several-flowered cymules, their number increasing to the top, several to many axes (of different orders) may form together a dense cluster of axes of about the same length; pedicels up to 3.5 mm long, 0.2–0.5 mm in diam.; bracts deltoid to linear, often persistent for a long time (even remaining in the infructescences); often bearing in the axil 2 serial buds, the lower of which developing into a flowering branch, the upper one sometimes developing into a cymule; bracteoles narrowly triangular, up to 1 mm. *Flowers* actinomorphic as a rule, 5-merous, functionally unisexual, ± regular, sometimes very irregular with different numbers of flower-parts; plant monoecious. *Calyx* (4–)5(–7)-merous, together with the large receptacle cup-shaped; sepals at the transition to the receptacle connate to free, aestivation apert or induplicate to quincuncial, ± persistent (in the infructescences), ± spreading after anthesis, equal to sometimes very unequal, broadly ovate to linear, flat to boat-shaped, entire, not petaloid, outside white to dark yellow pubescent to tomentose/velutinous, inside white sericeous, at the margin ciliate, glands absent. *Petals* (4–)5(–7), longer than sepals, aestivation apart, falling off quite late, still enlarging while the fruit develops, the plate variably shaped: obdeltoid, obtriangular, rhomboid, spatulate, ovate to half orbicular, sometimes nearly totally reduced, at the base slenderly unguiculate to broadly truncate, outside mostly glabrous to laxly woolly; petalar scale at base and lower margin adnate to the petal, larger to sometimes smaller than the petal, narrowly obtriangular to roundish, upper margin emarginate to medially divided into 2 separate lobes, upper (and side) margin erect to curved inwards, covering the disc entirely, ± undulate, both sides orange woolly, particularly at the upper margin. *Disc* composed of a flat ring but for the margin adnate to the receptacle and an erect rim to tubular collar up to 1 mm high (see fig. 3c), all thin fleshy and glabrous. *Stamens* 5–8(–9), ± free, exserted in male flowers, glabrous; filaments thread-like, red; staminodes reaching half their length; anthers attached at the base, rarely bearing sparse hairs, connective extremely narrow, dehiscence lateral. *Pistil:* ovary ± globular, sessile, 0.8–2 × 0.8–2 mm, densely set with tubercles, each tubercle bearing one thick erect hair up to 1 mm long, further glabrous to minutely hairy; (1 or 2) 3 (or 4) cells; style simple, apical on the connate pistil, longer than the ovary, 1–3.5 mm long and 0.3–0.5 mm in diam., laxly to densely short strigose; stigma flat to 1–4-lobed; lobes up to 1.5 mm long, erect to strongly curved backwards, densely set with short glandular hairs; pistillode 3-angled to conical, 0.5–1 × 0.5–1 mm, with or without a vestigial style, orange (stiff-)woolly. *Ovules* 1 per cell, on a knob at the thickened base of the central axis, ascending, epitropous. *Infructescences* strongly thickened and lignified, sometimes drooping, glabrous to tomentose. *Fruits* (see fig. 3d–g) capsular, (depressed-)globular, dehiscing either with 3 or 4 (unequal) valves, starting at the base, loculicidal, or irregularly tearing apart; fruit wall warty to densely spiny, ribbed or corrugated to smooth, outside glabrous to minutely hairy,

inside hairy, densely to loosely composed of radial woody fibres, wall (incl. spines if any) 2.5–12 mm thick; valves clearly separated by ridges to inconspicuous; top flat, sunken to bulging (composed of connate spines), sometimes protruding above the spines, sometimes still bearing the remainder of the style. *Seed* 1, sometimes a second one (vestigially) developed, horsechestnut-like, depressed-globular, ± slightly 2- or 3-lobed in accordance with the valves, 1.5–2.7 × 1.5–4 cm, no aril, attached with a short, thick, lignified funicle; testa a hard shell, 0.5–0.8 mm thick, thickened at the hilum, glossy dark to redbrown, often covered with the membranaceous remnants of the septae, on which the 2 (or 1) undeveloped ovules (see fig. 3i); hilum a large white spot covering up to ¾ of the surface of the testa (see fig. 3h); inner integument closely adhering to the embryo, coriaceous, forming a triangular pouch for the rootlet, 5–7 × 6–7 mm; rootlet ventral, slightly-bent; cotyledons ± equal, longitudinally superposed.

Distribution. Four species, from 25° N in Southeast Asia (Yunnan, Hainan, Burma) unto 5° S in West Malesia (Sumatra and Borneo), the most eastward found specimen on the Philippines (122° E), see figures 1 & 2. Radlkofer (1931: 16) mentions in his key *Paranephelium* from Celebes. He does not cite his source, nor does he confirm this statement later on in his treatment of the genus.

Ecology. Mainly trees of the lower canopy or higher understorey of the primary rain forest, mixed deciduous forest, or dry evergreen forest, especially in the moist part near streams, sometimes in secondary forest, rarely in scrub; typical of lowlands and the lower hillside; altitude 0–300(–700) m. Nothing is known about the dispersal of the seeds. In Borneo, the seeds are eaten by monkeys, possibly also by other mammals.

Uses. Economically the genus is not really important. The wood is merely good as firewood. The seeds are eaten, baked or cooked, and in the past the oil from the seeds was used as an illuminant; it is also used for skin complaints.

NOTES

Leaves

Although the main genus character is the presence of a terminal leaflet, there is only one species, *P. macrophyllum*, that hardly deviates from this rule. In the other species, paripinnate leaves are regularly found, though no collections were seen with exclusively paripinnate leaves. Remarkably, Gagnepain (1947: 165) calls the leaves of his new species *P. poilanei* 'paripenné', whereas among his syntypes, no paripinnate leaf has been found.

In two species, *P. xestophyllum* and *P. joannis*, the growth of the midrib seems to stop abruptly in very large leaflets, while the mesophyll is still developing; this causes a widely emarginate apex and towards the apex between the nerves bulging mesophyll.

Sex of the flowers and monoecism

The flowers are functionally unisexual, containing either a developed pistil and indehiscent staminodes or developed stamens and a small pistillode. Sometimes, both

organs are equally well developed, suggesting that the flower could be bisexual as well.

Most collections bear both male and female flowers, though some seem to bear flowers of one sex only. In the latter case dioecism may occur.

Flowers

In all species except *P. macrophyllum*, the flowers may show irregularities in number, size, and shape of sepals and petals. Only a few examples are given. Flowers occur, in which one or two of the sepal lobes are twice as big as the other lobes; one flower had a petal-like organ on the place of the fifth sepal. *Nooteboom 1317* shows a filiform hairy organ outside the disc alternating with the petals; this could be the initial of a petal, but not at the right place and wrongly grown. In an exceptional flower (*Poilane 20287*) the primordia of the organs seemed entirely mixed up, with for instance a vegetative bud replacing the pistil.

Gagnepain (1950: 972) incorrectly notes the filaments to be hairy and even indicates this in his drawings; he must have been misled by the local lengthwise detachment of the epidermis from the filaments or by loose hairs from the petals.

Fruits (see fig. 3d–g)

The arrival of new material from Borneo, *M. Leighton 59*, collected from the same tree with an interval of several months, has considerably contributed to the understanding of the development of the fruit.

From a very early stage on, the fruits are woody already, with a thick wall and a hard testa around the three small seeds. The wall is composed of very dense woody radial fibres and is densely covered with spines or bulbs. Finally, the surface may be smooth or laxly set with flattened spines or bulbs, or densely covered with stout spines when mature. It can hardly be stressed enough that different wall types even can be found within one collection.

The valves can be about equal in size, which is remarkable as in the whole fruit only one seed matures. The fruit opens either by dehiscence of the valves, or at random, or by a complete desintegration, the woody fibres loosing their structure and falling apart.

There seems to be some contradiction between Radlkofer's inclusion of *Paranephelium* in his tribe Cupanieae, which is characterised by fruits opening with valves, and the fact that the dehiscence may also be irregular. An irregular dehiscence characterises Radlkofer's Nephelieae. Muller & Leenhouts (1976: 418– 419) suggested a close connection between the Cupanieae and the Nephelieae.

In the description, only sizes of mature (that is, dehiscent) fruits have been given. Unfortunately, most fruits collected are immature.

Miquel (1861: 509) described an aril around the seed. This aril turned out to be the enlarged hilum with the membranaceous remnants of the septae.

Amesiodendron Hu

Amesiodendron is the genus most closely allied to *Paranephelium* in which genus it was at first described. It is monotypic, the only species being *A. chinense* (of which *A. integrifoliatum* and *A. tienlinensis* probably are synonyms).

The most striking resemblances between the two genera are in the seed and in the flowers. Still, the two genera differ sufficiently to keep them separate. The main points in which *Amesiodendron* differs from *Paranephelium* are as follows:

Leaves paripinnate, leaflets not accrescent in size towards the top; petiolule slender and short, up to 8 mm long. Leaflets small, always narrowly elliptic (3.5–4 times as long as wide); margin serrate; veins and veinlets very conspicuous. Inflorescences stout, even the branching in the cymules. Flowers relatively small; disc smaller than 1.5 mm in diam.; filaments hairy; ovary 3-lobed, without tubercles, shortly haired. Fruits globular (if one seed is developed) plus 2 bumps (being the suppressed lobes), bilobed plus 1 bump if 2 seeds are developed; fruit wall knotted and dark coloured, not woody when immature, smooth and light coloured, woody when mature.

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KEY TO THE SPECIES OF PARANEPHELIUM

1a. Margin of the leaflets dentate 2
b. Margin of the leaflets entire 3
2a. Midrib of the leaflets above visible ..... **1. P. spirei**
b. Midrib of the leaflets above entirely sunken, invisible .... **2. P. macrophyllum**
3a. Nerves straight, abruptly curving near the margin; veins densely scalariform (cf. fig. 3a) (leaflets up to 52 × 22 cm), if leaflets large, with petiolules at least 4 mm in diam., the veins may become more lax; inflorescences stout, at least 20 cm long ..... **3. P. joannis**
b. Nerves curving gradually; veins laxly reticulate (cf. fig. 3b) (outside Borneo sometimes scalariform; leaflets up to 42 × 14 cm), petiolules up to 4 mm in diam., inflorescences delicate, up to 20 cm (outside Borneo up to 30 cm) **4. P. xestophyllum**

1. Paranephelium spirei Lecomte

P. spirei Lecomte, Notul. Syst. 2 (1911) 6; Fl. Gén. Indo-Chine 1 (1912) 1026; Radlk., Engl. Pflanzenr. 98 (1933) 1326; Gagnep., Fl. Gén. Indo-Chine Suppl. 1 (1950) 972; How & Ho, Acta Phytotax. Sin. 3 (1955) 400. – Type: *Spire 1158* (P), Laos (Indochine): Cahn trap, fl.
P. hainanense Lo in Anon., Fl. Hainan 3 (1974) 89, 575, f. 587. – Type: *Wang 45007* (not seen), Hainan, Yaxian.

Tree, up to 25 m high, 20–30 cm in d.b.h., rarely a shrub. *Indumentum* often still present on twigs, axial parts of leaves and infructescences, tomentose to pubescent. *Twigs* 3.5–7.5 mm in diam., smooth, light to dark brown, often dark yellow, laxly tomentose. *Leaves* 2–4-jugate, mostly tomentose on the base of the petiole, rachis and petiolules, sometimes midrib above and beneath, and nerves beneath minutely hairy; petiole 1.6–11 cm long, 1.5–3 mm in diam., petiolules 1–18(–25) mm long, 1–2.5 mm in diam. *Leaflets* 5–34 × 2–14.5 cm, 2–3.7 times as long as wide, widest about the middle, thick papery, surface flat to bulging; base symmetrical to slightly asymmetrical, cuneate, acute to obtuse–rounded-attenuate; margin (sometimes weakly) dentate, a tooth up to 6 mm long; apex acuminate, cuspidate to strongly caudate (acumen up to 4 cm long), often rounded in the terminal leaflet. *Nervation:* above midrib and nerves raised (in a furrow) to flat; nerves at an angle to midrib of 55–75°, 5–25 mm distant, gradually curving, sometimes curving abruptly near the margin, every 2nd one ending in a tooth; veins laxly to densely reticulate, sometimes laxly scalariform. *Inflorescences* axillary to terminal, mostly a stout branched axis, rarely clustered, 8–28 cm long, densely hairy; branches up to 16 cm, bracts up to 5 mm. *Flowers* mostly regular. *Sepals* 5(–7), at the receptacle connate to sometimes free, aestivation quincuncial to induplicate, opening very early, equal or sometimes unequal, narrowly triangular, linear, or broadly ovate to elliptic, acute to rounded, 1.2–2 × 0.5–1.8 mm. *Petals* 5, variably shaped, 1.2–2 × 0.8–1.7 mm, outside laxly woolly to sometimes glabrous; petalar scale sometimes adnate to the petal except for the upper margin, emarginate to divided into 2 separate lobes, 1.5–2.5 × 1–2 mm. *Disc* up to 0.7 mm high, 2–3 mm in diam., erect rim sometimes absent. *Stamens* 7 or 8, filament up to 4.2 mm long. *Pistil:* (1) 2 or 3 cells. *Infructescences* mostly single, bearing up to 6 fruits, glabrous to laxly velutinous. *Fruits* 2.5–4 × 3–4.3 cm; fruit wall densely to laxly spiny, spines slender-conical or pyramidal to broadly ovate, curved to straight, acute and mucronate, glabrous to minutely hairy; top flat to a protruding rounded swelling.

Field notes. Bole may be coppicing or shortly fluted. Bark smooth to rugulose, not dippled nor reddish (like a *Pometia*); inner bark firm, hard lamellate; wood hard and dense, but said to be attacked by termites. Leaves all green. Flowers strongly scented, white to yellow. Fruits dull brown to brownish black.

Distribution. China (Hainan), Indochina (Laos, Vietnam) and the Malay Peninsula. Fig. 1.

CHINA. Hainan. How 70602, 70746, Yaichow; Lau 584, Wong Kam Shan, Ngai Dist. INDOCHINA. Laos. Spire 1158, Cahn trap, type of *P. spirei*. – Vietnam. 9 collections. MALAY PENINSULA. Peninsular Thailand. Sangkhachand 110 = BKF 32388, Narathiwat; Santisuk & B. N. 362 (BKF), Banang Sata, Than To Waterfall; Smitinand 10999 = BKF 46662, Pen Yala, Than To. – Perlis. Ridley 15108, Chupung. – Perak. KEP/FRI 15810, Hulu Perak, K. Tiang, Jeram Benuas.

Ecology. In evergreen forest or sometimes in thicket, often along rivers, also recorded from moist gentle slopes; soil clay, loam, or rocky sand; alt. 100–500 m. Recorded fl. in March and May, fr. mainly in May–July, though also in other months.

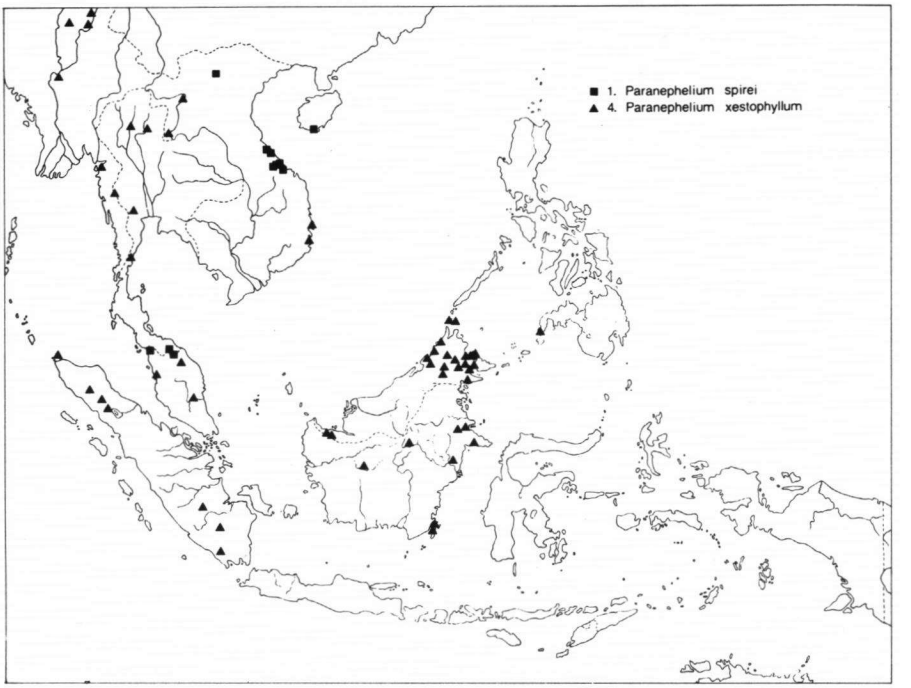

Fig. 1. Range of *Paranephelium spirei* Lecomte and *P. xestophyllum* Miq.

Uses. The seed may be eaten.

Note. The slight disjunction in the distribution area is paralleled by some minor morphological differences. In Indochina, twigs and leaves are much more hairy and the apex of the terminal leaflet is much shorter than in the Malay Peninsula.

2. Paranephelium macrophyllum King

P. macrophyllum King, J. As. Soc. Beng. 65, ii (1896) 450; Ridley, Fl. Mal. Pen. 1 (1922) 509; Craib, Fl. Siam. En. 1 (1926) 334; Radlk., Engl. Pflanzenr. 98 (1933) 1323; Corner, Wayside Trees (1952) 594, f. 211; Keng, Malayan Seed Plants (1969) f. 118. – Lectotype (present author): *King's coll. 7027* (CAL, not seen; iso K, L, M), Malacca, Perak, on limestone rocks near G. Bujong Malaka, I-1885.

Tree, sometimes shrub, 4.5–12 m high, 10–40(–60) cm in d.b.h. *Indumentum* on buds, young shoots and inflorescences, tomentose. *Twigs* 10–15 mm in diam., light to dark brown. *Leaves* 3–5-jugate, glabrous or sometimes midrib beneath sparsely hairy; petiole 11.5–20 cm long, 3–6 mm in diam.; petiolules 5–17(–27) mm long, 1.5–4 mm in diam. *Leaflets* 6–32 × 3–13 cm, 1.3–3.3 times as long as wide, widest about the middle, thick pergamentaceous, surface often bulging between the nerves; base symmetrical to asymmetrical, cuneate, especially in the terminal leaflet,

to rounded, sometimes slightly attenuate; margin dentate, a tooth up to 4 mm long; apex emarginate to rounded, sometimes ± abruptly short-acuminate, mucronate or not. *Nervation:* above midrib and nerves deeply sunken, midrib invisible; nerves at an angle to midrib from 90° at the base, to 65–80° in the central part of the leaf, and 45° at the apex, 5–26 mm distant, straight to slightly curved, ± abruptly curving near the margin, every 2nd one ending in a tooth; venation lax, reticulate to scalariform, ± inconspicuous. *Inflorescences* axillary to sometimes terminal, stout, often single, 25–60 cm, tomentose; branches up to 40 cm; bracts up to 15 mm. *Flowers* regular. *Sepals* 5, at the receptacle connate, aestivation quincuncial, opening relatively late, equal, deltoid to broadly ovate, acute, 1.0–2.1 × 1.2–2.3 mm. *Petals* 5, obtriangular to roundish, 1.0–2.0 × 0.8–1.8 mm, outside glabrous; petalar scale lobed to emarginate, 1.0–2.0 × 1.5–3.3 mm. *Disc* up to 1 mm high, 2–3 mm in diam. *Stamens* 7 or 8, filament up to 3.5 mm long. *Pistil:* 3 (or 4) cells. *Infructescences* bearing up to 16 fruits, up to 6 per branch; glabrous. *Fruits* 2–3 × 2.5–3.7 cm, densely spiny, the spines slender conical, curved, sharp pointed, glabrous; top flat to protruding.

Field notes. Erect tree to a weak flopping shrub, bole erect or slightly slanting, scarcely to strongly branched, the branches spreading. Bark smooth, greenish grey to pale greyish brown; inner bark light red; wood white. Twigs reddish brown. Leaflets drooping, rather hard, leathery, glossy, dark to light green above, paler beneath, young leaves bright pink to red, with the edge almost spiny, strongly ribbed by the numerous veins. Inflorescences pinkish to reddish. Flowers fragrant; sepals cherry pink or light crimson to red; petals pink to white, petalar scale (bright) yellow hairy; stamens white to red; ovary and style crimson; said to be a splendid looking tree when in full flower. Fruit greyish brown, silvery grey, rich red towards the centre, to red (immature).

Distribution. Malay Peninsula. Fig. 2.

MALAY PENINSULA. Peninsular Thailand. 5 collections. – Kedah. Bell & Haniff s.n. (K), Kedah Peak, Sunling. – Perak. 17 collections.

Cultivated at Bogor (Indonesia, Java: Botanic Garden, III.J.25), at Ceylon (Peradeniya Gardens, De Silva 96, 111), at Leiden (Netherlands: Botanic Garden, Leenhouts 1947), and at Singapore (Malay Peninsula: Botanic Gardens, Sappi bin Hassan SF 18184).

Doubtful:

MALAY PENINSULA. Perak. Cantley's coll. 50 (SING), Lambasu Bukit.

Ecology. In open, secondary forest and evergreen scrub, along rivers, in plains, less frequently on a cliff or the top of a hill, on rocky localities; soil rich, often on limestone; alt. 0–300 m. Fl. in two periods, March–April and July–Sept. and fr. in July and Oct.–Feb.(–April).

Uses. The oil of the seed is used as lighting oil and skin oil.

Notes. Corner (1952) notes the following about the species: 'The striking small tree much resembles a sapling Kasai (*Pometia*) in its flushes of reddish pink leaves with toothed, ribbed leaflets, but the flopping habit, smaller number of leaflets and absence of stipule-like leaflets at the base of the leafstalk will easily distinguish it when sterile. Formerly, it was much grown in villages in the North of the country, because the oil from the large seed was used as an illuminant in lamps, but with the

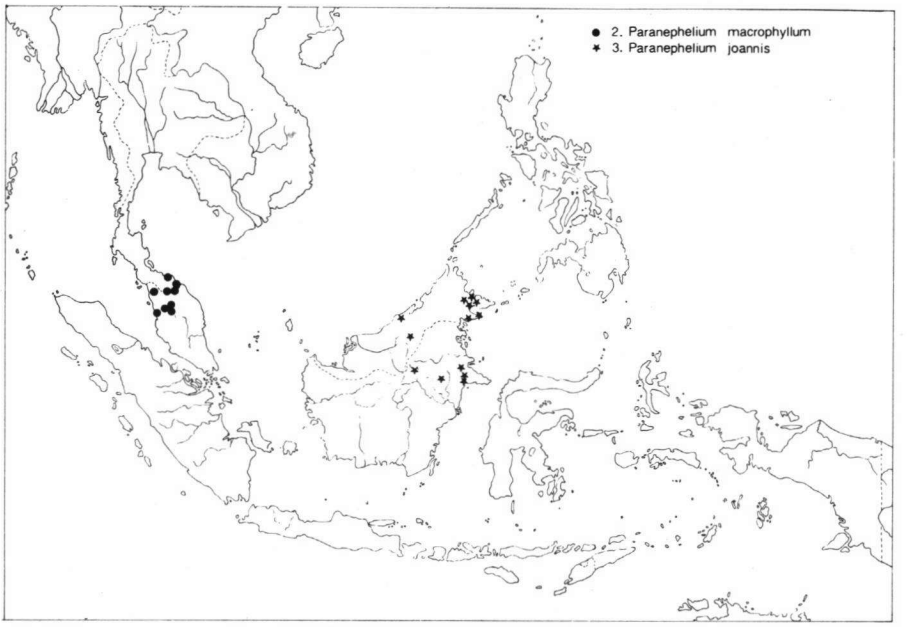

Fig. 2. Range of *Paranephelium macrophyllum* King and *P. joannis* M. Davids.

advent of kerosene, the plant has become little else than a weed and is not likely to be met with except in Perak. The oil of the seed is also used for skin complaints.'

The collection *Leenhouts 1947* is a seedling being clearly *P. macrophyllum*, but the leaflets are more slender with a cuspidate apex, and the leaves are 1- or 2-jugate with a slender petiole (1.5 mm in diam.).

The collection *Cantley's coll. 50* looks like *P. macrophyllum*, but differs in an apparently constant character: the midrib of the leaflets is visible above. Other differences are in the indumentum, which is much denser and is also found on the twigs, petiole, petiolules and leaflets (midrib and nerves beneath), all parts are often relatively small, and the leaves are 2–4-jugate.

3. Paranephelium joannis M. Davids, *spec. nov.* – Fig. 3a.

Descriptio typi: Arbor 20 m alta, 35 cm crassa. *Indumentum* usque praesens in ramulis, partibus axialibus foliarum et in inflorecentils, flavum (sparse) tomentosum. *Ramuli* 6 mm in diam., puberuli. *Folia* 2-jugata, tomentosa in rhachi, petiolulis et foliolis (inferiore parte in costa nervisque, superiore parte in costa); petiolus 11–15 cm longus, 2.5–4 mm in diam.; petioluli 6–8 mm longi, 2–4.5 mm in diam. *Foliola* 10–28 × 4.7–9.5 cm, ratione 2–2.9, medio latissima, coriacea, superficiei planae, supra infraque nitida; basis aequilateralis, acuta ac cuneata; margo integer; apex admittens non descriptionem, laesus; supra: costa prominens in fossula, nervi plani vel prominuli, infra: costa nervique maxime prominentes; nervi 6–15 mm distantes, angula ad costam 60–70°, linea recta abeuntes ab costa, incurvantes subito prope marginem, venae dense

scalariformae. *Inflorescentiae* axillares ac solitariae vel terminales ac fasciformae; rhachis circa 20 cm longa, dense tomentosa; bracteae ad 3 mm longae. *Flores* regulares. *Sepala* 5, aestivatione quincunciali, se aperientes satis tarde, deltoidi; apex mucronatus, 0.8–1.8 × 1.1–1.6 mm. *Petala* 5; lamina parva, 0.2–1 × 0.2–0.7 mm, exteriore parte saepe pilosa, squama undulata, 1.5–2 × 1.5–2 mm. *Discus* 2.5–3 mm in diam. *Stamina* 7 vel 8; filamentum ad 4.5 mm longum. *Pistillum* 3-loculare. Fructus absentes. – Typus: *F.H. Endert 3460* (L), Central East Borneo, W. Koetai, no 36, near L. Petah, 20-IX-1925, fl.

Tree, sometimes shrub, 6–24 m high and 10–40(–60) cm d.b.h. *Indumentum* still present on twigs, axial parts of leaves and infructescences, tomentose. *Twigs* 6–13 mm in diam. *Leaves* 2- or 3-jugate, (laxly) tomentose, glabrescent on the petiole, rachis, petiolules, leaflets beneath: midrib, often nerves, rarely veins and veinlets, leaflets above: midrib; petiole 8–25 cm long, 3–7 mm in diam.; petiolules 7–22 mm long, 1–8 mm in diam. *Leaflets* 10–51 × 4–22 cm, 1.7–3.7 times as long as wide, widest above (mostly) or about the middle, coriaceous, surface entirely flat to bulging between the nerves; base symmetrical to asymmetrical, acute; margin entire; apex emarginate to rounded, mucronate or not, acute to cuspidate, when dried mostly damaged. *Nervation:* above midrib (slightly) raised in a furrow (always visible), nerves sunken to slightly raised; angle to midrib 45–80°, 6–25 mm distant, straight to slightly curved, abruptly curving near the margin; veins densely to in very large leaflets laxly scalariform. *Inflorescences* axillary to terminal, stout and often clustered, 20–38 cm long, densely yellow tomentose to strigose; branches up to 36 cm; bracts up to 8 mm. *Flowers* regular or sometimes irregular. *Sepals* 5 or 6 (in case of 6, very unequal), at the receptacle connate, aestivation quincuncial, opening relatively late, deltoid to ovate, acute to mucronate, 0.8–2.3 × 0.6–1.8 mm. *Petals* 5, plate small to absent (in the latter case, mind the scale), narrowly spatulate, a little lobe above the claw to invisible, 0–1.7 × 0–1.0 mm, outside glabrous to pilose; petalar scale lobed, 1.5–2.1 × 0.9–2.0 mm. *Disc* up to 1 mm high, 2.5–3.5 mm in diam. *Stamens* 7 or 8, filament 2–4.5 mm long. *Pistil:* 3 cells. *Infructescences* with up to 6 fruits. *Fruits* 2.5–4 × 3.5–4.5 cm, laxly to densely spiny, the spines slender conical or pyramidal to ± rounded mucronate tubercles with slender spines in between, glabrous to densely short-strigose; top flat to a protruding rounded bulge.

Field notes. Bole straight, sometimes with buttresses up to 1.5 m high, or with stilt roots. Bark smooth, grey to brown, sometimes green or whitish, soft to hard, up to 1 cm thick, fibrous; sapwood pale, whitish to yellowish brown, hard. Flowers sweetly fragrant, white, in bud grey white. Fruit yellowish, (pale to greenish) brown, red to black.

Distribution. Borneo. Fig. 2.

BORNEO. Sarawak. Chew Wee Lek 1053, Baram Dist., Sungei Melinau, 4°03′ N, 114°50′ E; Sarawak For. Dept. S 23473, Ulu Dapoi, Tinjar, Marudi, 4th Div. – Northeast Kalimantan. 7 collections. – Sabah. 9 collections.

Ecology. In primary (dipterocarp) forest, often on river banks, low, sometimes on slopes; soil alluvial, clay or sand, on sandstone or limestone; alt. 0–300(–450) m. Fl. in two periods a year, March–April and August–Sept., fr. periods July–Nov. and Jan.–Feb.

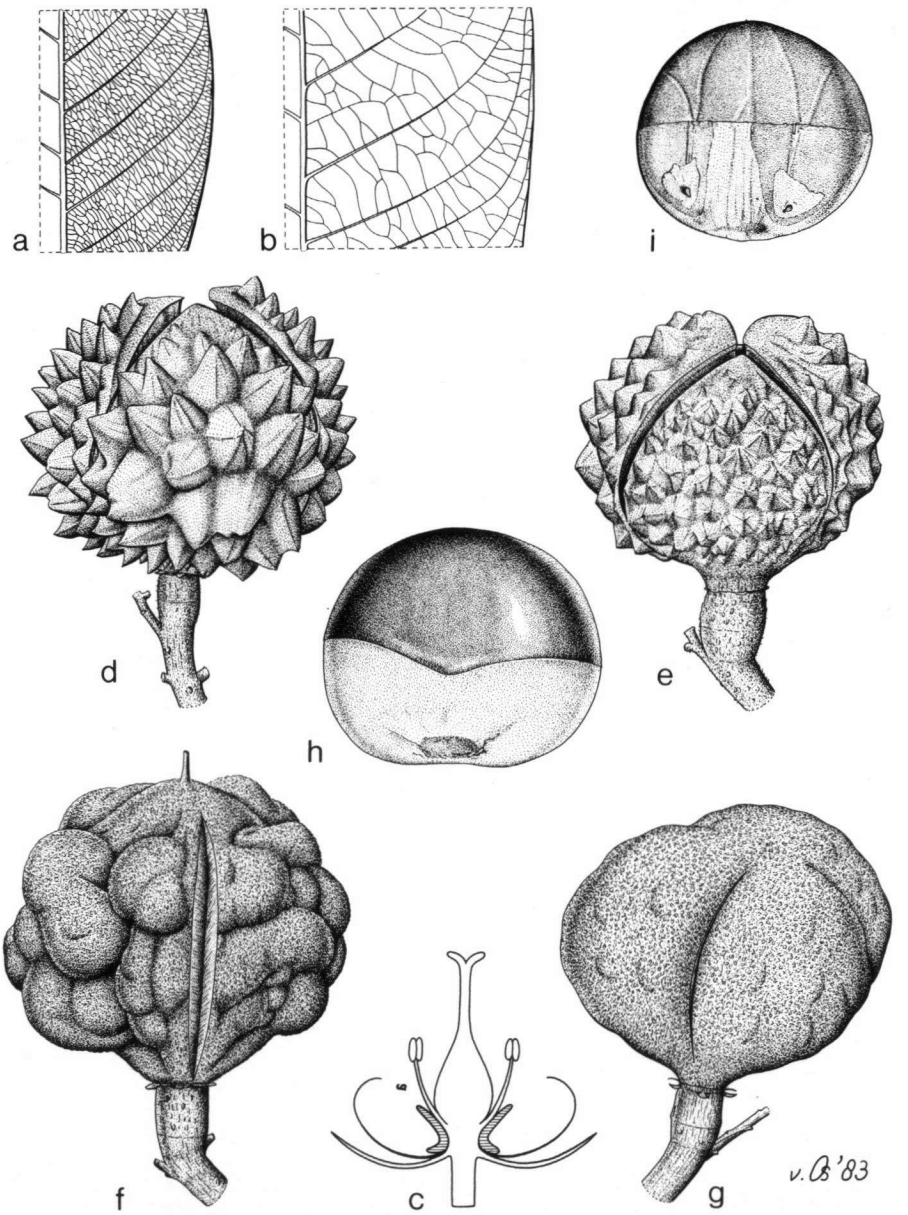

Fig. 3. *Paranephelium joannis* M. Davids. a. Nervature, x ½. — *P. xestophyllum* Miq. b. Nervature, x ½; c. schematical longitudinal section of flower with the disc hatched; d–g. fruits; h. seed with the large white hilum; i. seed with the appressed remnants of the septae and the undeveloped ovules, all x 1½ (a. *Chew Wee Lek 1053*; b. *Kostermans 21141*; d. *Bogor Bot. Gard. III.J.26*; e, h. *Boerlage s.n.* in L 908.270-13/14/15; f. *Kostermans 13238*; g. *SAN 79936*; i. *Soepadmo 853*).

Uses. The seed is edible when cooked.

Notes. Joannes is the Christian name of my father, J.A.G. Davids, after whom I wish to name this new species. He is a biologist, though in a field slightly different from botany, viz. radiobiology.

Paranephelium joannis, endemic to Borneo, can easily be separated from the Bornean (and Sumatran) material of *P. xestophyllum* on the characters used in the key. However, the area of *P. xestophyllum* is much wider, correlated with a wider range of variation, and especially in the northern part of its continental Asian area, some character or other may become less clearly different: the petiolules may be longer, the venation may tend to be vaguely and laxly scalariform, and the inflorescences may be bigger. Still, in practice the two species can be separated easily.

4. Paranephelium xestophyllum Miq. – Fig. 3b–i.

P. xestophyllum Miq., Sumatra (1861) 198, 509; Kurz, For. Fl. Burma (1877) 286; Radlk., Sapind. Holl.-Ind. (1879) 80; Pierre, Fl. Cochinchine fasc. 21 (1895) 327A; Brandis, Indian Trees (1906) 187; Merr., Enum. Philip. Fl. Pl. 2 (1923) 514; Radlk., Engl. Pflanzenr. 98 (1933) 1324. – *Mildea xestophylla* Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 89, comb. illeg. – Lectotype (present author): *Teysmann 4218 HB* (L; iso K), Sumatra, Prov. Lampongs, M. Gunungbatin.

P. gibbosum Teysm. & Binnend., Natuurk. Tijdschr. Ned.-Indië 29 (1866) 254; Radlk., Sapind. Holl.-Ind. (1879) 29, 79, 80; Engl. Pflanzenr. 98 (1933) 1325. – *Mildea gibbosa* Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 89, t. 5: A, comb. illeg. – Type: *Teysmann & Binnendijk s.n. (herb. J. Kurz)* (BO, not seen; iso FI, M), W. Sumatra, Loeboe Aloeng, fl.

Scyphopetalum ramiflorum Hiern in Hook.f., Fl. Brit. India 1 (1875) 675; Kurz, J. As. Soc. Beng. 44, ii (1876) 188; Radlk., Sapind. Holl.-Ind. (1879) 29. – Type: *Griffith 985* (K), Burma, 3-II-1837, fl.

P. nitidum King, J. As. Soc. Beng. 65, ii (1896) 450; Ridley, Fl. Mal. Pen. 1 (1922) 509; Radlk., Engl. Pflanzenr. 98 (1933) 1326. – Syntypes: *King's coll. 7416*, Malay Peninsula, rocky locality near G. Bubu, III-1885, fl.; *7410* (= *7710*?), Malay Peninsula, Larut, Cugunong Boobo Range, IV-1885, fr. (both K, M, SING).

P. hystrix W.W. Smith, Rec. Bot. Surv. India 4 (1911) 275; Radlk., Engl. Pflanzenr. 98 (1933) 1323; Lo & Chen, Acta Phytotax. Sin. 17 (2) (1979) 37. – Syntypes: *Rodger 4, Cubitt 638* (both not seen) and *Lace 5177* (K), Burma, Muyitkyina Dist., Nammun & Namma, 7-III-1910, fl.

P. longifoliolatum Lecomte, Notul. Syst. 2 (1911) 7; Fl. Gén. Indo-Chine 1 (1912) 1027, f. 131: 8, p. 1048; Craib, Fl. Siam. En. 1 (1926) 334; Radlk., Engl. Pflanzenr. 98 (1933) 1323; Gagnep., Fl. Gén. Indo-Chine Suppl. 1 (1950) 974. – Type: *Thorel s.n.* (P; iso M), (Laos) Vietnam: Expédition du Me-Kong, B. Paklaï, 1866–1868, fl.

P. acanthocarpum Radlk. ex Koord.-Schum., Syst. Verz. 2 (1914) 61; Radlk., Feddes Repert. 18 (1922) 344; Engl. Pflanzenr. 98 (1933) 1324. – *Sapindacea sp. A* Koord.-Schum., Syst. Verz. 2 (1910) 5. – Type: *Koorders 10515* (M; iso L), Sumatra, Atjeh, P. Beras, 6-II-1890, fr.

Nephelium forbesii E.G. Baker, J. Bot. 62, Suppl. (1924) 25; Radlk., Engl. Pflanzenr. 98 (1933) 982. – Type: *Forbes 1592* (BM, not seen; iso FI, K, L, P, SING), Sumatra, hill north of G. Trang, Lampongs, 1881, fl.

Pometia forbesii E.G. Baker, J. Bot. 62, Suppl. (1924) 26; Radlk., Engl. Pflanzenr. 98 (1932) 936; Jacobs, Reinwardtia 6 (1962) 141. – Type: *Forbes 2825* (BM, not seen; iso L), Sumatra, Tandjong Ning, R. Bliti, Palembang, 1881, fl.

P. poilanei Gagnep., Notul. Syst. 13 (1947) 65; Fl. Gén. Indo-Chine Suppl. 1 (1950) 973, f. 123: 1–7. – Syntypes: *Evrard 611* (K, P), Vietnam (Annam), Song Cay près Nhatrang, 18-VII-1921, fr.; *Poilane 6689* resp. *6771* (K, P resp. P), Annam, Massif de la Mère et l'Enfant, Prov. Nhatrang, 24-V-1923, fl.; *Poilane 17940* (P), Annam, reçu le 13-I-1931, fr.

Tree, sometimes shrub, (3–)10–20(–40) m high, 10–45(–75) cm in d.b.h. *Indumentum* mostly still present on twigs, axial part of leaves and infructescences (except on the fruit), puberulous to sometimes tomentose. *Twigs* 3–10 mm in diam., mostly light brown, minutely laxly hairy to glabrous, sometimes up to dark yellow tomentose. *Leaves* 1–6-jugate, minutely hairy in the axial parts; ± densely so on the petiole (especially the base), rachis, petiolules, midrib above and beneath (mainly at the base), sometimes on the nerves beneath; petiole 0.8–17 cm long, 1–4 mm in diam.; petiolules 1–20 mm long, 0.8–4 mm in diam. *Leaflets* mostly opposite or nearly so, 3–42 × 1.1–14 cm, 1.4–5 times as long as wide, widest about or (in the lowermost pair) seldom beneath the middle, thick papery, surface ± flat; base in the lowermost pair sometimes strongly asymmetrical, (narrowly) cuneate to obtuse, attenuate or not; margin entire, sometimes ± undulate, apex acute to rounded, acuminate or not. *Nervation:* above midrib ± raised (in a furrow) to slightly prominent, nerves sunken or flat to slightly raised in a furrow; nerves at an angle to midrib of 45–75°, 3–40 mm distant, first straight to curving, near the margin stronger curving; veins ± laxly reticulate to (laxly) scalariform. *Inflorescences* mostly ramiflorous, sometimes axillary to terminal, delicate and clustered, 2–29 cm, laxly to densely velutinous and hispid; branches up to 17 cm; bracts up to 7 mm, sometimes 3–5-forked as a leaf primordium. *Flowers* mostly regular. *Sepals* (4–)5(–6), at the receptacle connate to free, aestivation apert or induplicate to quincuncial, opening very early, mutually equal to very unequal, deltoid or narrowly triangular to broadly ovate, sometimes linear, acute to acuminate, sometimes 2-tipped, 0.8–2 × 0.5–1.8 mm. *Petals* (4 or) 5(–7), variably shaped, 1–2.5 × 0.7–2.7 mm, outside glabrous, rarely woolly; petalar scale sometimes emarginate to divided into 2 lobes, 1.1–2.2 × 1.2–3.0 mm. *Disc* 0.7–1.5 mm high, 1.0–2.8 mm in diam., sometimes at the base a few hair tufts alternating with the petals. *Stamens* 5–8 (rarely 9), filament up to 4 mm long. *Pistil:* (2) 3 (4) cells. *Infructescences* mostly consisting of a short and simple axis only, sometimes branched, erect or drooping, bearing mostly one, but up to 6 fruits, glabrous to minutely hairy. *Fruits* 2.3–3.2 × 3.0–3.8 cm, ± 2- or 3-lobed; smooth or laxly to densely ± irregularly gibbose, warty to spiny, glabrous; top flat, sunken to bulging.

Field notes. Bole straight, sometimes bending, with bumps and grooves, often with stilt roots up to 60 cm, or with buttresses up to 70 cm high. Bark smooth, with lenticels, finely fissured, or scaly; whitish, grey, dirty yellow, green to dark brown, hard to soft, 1–5 mm thick; inner bark orange-red outside, white, pinkish, yellow, finally orange-red to brown inside, laminated to fibrous, brittle, 4–5 mm thick; cambium pale, yellow, red to brown; sapwood white to yellow, hard. Leaves glossy dark to bright green, hard. Flowers fragrant or not much scented, white or greenish white to yellowish, calyx white with pink, corolla white. Fruits brown, yellow to grey, taste a bit astringent.

Distribution. China (Yunnan), Burma, Thailand, Indochina (Laos, Annam), Malay Peninsula, Sumatra, Borneo, and the Philippines (Mindanao). Fig. 1.

CHINA. Yunnan. Ying Yang: Pei 12254; Tao 13217, both not seen, see Lo & Chen, Acta Phytotax. Sin. 17 (2) (1979) 37.

BURMA. 7 collections.

THAILAND. 8 collections.

INDOCHINA. Laos. Poilane 20287, Phou-Phung, Prov. Luang-Prabang. – Annam. 4 collections.

MALAY PENINSULA. Perak. 4 collections. – Kelantan. Chin 1426, Gua Musang. – Pahang. KEP/FRI 14345, Taman Negara Exp.; Soepadmo 853, Bk. Tersik, Taman Negara.

SUMATRA. Atjeh. 9 collections. – Tapanuli. Junghuhn 14, S. Hochankola. – Westcoast. Teysmann & Binnendijk s.n. (FI, M), Loeboe Aloeng, type of *P. gibbosum* and paratype of *P. xestophyllum*. – Eastcoast. Yates 1357. – Palembang. 6 collections. – Lampong Dist. 7 collections.

BORNEO. Sarawak. Jacobs 5152, 1st Div., Passage of Sungei Serin (30 miles S of Kuching) c. 1°10′ N, 110°20′ E; Sarawak For. Dept. S 31634, Bukit Krian, Bau Limestone Hills. – West Kalimantan. nn 28109, Melawi, B. Kelawai deras. – P. Laut. bb 12915, Bekatan, Sci Paring Boschproefstation; Verhoef 82, Bakatan, Bovenkamp Sci Paring; van Slooten 2275, NE of Stagen. – Northeast Kalimantan. 7 collections. – Sabah. 46 collections.

PHILIPPINES. Mindanao. Williams 2361, Dist. of Zamboanga, Sax River.

Cultivated at Bogor (Indonesia, Java: Botanic Garden, III.8.10, III.J.26, III.J.30a, III.J.34a, III.J.38, III.I.41) and at Leiden (Netherlands, Leiden Botanic Garden, grown from seeds received from Hort. Bot. Bogor, Leenhouts 1962).

Ecology. Mainly in the primary rain forest, a tree of the lower canopy or higher understorey, also in mixed deciduous, dry evergreen, partly secondary or disturbed forest, rarely in (seasonal) swamp; often along rivers in shaded riparian forest, on the occasionally flooded flat area, also on (gently sloping) hillsides, rarely on dry ridges or summits; typical of wetter soils, alluvial clay, red-yellow podzolic, sandy or igneous derived soils, mostly over limestone, sometimes over sandstone; alt. 0–300 (–700) m, once found at 1100 m. Fl. and fr. nearly the year round, but mainly fl. in Feb.–July and fr. in May–Sept. In Borneo, the fruit is eaten by proboscis monkeys (M. Leighton, personal comm.).

Uses. The wood is seldom used for timber, though it is good as firewood. The seeds yield a lighting oil and are eaten, baked or cooked, tasting, according to a Malay templekeeper, like the Chinese waterchestnut, though they would be containing a drug: 'Too much causes giddyness.'

Notes. *Stamens:* The number of the stamens varies with the island; in Sumatra it is always 5 or 6, in Borneo 7 or 8, rarely 6, and in the Malay Peninsula it is 5 or 6, rarely 8.

Leaflets: Two collections (*Evrard 611, Poilane 6689*) have very faint dentations at the margin of the leaflets. However, the resemblance to *P. xestophyllum* is too great to place these two in *P. spirei.*

Fruits: The swellings on the fruit wall are very variable; they might be uneven and rounded, broadly ovate, pyramidal to slender conical, curved to straight, obtuse, acute or mucronate. Collections bearing both spines and bulbs are: Borneo: *Castro & Melegrito 1564, Verhoef 82*; Sumatra: *bb 22405, Junghuhn 14* (see fig. 3d–g).

Distribution: This is a complex, greatly variable species. In the everwet area, Sumatra, the Malay Peninsula, and Borneo, it is quite homogeneous (with some exceptions in the Malay Peninsula), but further on northwards, in the seasonal monsoon climate region, in general the number of leaflet pairs tends to increase, the hairiness increases, the inflorescences become stouter, and the fruits become mainly prickly.

The find of *P. xestophyllum* in China does not add much to the distribution area: Ying Yang is just across the border with Muyitkina in N. Burma (*Lace 5177*).

EXCLUDED TAXA

Paranephelium chinense Merr., Lingnan Sci. J. 14 (1935) 30, f. 10, = **Amesiodendron chinense** Hu, Bull. Fan Mem. Inst. Biol. 7 (1936) 209.

Paranephelium chinense Merr. var. *laoticum* Gagnep., Fl. Gén. Indo-Chine Suppl. 1 (1950) 972, nom. inval. = **Amesiodendron chinense** Hu, Bull. Fan Mem. Inst. Biol. 7 (1936) 209.

Paranephelium fallax Gagnep., Notul. Syst. 13 (1947) 66, = **Sisyrolepis muricata** (Pierre) Leenh., Blumea 23 (1977) 336.

Paranephelium muricatum Pierre, Fl. Cochinchine (1895) t. 328, = **Sisyrolepis muricata** (Pierre) Leenh., Blumea 23 (1977) 336.

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