PARAMYRISTICA, A NEW GENUS OF MYRISTICACEAE

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SUMMARY

The new genus Paramyristica from New Guinea, based on Myristica sepicana Foreman, is described and discussed, and included in keys to the Asian genera of Myristicaceae. Detailed drawings of the androecia of Paramyristica sepicana and of Myristica hooglandii and M. hollrungii are presented for comparison.

The New Guinean species Myristica sepicana Foreman is so distinct from all other species of Myristica that it cannot be kept within that genus. In the original description of M. sepicana, Foreman (1974) noted "bracteole not seen". On close inspection the staminate flowers appear to lack a bracteole, in this approaching those of Gymnacranthera (see Schouten, 1986) and Horsfieldia (see De Wilde, 1984b, 1985, 1986). Although the species shares other important features with Myristica, and has apparently no single traits that are unique in the family, the combination of characters it shows are unlike those of any of the currently recognized genera in Myristicaceae. Therefore, M. sepicana is placed in a new genus, Paramyristica. This can be keyed out from the other Asian genera of Myristicaceae as shown in the two keys below. A summary of the pertinent generic-level characters is given in Table 1.

KEY TO THE ASIAN GENERA OF MYRISTICACEAE Based on staminate flowering specimens

1a.	Inflorescence a sessile or to 3(-5) mm peduncled, short, tubercle-like or worm-like protuberance, usually woody, with scars of fallen pedicels and bracts. Bracteole present
b.	Inflorescence branched, panicle-like, short- or long-peduncled, the distal parts of the branches woody and with scars, or not. Bracteole present or absent 3
	Androecium a stalked disc, the anthers sessile, contiguous or largely free, radiating. Bracteole mostly small, apical to median
b.	Androecium a stalked elongated column, to which the anthers are completely fused by their backs, the apex of the column often a sterile protuberance, or flattish, very rarely shallowly excavated (<i>M. markgraviana</i> , <i>M. hooglandii</i>). Bracteole embracing (the base of) the perianth, apical or nearly so Myristica
3a.	Bracteole present, inserted at or towards the top of the pedicel. [Inflorescences with scar-covered perennial distal portions present or not]
b.	Bracteole absent

Table 1. Pertinent generic-level characters of Asian genera (vegetative characters excluded).

Characters	Myristica	Paramyristica	Gymnacranthera	Endocomia	Horsfieldia	Кпета
Status of flowers	dioecious	dioecious	dioecious	monoecious	dioecious	dioecious
Inflorescences .	1) panicle-like, peduncle without cataphyll scars at base 2) scar-covered (woody) protuberances as in Knema 3) as in Paramyristica: M. carrii, M. hooglandii	panicle-like partial inflorescences arranged into compound panicle, both cataphyll sears at base, and terminal vegetative bud present	compound-panicu- late; cataphyll scars at base present, terminal bud absent	compound-paniculate (cataphyll scars at base present, termi- nal bud absent)	compound- panicu- ulate (cataphyll scars at base present, terminal bud absent)	scar-covered (sessile or subsessile) (woody) protuberance
Bracteole	present	absent	absent	absent	absent	present
Perianth lobes (staminate flowers)	mostly ± out-curved at anthesis; inner surface glabrous	erect; glabrous inside	erect; glabrous inside	out-curved or reflexed; papillose-hairy inside	erect; glabrous inside	out-curved or spreading; glabrous inside
Androecium - synandrium (androphore)	subsessile or short- or ± long-stalked	long-stalked	(sub)sessile	short- or long-stalked	sessile or shortly stalked	short- or long-stalked
- anthers	completely fused	completely connate	free in apical por- tions	completely connate	connate or partially free	connate or partially or entirely free
- central column	central column frequently prolonged into sterile apex not or but little widened (at apex shallowly excavated in M. carrii, M. hooglandii)	broadly widened and deeply excavated	not widened	not widened, not ex- cavated	widened and deeply excavated	not or slightly widened, disc-shaped, not excavated
Stigma	minutely 2-lobed	unknown	minutely 2-lobed	minutely 2-lobed	minutely 2-lobed	few- to many-lobulate
Aril	laciniate to the base	laciniate to the base	laciniate to the base	laciniate to about halfway	(almost) undivided, completely envelop- ing the seed	(almost) undivided, completely enveloping the seed
Seed (seed coat)	not variegated	not variegated	not variegated	variegated; pointed at one end	not variegated	not variegated

4a.	Synandrium various, with the central column solid or excavated, usually considerably broader than the androphore. Perianth inside glabrous, perianth lobes no reflected at anthonic
b.	reflexed at anthesis
	or papillate hairy, perianth lobes erect or reflexed. [Inflorescences panicle-like usually branched at or near the base, some basal cataphyll scars present] 6
5a.	Perianth of staminate flower small, less than 4 mm long (6–7 mm in <i>H. superba</i>); androphore much shorter than synandrium, glabrous. Inflorescence pedunculate with scars of cataphylls at base, not branched at the base; vegetative but
b.	absent
6a.	type partial inflorescences, ending in a vegetative bud Paramyristica Synandrium elongate, anthers free apically. Perianth lobes erect at anthesis
	Gymnacranthera
b.	Synandrium short, (depressed-)globose; anthers completely connate. Perianth lobes spreading or reflexed in anthesis Endocomia
	KEY TO THE ASIAN GENERA OF MYRISTICACEAE
	Based on fruiting specimens and on vegetative characters
1 a.	Aril divided into segments to or almost to the base
	Aril entire, or laciniate only apically to up to halfway the top
2a.	Inflorescences or infructescences paniculate, with scars of cataphylls at base,
	without vegetative terminal bud. Bark of twigs smooth or but little striate. Fruit
ı.	1.5-3 cm long. [Bracteole absent]
D.	Inflorescences either short, (sub)sessile (as in <i>Knema</i>) or panicle-like, with peduncle, lacking both scars of basal cataphylls and terminal bud; or compound,
	consisting of those of both foregoing types distichously arranged in short-shoots
	ending in a vegetative bud. Bark of twigs usually striate, longitudinally cracked,
	or flaking. Fruit 1.5–8 cm long
3a.	Inflorescences compound, provided with a vegetative terminal bud. Bracteole
	scar on fruiting pedicel absent (pistillate flowers not seen). Fruit c. 5 cm long,
	conspicuously pubescent. Crowded line-shaped cataphyll scars usually present at base of innovations
b.	Inflorescences without a vegetative terminal bud (except for M. carrii, M. hoog-
	landii and M. markgraviana which resemble Paramyristica). Bracteole scar on
	fruiting pedicel present. Fruit size variable, pubescent or glabrescent. Cataphyll
	scars on twigs usually absent
4a.	Aril at apex convoluted or shallowly laciniate. Seed not variegated, not pointed at one end
b.	Aril coarsely incised for about the upper 1/3, or ± entire in the Philippines. Seed
	usually variegated, often bluntly pointed at one end. [Leaves not whitish below.
	Bracteole absent. Stigma narrowly 2-few-lobed. Inflorescence paniculate].
	Monoecious Endocomia

- 5a. Bracteole absent. Inflorescence paniculate, open. Stigma usually minutely 2-lobed (or few-lobed in *H. iryaghedhi* from Sri Lanka). Leaves usually not whitish below (papillose and whitish below only in *H. iryaghedhi*) Horsfieldia

PARAMYRISTICA W.J. de Wilde, gen. nov.

Genus novum fam. Myristicacearum, a genere Myristica Gronov. floribus ebracteolatis atque synandrio profunde excavato diversum. Ab Horsfieldia Willd. inflorescentiis gemma vegetativa terminali differt. — Type species: Paramyristica sepicana (Foreman) W.J. de Wilde, based on Myristica sepicana Foreman.

Trees dioecious; twigs and leaves stout. Twigs early glabrescent, bark pale, when older flaking, crowded cataphyll scars at base of innovations usually present. Leaves distichous, lower surface papillose. Inflorescences 1-5 cm long, mostly axillary to scars of foliage leaves, panicle-like, terminating in a vegetative bud. Staminate flowers in subumbels of 5-10, fewer in pistillate specimens. Flowers densely woolly pubescent, pedicellate, bracteole absent. Staminate flower: perianth broadly ellipsoid, inside glabrous except at base of androphore, $(5-)6-7 \times 4-5$ mm, lobes 2.5-3 mm long, i.e. splitting the perianth for 1/3 to nearly halfway, not reflexed in anthesis; androecium c. 4(-4.2) mm long, synandrium \pm subglobose, $2-2.4 \times 2$ mm, the central column deeply and broadly excavated nearly to the base, sterile apex absent; androphore slender, 1.5-2 mm long, glabrous, except for a dense collar of fine hairs at base. Pistillate flowers not seen. Infructescences on the older wood below the leaves, 2-5 cm long, with 2-6 fruits; fruiting pedicel without scar of bracteole. Fruit ovoid-ellipsoid, (4-)5-5.5 cm long, densely woolly tomentose; seed ellipsoid-oblong, c. 3 cm long, not variegated, aril completely enveloping the seed but deeply laciniated from the base.

Distribution - Papua New Guinea (Sepik Prov.).

Explanatory notes – *Paramyristica* can be split off from the genus *Myristica*, to which it is very close, especially in a puzzling similarity with *M. hooglandii* and allies.

The genus Myristica is large, with more than 150 species, and is especially rich in species in New Guinea (Sinclair, 1968; Foreman, 1978). It contains two sections distinguished by the shape of inflorescence: sect. Myristica and sect. Fatua (for a discussion see Sinclair, 1968: 41–44; De Wilde, 1991a). Myristica is well-defined and demarcated against the other genera of Myristicaceae (see Sinclair, 1958, 1968; De Wilde, 1984a, 1991a), but within the genus there is much variation, notably in the morphology of the inflorescences, and in the size and shape of the flowers, especially the androecium. Paramyristica is linked with some species of Myristica which in turn are exceptional within the genus on account of the position of the inflorescence and their floral morphology. These species are M. hooglandii Sinclair and M. carrii Sinclair,

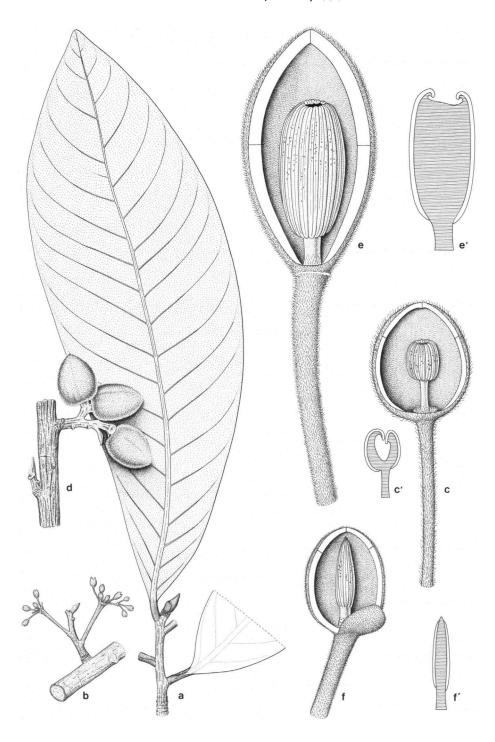
and, to a lesser extent, M. markgraviana A.C. Smith and M. philippensis Lam. Paramyristica, however, also shares important characters with Horsfieldia, and some less important ones with other genera of the family.

Apart from anatomical characters (see Koster & Baas, 1981, 1982; Armstrong & Wilson, 1980; but see also the paragraph on leaf anatomy on p. 347), the main characters defining *Myristica* are in the inflorescences, the (staminate) flowers, and the fruit. *Paramyristica* has the fruit with deeply lacerated aril around the seed in common with *Myristica*, but shows significant differences in the following features:

Inflorescences - The inflorescences in Myristica are of the single-type (for explanation, see De Wilde, 1991a), axillary either to foliage leaves or to scars of normal foliage leaves; in sect. Fatua the inflorescences are short, (sub)sessile, of long duratior like those in the genus Knema, in sect. Myristica they are panicle-like with a distinct peduncle (hypopodium). In some exceptional species of this latter section, M. hooglandii and M. carrii (both from New Guinea), the inflorescences are also panicle-like, but they may consist of several inflorescences of the type normally found in sect. Myristica, distichously arranged in short-shoots of a few centimetres long, with caducous cataphylls, and ending in a vegetative bud (see the figures in Sinclair, 1968: 157, fig. 7; 161, fig. 8). I have never seen material in which this bud has proliferated. In M. markgraviana (New Guinea) and in M. philippensis (Philippines) there may be shortened portions of twigs with crowded inflorescences, but here the twig normally proliferates. The inflorescences of *Paramyristica* are similar to the compound ones as found in M. carrii and M. hooglandii (partly) (see Fig. 1). The other genera of Asian Myristicaceae have inflorescences of the plural-type, i.e. compound with cataphyll scars at base (see De Wilde, 1991a), without a terminal bud.

Bracteoles – In Myristica there always is one bracteole on the pedicel. Usually it is large and conspicuous, sometimes small, persistent or caducous, usually inserted at or near the transition to the perianth, and it envelopes most of the perianth, especially in bud. In M. hooglandii the bracteole is caducous, leaving a conspicuous collarlike scar below the perianth. In Paramyristica the bracteole is absent, as in Horsfieldia, Gymnacranthera and Endocomia. Flowers in the genus Knema always have a bracteole (Sinclair, 1958, 1961; De Wilde, 1979).

Androecium – The typical androecium of Myristica has often been described and depicted for many species (e.g. Warburg, 1897; Sinclair 1958, 1968; De Wilde 1990). The anthers are fused by their backs into an elongated synandrium; the central column (around which the anthers are attached) is about as wide as the short or long but always distinct androphore, the apical portion of the central column is usually elongated into a sterile apex, more rarely the latter is truncated or absent. In a few exceptional cases, again species M. hooglandii, M. carrii and M. markgraviana, the central column is wider than the androphore, and is flattish or shallowly exacavated at the apex, with the tips of the anthers bent back into the apical depression. The androecium of Horsfieldia (almost) always has a central column that is much wider than the androphore, and it is frequently hollowed out at the top to various depths depending on the species (see De Wilde, 1984b: fig IA-D, 1985, 1986, 1987). That the androecial morphology of M. hooglandii somewhat resembles that of Horsfieldia was already noted by Sinclair (1968: 158). In Paramyristica, however, the androecium is very much like that of Horsfieldia, with a broad, almost globose synandrium



in which the wide central column is deeply excavated; there is a remarkably long, slender, glabrous androphore, with a collar of short hairs at the bottom of the perianth (see Fig. 1).

Further noteworthy features of *Paramyristica*, found frequently or irregularly in other genera of Asian Myristicaceae are:

- The lower leaf surface is distinctly papillose. This phenomenon occurs quite frequently in *Myristica*, where it is useful in distinguishing species.
- The colour of the bark of the twigs is markedly pale, contrasting with the blackish-drying colour of the petioles. This feature is not so well developed elsewhere in *Myristica*, but it is striking in some species of *Horsfieldia*, where it is used for the distinction of certain (groups of) species in the keys.
- The terminal vegetative bud is made up of a number of cataphylls (or scales), often with the apical portion broken off; these cataphylls leave distinctive crowded semi-circular scars at the bases of the innovations. This feature is absent or indistinct in *Myristica*, but occurs in *Gymnacranthera ocellata* (Borneo). The sterile terminal bud in most Myristicaceae usually consists of only a single conduplicate leaf beginning. When growth is renewed none or only one or two scales are shed.

Leaf anatomy – The leaf anatomy of Paramyristica is very similar to that of many Myristica species (cf. Koster & Baas, 1981). Hair bases are found on both adaxial and abaxial surface. The lower leaf surface is strongly papillate and the papillae are covered with alveolar material. The paracytic stomatal complex is sunken and overarched by a ring of papillate cells (as uniquely present in Myristica among the SE Asian Myristicaceae). Mesophyll structure, and midrib and petiole anatomy agree completely with Myristica.

A close affinity with Myristica hooglandii and M. carrii (Hoogland 4534 and LAE 74880, respectively) as deduced from superficial (macromorphological) resemblance is contradicted by leaf anatomical evidence. The epidermis of both specimens is not papillate, and the stomatal complex is overarched by a ring of cells with horizontal, nipple-shaped protrusions, collectively leaving a star-shaped opening above the guard cell pairs. Thus far such a structure is only known from and constant for Knema. The specimens mentioned above are of considerable interest because they combine this feature with two-armed hair cells – a constant feature of Myristica and Gymnacranthera according to Koster & Baas (1981). A papillate epidermis as reported here for Paramyristica (Fig. 2) also occurs in Myristica maingayi and M. gigantea (in the limited sample of 13 species seen by Koster & Baas).

Fig. 1. Paramyristica sepicana (Foreman) W.J. de Wilde. a. Habit of leafy twig apex; note sterile terminal bud with scale and scale scars, and congested scars of scales lower down at transition with previous innovation; × 0.5; b. staminate synflorescence; note terminal bud; × 0.5; c & c'. staminate flower, perianth opened, and schematic longitudinal section of androecium showing hollowed-out central column; × 5; d. infructescence on older wood of twig, fruit somewhat immature; × 0.5. — Myristica hooglandii Sinclair. e & e'. Opened male flower (note scar of bracteole) and schematic longitudinal section of androecium; × 5. — Myristica hollrungii Warb. f & f'. Opened male flower and schematic longitudinal section of androecium; × 5 (a: LAE 52983 (and NGF 48265); b, c, c': NGF 19516 (type); d: LAE 73769; e, e': Brass 25471; f, f': Demoulin 5958).

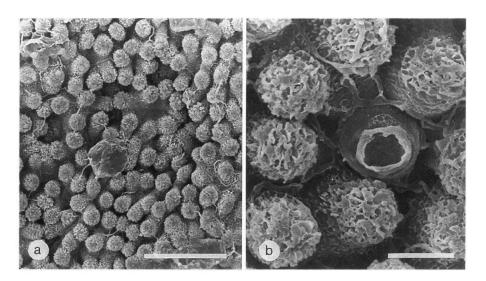


Fig. 2. Lower leaf surface in Paramyristica. – a. Papillae, hair bases and rings of papillae above stomatal complexes (LAE 73587), scale bar = 50 μ m. – b. Papillae covered with alveolar material and hair base (LAE 73769), scale bar = 10 μ m.

Paramyristica sepicana (Foreman) W.J. de Wilde, comb. nov. — Fig. 1a-d

Myristica sepicana Foreman, Contr. Herb. Austral. No. 9 (1974) 40, f. 2; Handb. Fl. Papua New Guinea 1 (1978) 209. — Type: Sayers NGF 19516 (LAE, n.v.; iso K, L).

Tree 5-25 m. Twigs (sub)terete, towards the apex 3-6(-7) mm in diameter, at first with minute tomentum consisting of ± appressed pale brown or bright rusty hairs 0.2-0.5 mm long, glabrescent; bark of older twigs ashy, dark grey, or blackish, conspicuously cracked and flaky, with ± concolorous lenticels. Leaves chartaceous: blades elliptic-oblong or oblong-lanceolate, broadest generally above the middle, $21-45 \times (5-)8-17$ cm, base rather gradually cuneate, top broadly acute with acute or bluntish tip, sometimes acute-acuminate; upper surface drying (greenish) olivaceous, lower surface glabrous, pale, brownish grey, with the nerves yellowish brown, contrasting, lower leaf surface strongly papillose, non-traumatic dots absent; midrib slender or medium, in large leaves to 5 mm wide, flat or slightly raised above; lateral nerves 15-22 per side, at an angle of 45-60(-70)° with the midrib, slender, flat or slightly sunken above, distinct and much raised below, lines of interarching indistinct; tertiary veining faint or invisible on both surfaces; petiole stoutish, (6-)10-20 × 4-6 mm, glabrous, brown or blackish, contrasting with light brown midrib and greyish (to whitish) twigs; sterile terminal leaf bud rather broad, (sub)acute, 10-15 × 4-6 mm, appressed-pubescent with dull brown hairs c. 0.5 mm, bud at base with few or several scale-like cataphylls, sometimes with the apical portion broken off, when shed leaving line-shaped crowded scars. Inflorescence compound, consisting of partial inflorescences each with a short flattened peduncle, of which there are 3-5

distichously arranged in the axils of fallen cataphylls along a short shoot (brachyblast) (1-)2-4 cm long, forming a panicle-like synflorescence; main axis always ending in a sterile vegetative bud 0.5(-1) cm long, scars of fallen cataphylls at base of main peduncle present; whole synflorescence shaggy bright rusty pubescent, hairs 0.5(-1) mm; flowers shaggy-pubescent, hairs yellow-brown, 0.5(-1) mm long; bracts irregularly broadly rounded, ± convex, 5-10 mm in diameter, pubescent, early shed, leaving distinct scars. Synflorescences of staminate flowers 3-6 cm long; partial inflorescences with peduncle (1-)2-2.5(-3) cm long, simple or with central axis up to 15 mm elongated, with 1 or 2 (or 3) clusters of 5-10 flowers of almost equal stage of development. Infructescences on the older wood, 1-4 cm long, with partial inflorescences shorter than in staminate, c. 1 cm long, each few-flowered; pistillate flow s not seen. Staminate flower: pedicel slender, $(5-)8-10 \times 0.8(-1)$ mm, bracteole absent; mature perianth in bud (broadly) ovoid-ellipsoid, $(5-)6-7 \times (4-)5$ mm, top rounded, base broadly rounded, the apical portion not angular in transverse section, inside glabrous, smooth, perianth lobes 3 (or 4?), c. 2.5(-3) mm long, splitting the bud for c. 1/3 to nearly halfway, at sutures 0.2-0.3 mm in diameter; androecium 4-4.2 mm long, androphore slender, slightly shorter than the synandrium, 1.5(-2) \times (0.3–)0.4 mm long, finely striate, glabrous, but at base with a 'collar' of densely set curly brown hairs 0.3-0.4 mm long, synandrium subglobose or broadly ellipsoid, subcircular in transverse section, ± truncate or depressed at both ends, c. 2-2.4 × 2 mm, inside deeply hollowed out nearly to the base; anthers probably c. 20 (i.e., c. 40 thecae), narrow, contiguous, partially curved to within the apical hollow of the synandrium (similar as in many Horsfieldia species). Infructescences (synfructescences) on the older wood below the leaves, 2-4(-5) cm long, branched, bark fissured and \pm flaking. Fruit 2-6 per infructescence; fruiting pedicel 3-6 \times 3-5 mm, pubescent; fruit ovoid-ellipsoid, $(4-)5-5.5 \times 2.5(-3)$ cm, base rounded or truncate, top narrowed, subacute, sometimes somewhat uncinate, (dry) pericarp rather woody, 5-7 mm thick, with woolly rusty tomentum, hairs 1-1.5 mm long; mature seed ellipsoid-oblong, with impressions of the aril lobes, brown, c. 3×1.5 cm.

Distribution – Papua New Guinea (a restricted area in West and East Sepik Province).

Habitat & Ecology – Lowland forest on ridges, forest of flats near creeks, and swamp forest dominated by *Calamus* species; 30–300 m altitude. Fl. March, fr. throughout the year.

Notes – 1. Fieldnotes. Straight-boled tree, branches horizontal or slightly pendulous. Bole 1–8 m. Bark finely longitudinally fissured, or smooth, once reported as peeling in large sheets; bark colour brown or black, inner bark light brown or light reddish brown, with red sap. Wood soft, straw, or pale reddish brown. Leaves shiny above, light green, whitish, or almost glaucous below. Flowers cream; inflorescence covered with brown indumentum; inflorescences and infructescences reported as cauliflorous, on branches only; fruit with dark brown or reddish brown indumentum, aril red.

2. Paramyristica sepicana much resembles some species of Myristica. Because of its papillate leaf undersurface it keys out beside M. ornata in a key to the species of Myristica for New Guinea. However, it does not at all resemble the latter in habit or

in fruit. Paramyristica sepicana is more probably related to Myristica markgraviana, M. carrii, and M. hooglandii, and, indeed, in habit superficially approaches these latter two species (see above for further discussion).

Specimens seen:

PAPUA NEW GUINEA. Sepik Prov.: NGF (Sayers) 19516 (type), NGF (Katik) 46690, NGF (Foreman & Kumul) 48161, 48265, 48345; LAE (Streimann & Martin) 52884, LAE (Streimann) 52983, LAE (Wiakabu et al.) 73587, 73769.

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