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THE MYRMECOPHILOUS SPECIES OF MYRISTICA (MYRISTICACEAE) FROM NEW GUINEA

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SUMMARY

The phenomenon of myrmecosymbiosis in *Myristica*, only occurring in some species from New Guinea, is reviewed here. A key to myrmecophilous taxa (and resembling species) is presented, and the status of their myrmecophily is briefly discussed. Three myrmecophytes are described as new species (*M. dasycarpa, M. sarcantha, M. verruculosa*), and *M. subcordata* var. *rimosa* is described as a new variety in a species liable to be confused with a myrmecophyte.

Key words: *Myristica*, New Guinea, myrmecophily, ants, coccids.

INTRODUCTION

In the elaborate taxonomic treatment of the genus *Myristica* by Sinclair (1968) the species *M. subalulata* Miq. is the only one identified as myrmecophytic. Herbarium collections of this species almost always show characteristic ant-swellings in the twigs, and this character, together with the marked wing-like ridges at two sides running from petiole base to petiole base, serve as major characters for defining his series Subalulatae (l.c.: 66, 384). Sinclair accepted *M. subalulata* in a wide sense, and hence the herbarium material of this common species has a wide ecological range and shows a large variability.

In my enumeration of *Myristica* in New Guinea (De Wilde, 1995) this variability was partly covered, for various morphological reasons, by accepting several varieties, viz. var. *subalulata*, var. *hagensis* (coriaceous-leaved mountainous plants), var. *leptantha* (with slender male flowers), var. *paucifructa* (infructescences with few, somewhat larger fruit, as compared with the type-variety), and var. *pedunculata* (with peduncled inflorescences). Besides, because considerably more material has become available for study since Sinclair's revision, a few additional new species, also characteristically with ant-swellings in the twigs, have been described by me (De Wilde, 1995; and the present paper). I now have the conviction that ant-swellings in the twigs, and more generally the inhabitation or the visible potential to be inhabited by ants (i.e., a distinct hollow stem and/or the presence of ant-holes), is a preponderant character on the species-level in *Myristica*, and in the key to New Guinean species (De Wilde, 1995) it is used in an early fork, leading to the myristicaceous ant-plant species of New Guinea. Including the three new species described here, these are: *Myristica bialata, M. dasycarpa, M. fasciculata, M. fissiflora, M. ingrata, M. sarcantha, M. subalulata*, and *M. verruculosa*.

The habit of housing ants in *Myristica*, in hollow twigs and more conspicuously in twigs with ant-swellings and perforation holes, is exclusive for New Guinea (including the Kai and Aru Islands). Plants of these species have twigs and leaves of comparatively stout habit, with leaves generally more than 20 cm long, the twigs (with a tendency to be) lined or ridged or low-winged. However, these species can be confused with species without ant-inhabitation but with angled or lined (or ridged) twigs, especially when the collected twig portions are inadequate and too short to ascertain if the character is present. Moreover, some of the myrmecophilous species are supposedly merely facultatively inhabited by ants, and only when actually sheltering ants they produce swellings (e.g. the mountainous *M. subalulata* var. *hagensis*). Other species, supposedly obligatory inhabited by ants (and ant-holes always present) do not normally produce swellings, hence have normal-looking, not swollen though hollow twigs (i.e. in *M. bialata* and in the newly described *M. dasycarpa* and *M. verruculosa*). As said above, still other species may have (partly) hollow twigs but are apparently never inhabited by ants and hence these are not ant-species (i.e., *M. sulcata*, *M. hollrungii*, *M. subcordata*). Finally, some species with terete, not or hardly lined solid twigs may vegetatively look deceptively like myrmecophilous species (e.g. *M. inutilis*, partly, or specimens of *M. subcordata* with hollow or solid twigs), and these have been listed and entered in the key to myrmecophilous species for convenience sake.

HISTORY AND STATUS OF THE PHENOMENON OF MYRMECOSYMBIOSIS

With the treatment of the widely conceived species *M. subalulata* Miq. by Sinclair (1968) (with elements now in segregated species) the condition of the twigs is described as "myrmecophilous with hollow, swollen, ant-inhabited deformities, reddish-brown, smooth and often shining in such parts, the older non-myrmecophilous parts generally solid, ..., the apical parts quadrate, smooth and also solid, two lines or often two narrow wings running from leaf base to leaf base, one on each side, the lines present throughout the length of the twig but becoming modified into wings in the swollen parts." (l.c.: 386). In his fig. 64 (l.c.: 387) twigs with swollen parts are illustrated, with circular as well as elongated ant-holes. From the notes to the species (l.c.: 393–396), I quote: "*Myristica subalulata* is distinct from all other members of the family in being an ant-plant and the special morphological modifications that have been evolved as a result of the myrmecophilous habit are well-known and useful diagnostic characters. Such portions of the twigs that are inhabited by ants are hollow and often swollen or variously deformed. The swellings seem to be absent from the extreme apical portions as well as from the older, solid, striate parts. The two lateral lines which run down from petiole base to petiole base (also found in certain species of *Horsfieldia*) are very distinct in the myrmecophilous parts where they form thin wings on each side of the twig. *Myristica hollrungii* and *M. sulcata* also have the lines but lack the wings and the swollen portions and are not inhabited by ants," and "... although the ant-swellings on the twigs seem to be fewer in (such) mountain plants, some of the specimens do show them. It seems that such portions without them are mostly the younger or apical parts of the twigs and that the portions showing them have just not been collected. On the other hand it may be that they have not been invaded yet by ants or that the ants which prefer them are absent in the district. Ants cannot always be present."

Beccari (1884) published on myrmecophilous plants, describing *Myristica myrmecophila* Becc., a later synonym of *M. subalulata* Miq. In Sinclair's notes (l.c.: 396) a transcript of a portion of a publication by Bower (1889) concerning Beccari's observations is reproduced and partly repeated here: "Of the myrmekophilous plants cited by Beccari ... is *Clerodendron fistulosum*, a new species, here also the internodes are swollen, and hollowed, and inhabited by ants, which gain access to the interior of the slit-like holes, two of which are situated, one on either side, at the upper end of each internode. Beccari is of opinion that both the swollen form of the internodes and the first origin of the holes have become inherited characters of the species, as an adaptation to the requirement of the protecting ants. Somewhat similar slit-like holes are to be found in *M. myrmecophila*, also a new species. The form of the orifice in this case also would suggest that the initiative in their formation is taken by the plant."

In a recent publication Maschwitz et al. (1994) report on *Clerodendron fistulosum* Becc., grown in the greenhouse, without the presence of ants, as being an unspecific myrmecophyte with extra-floral nectaries, of which the inflated hollow internodes open spontaneously, i.e., the entrance holes develop by themselves, a notion already held by Beccari in 1884 for this species as well as for *M. myrmecophila*. The spontaneously formed holes remain open for a long time and offer nesting space for a number of different opportunistic ant species. Likewise, Maschwitz et al. (1996) describe a newly discovered case of a myrmecophyte, *Capparis buwaldae* Jacobs, with similarly spontaneously formed stomata and inhabited by several opportunistic ant-species; it is the first and apparently only myrmecophyte in Capparaceae (*Capparis* has some 65 species). Both articles provide references to related literature.

About one hundred years ago, Schumann (1889) and Warburg (1890, 1897) had already published notes and a short essay on the phenomenon of what is called myrmecosymbiosis in the Myristicaceae, as only occurring in some species of *Myristica* in New Guinea (including the Kai and Aru Islands). In essence Warburg found that the ant-swellings originate from the pith tissue of the growing twigs and are formed irregularly, on morphologically not pre-indicated internodes of the twigs. Besides the habitation by ants he recorded the frequent occurrence of fairly large coccids in the ant-hollows, and further he assumed that these were even always present in two *Myristica* species, viz. *M. heterophylla* K. Schum. (= *M. hollrungii* Warb., p.p. and ?*M. subalulata* Miq.) and *M. myrmecophila* Becc. (= *M. subalulata* Miq.). He assumed that the phenomenon, as well as the ant-species, particularly belong to the concerned *Myristica* species. Swellings were found by him in sterile as well as in fertile twigs, even apically in very young stages, but were definitely located on irregular sites on the twigs. The question of whether the formation of ant-swellings is inherent to the plant itself or rather that a stimulus from the ants should have preceded is amply discussed, and he was of the opinion that in *Myristica* a truly genetically fixed myrmecosymbiosis is not the case, and that the ant-swellings are to be regarded as a sort of galls, rather than true myrmecodomatia. Queries discussed by him as still to be resolved are the way the ants disperse to the young plants, and how the coccids, which are in the adult stage sometimes too big to pass the ant-holes, enter the hollow nodes.

Meanwhile I found in recent collections of *M. subalulata* the coccids frequently present inside the ant-swellings. Notwithstanding the rather irregular location of the

morphologically well-defined ant-swellings on the twigs, always present in several species, I myself regard the syndrome, following previous authors, as a good taxonomic character. Besides, in other species and apparently less obligatory, ant-habitation in not or but little swollen though hollow twigs (and with ant-holes in the bark) is quite evident in part of the material, and hence can serve as a useful additional specific character (see Fig. 1).

Fig. 1. *Myristica subalulata* Miq. var. *subalulata*. Male twig with immature flowers (bracteoles partly still present), ant-swellings, and ant-openings; stem partly opened to show ant-cavities with two coccids, × 0.5 (*Polak MP 750*).

About the biology of the syndrome in *Myristica*, i.e., the swellings, the species of ants concerned, and the coccids, little is known yet. According to Warburg (1890) the coccids likely belong to the genus *Myzolecanium* Targ. Field study and greenhouse experiments (without and where possible with ants) may yield more facts.

KEY TO MYRMECOPHILOUS SPECIES OF MYRISTICA
(including also resembling non-myrmecophilous species)

This key is applicable only to specimens from New Guinea (incl. Kai and Aru Islands), essentially of the larger size class, i.e., twigs towards apex c. 5 mm im diameter or more, leaves c. 20 cm long or more, the twigs with or without ant-swellings, and with or without ant-holes, inside hollow or occasionally not, outside low-winged or ridged, angled, lined, or not.

1a. Plants myrmecophilous, i.e. twigs hollow or partly hollow, locally swollen or not, usually with ant-holes (perforations), frequently ± winged, or ridged, lined, or angular. Male perianth usually large, c. 10 mm long or more (c. 7 mm in *M. ingrata*) 2
b. Plants not myrmecophilous, twigs terete, or lined, or angular, solid or but narrowly hollow, without ant-holes. Male perianth usually less than 10 mm long 11
2a. Twigs usually with swellings and with ant-holes, usually winged or ridged .. 3
b. Twigs (sub)terete, hollow, without swellings, ant-holes present or absent (twig portion with ant-holes may not have been collected) 9
3a. Twig and leaves exceedingly stout, twig towards apex c. 10 mm diam., leaf blade to 43 by 18 cm. Fruit c. 3.5 cm long, with conspicuous indumentum with hairs (0.5–)1 mm long ..... **2. M. dasycarpa**
b. Plants generally less stout, twig up to 8 mm diam. Fruit with shorter indumentum 4
4a. Male perianth at anthesis split into lobes to halfway or over; flowers in one cluster in various stages of development; bracteole small or large. (Fruit not known with certainty.) — Lowlands of northern New Guinea .... **4. M. fissiflora** (2 subspecies)
b. Male perianth split for 1/3 or less, bracteole small, 2–3 mm 5
5a. Mature male perianth in bud ovoid or ellipsoid or ellipsoid-oblong, at anthesis split into lobes for 1/3–1/4. Synandrium obtuse, or with sterile apex to 0.2 mm long only. Fruit rather small, up to 4 cm long 7
b. Male perianth in bud oblong or oblong-lanceolate (tubiform), lobes 1–1.5 mm, splitting the perianth at anthesis for 1/6–1/8. Sterile apex of synandrium acute, 0.5–1 mm long. Flower buds in the same inflorescence either of ± the same stage or of different stages according to age. Fruit small or large, 1.5–7 cm long .. 6
6a. Bracteole caducous. Fruit rather small, subglobose, or ovoid, or ellipsoid, with acute apex, 1.5–2.5(–3) cm long, generally with persistent short tomentum, fruiting pedicel 2–10 mm long. Lower leaf surface glabrous or minutely pubescent, the tertiary veins generally faint. — Throughout New Guinea, incl. the Kai and Aru Islands, not in the Bismarck Archipelago; 0–2100 m altitude .... **7. M. subalulata** (5 varieties, excl. var. *hagensis*)

b. Bracteole persistent in anthesis. Fruit 5–7 cm long, (late) glabrescent. Tertiary veins faint or rather distinct. — Lowland, Papua New Guinea: Bismarck Archipelago ..... **1. M. bialata** (2 varieties)

7a. Flower buds before anthesis in one inflorescence generally of different size according to age. Bracteole persistent. Female flower pedicel 2–5(–6) mm. Fruit ovoid-ellipsoid, c. 2.5 cm long, apex narrowly or broadly rounded (with minute apiculum); fruiting pedicel stoutish, 3–10 mm long. Lower leaf surface with marginal arching of nerves and tertiary veins generally faint. (Fruiting specimens may be confused with *M. subalulata*.) — Montane and lowland areas of northern and southern New Guinea ..... **5. M. ingrata** (2 subspecies)

b. Flower buds in one inflorescence all of about the same size (same stage of development). Bracteole caducous. Lower leaf surface with lines of interarching of lateral nerves and tertiary veins generally distinct 8

8a. Male perianth stout, carnose, pedicel 7–8 mm; bracteole scar situated well below the perianth. (Female flowers and fruit not known.) — Lowland of northern Irian Jaya (West New Guinea) ..... **6. M. sarcantha**

b. Perianth smaller, pedicel longer with bracteole scar at the transition of pedicel and perianth. Female flower pedicel c. 10 mm long; fruiting pedicel 10–15 mm long. — Lowland, Papua New Guinea: Upper Sepik River area (W Sepik Prov.) ..... **3. M. fasciculata**

9a. Plants montane, found at c. 2000 m altitude .. **12. M. subalulata** var. **hagensis**

b. Plants from lowland area 10

10a. Male perianth inside not or hardly finely warty; lobes c. 1.5 mm, splitting perianth to about 1/8; anthers 5 or 6. Lower leaf surface glabrescent. — Papua New Guinea: Bismarck Archipelago and Manus Island ... **1. M. bialata** (2 varieties)

b. Male perianth inside towards the base densely finely warty; lobes splitting perianth to about 1/3; anthers 6–9. Lower leaf surface with persistent dense tomentum. — W Irian Jaya: Bird's Head & Bomberai Peninsula ..... **8. M. verruculosa**

11a. Twig strongly angular. — Montane, 1500–2000 m altitude 12

b. Male perianth (in some taxa not known) less than 10 mm long. — Lowland or montane, 0–1500 m altitude (*M. subcordata* var. *gigacarpa* mountainous) . 13

12a. Fruit 5(–6) cm long, dry pericarp c. 20 mm thick. (Flowers not known.) — E Papua New Guinea: Mt Dayman, Milne Bay Prov. ... **11. M. pachycarpidia**

b. Fruit c. 2 cm long, dry pericarp 2(–3) mm thick. Male perianth 10–14 mm long, bracteole caducous. — Papua New Guinea: Western Highlands Prov. ..... **12. M. subalulata** var. **hagensis**

13a. Twigs distinctly angular. — Lowland ..... **14. M. sulcata**

b. Twigs ± terete, lined or not. — Lowland or montane 14

14a. Leaves below (sub)glabrous (i.e., glabrescent, at first with weak or dense minute tomentum). Mature male perianth ellipsoid-ovoid, 4–6.5 mm long, anthers 8–10, bracteole subpersistent. Fruit 2.5–5 cm long, subsessile, largely late-glabrescent. — Mostly lowland marshy forest; 0–1000 m altitude ..... **9. M. hollrungii**

b. Leaves below with (sub)persistent dense tomentum. — Dry land forest of low and medium altitudes (but see *M. subcordata* var. *gigacarpa*) 15

15a. Leaves of medium size class, 12–24 mm long. Mature male perianth in bud ellipsoid-oblong, 3–4.5 mm long; anthers (3–)5; bracteole persistent. Fruit 2.5–5 cm long; fruiting pedicel 1–3 mm long ..... **10. M. inutilis** subsp. **papuana**

b. Leaves medium or large, 12–40 cm long. Mature male perianth in bud narrow, almost tubiform, (6.5–)7–8(–10) mm long; anthers 5 or 6; bracteole caducous (male flowers not known in *M. subcordata* var. *gigacarpa* and var. *rimosa*). Fruit (3.5–)4–5.5 cm long; fruiting pedicel 1–10 mm long .... **13. M. subcordata** (4 varieties)

ENUMERATION OF MYRMECOPHILOUS TAXA

1. Myristica bialata Warb., Bot. Jahrb. 13 (1891) 308; W.J. de Wilde, Blumea 40 (1995) 264, f. 1, 2a, b.

a. var. **bialata** W.J. de Wilde, l.c.: 264, f. 1, 2a.

b. var. **brevipila** W.J. de Wilde, l.c.: 264, f. 2b.

Distribution — Lowland area of Manus Island and Bismarck Archipelago.

Notes — The species was included by Sinclair (1968) in *M. subalulata* Miq.

This species possibly is a facultative myrmecophyte, because hollow stems with ant-perforations are not manifest in part of the material; in these latter cases their absence may be due to inadequate collecting, however.

2. Myristica dasycarpa W.J. de Wilde, *spec. nov.* — Fig. 2

Arbor myrmecophila habitu valido, ramunculi apicem versus c. 10 mm diam. alati, laminae ad 47 cm longae 19 cm latae, fructus in sicco 3.5–4 cm longi indumento velutino pilis 0.5–1 mm longis. — Typus: *Regalado & Takeuchi 1520* (L), Papua New Guinea.

Tree, c. 10 m high. *Twigs* stout, 8–10 mm diam. towards the apex, subterete, with conspicuous wings 2(–3) mm high running at both sides from petiole to petiole, bright brown, with scattered ± concolorous lenticels, twig partially somewhat swollen and hollow, ant-holes present; bark of twigs lower down (where bearing the fruits, below the leaves, stem 15–20 mm diam.) coarsely rectangular cracked and flaking, grey-brown. *Leaves:* blade membranous or thinly chartaceous, ± brittle when dry, oblong, 32–47 by 13–19 cm, broadest at about the middle, base (narrowly) cordate, apex broadly acute-acuminate; upper surface drying olivaceous(-brown), lower surface densely cinnamon tomentose with interwoven hairs 0.1(–0.3) mm; not or indistinctly papillose; dark dots absent; midrib slender, flat or slightly raised above, nerves 20–25 per side, at an angle of 70–80° with the midrib, flat, lines of interarching fairly distinct, tertiary veining finely trabeculate, indistinct; petiole comparatively short, thick, almost pulvinate, 15–20 by 8 mm, glabrous; terminal leaf bud not seen. *Female inflorescences* (known from the infructescences) of the *Knema*-type, i.e. woody wart-like brachyblasts c. 5 mm diam. *Male inflorescences* not known (but see note 2). *Fruit* subsessile, 2 or 3 per sessile knotty infructescence, on the older twigs below the leaves; fruit ovoid-ellipsoid, base broadly rounded, apex narrowly rounded or (sub)acute, with rufous-rusty velutinous indumentum with hairs 0.5–1 mm; dry pericarp strongly

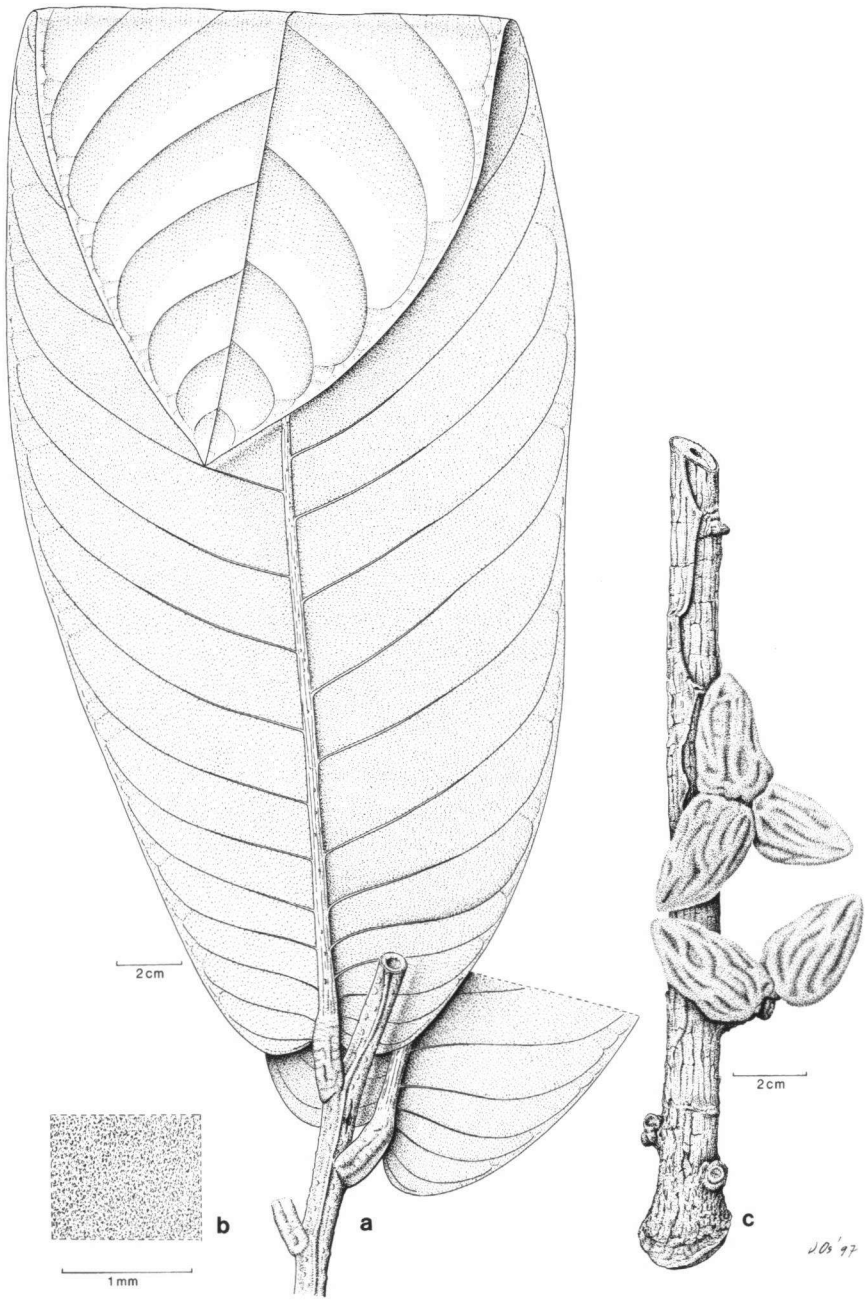

Fig. 2. *Myristica dasycarpa* W.J. de Wilde. a. Habit of portion of leafy twig, × 0.5; b. detail of tomentum of lower leaf surface, × 20; c. lower portion of older twig with ramiflorous infructescences, × 0.5 (*Regalado & Takeuchi 1520*, type).

creased (and apparently much shrunken on drying), c. 3 mm thick; fruiting pedicel stoutish, 2(–3) mm long; mature seed oblong, c. 2.5 cm long, greyish, the aril impressed into the seed.

Field-notes — Tree c. 10 m, myrmecophilous, leaves brown tomentose beneath; fruits rich brown to orange-brown; crushed dried fruit strongly smelling of nutmeg.

Distribution — Known only from the type (but see note 2), collected in northern Papua New Guinea, East Sepik Province, Ambunti subprovince, Waskuk Hills, area around Langu and Garuka villages, 4° 11' S, 142° 44' E.

Habitat & Ecology — Subcanopy tree; on a side ridge from the trail Garuka to Waskuk, at 50–70 m altitude; fruits July, 1995.

Notes — 1. This species is readily distinct among the New Guinean myrmecophilous *Myristicas* because of its stout habit, with thick alate twigs and large leaves, and by the subsessile fruit, 3.5–4 cm long, with for the group the most conspicuous indumentum: velvety with hairs to c. 1 mm long.

2. Male flowers of this species are not known with certainty. The specimen *Brass 13706*, from Irian Jaya, 4 km SW of Bernhard Camp, on the Idenburg River, in flood plain forest at 850 m, possibly belongs here. In L this collection consists of a portion of a leafy twig with inflorescences with immature male flowers and separately added fruit, the latter obviously belonging to *M. subalulata*. The immature male flowers can be briefly described as follows: inflorescence a wart-like brachyblast, 3–4 mm long, pubescent, glabrescent, bracts c. 1.5 mm, with a subumbel of 5 or 6 flower (buds) of various stages of development; male flowers: pedicel slender, c. 6 mm, bracteole c. 2 mm, apical; (immature) bud ellipsoid, 5–6 by 3.5 mm, ± woody (not collapsing on drying), valves c. 0.5 mm thick, splitting bud for about 1/3 (?); androecium c. 4 mm long, synandrium c. 3 by 1 mm, acute, anthers 14 (?); androphore narrow, c. 1 mm long, almost glabrous.

3. *Myristica dasycarpa* can be inserted in the general key to New Guinean species of *Myristica* as published in Blumea 40 (1995) 241 after lead 22 as follows:

22-bis a. Twig and leaves exceedingly stout, twig towards apex c. 10 mm diam., leaf blade to 43 by 18 cm. Fruit c. 3.5 cm long, with conspicuous indumentum with hairs c. 1 mm long ..... **M. dasycarpa**

b. Plants generally less stout. Fruit with shorter indumentum 23

3. Myristica fasciculata W.J. de Wilde, Blumea 40 (1995) 278.

Distribution — Papua New Guinea, Upper Sepik River area; in forest at low altitudes.

Note — The limited number of collections known suggests that this species is an obligate myrmecophyte.

4. Myristica fissiflora W.J. de Wilde, Blumea 40 (1995) 281.

a. subsp. **fissiflora**; W.J. de Wilde, l.c.: 282.

b. subsp. **kostermansii** W.J. de Wilde, l.c.: 283.

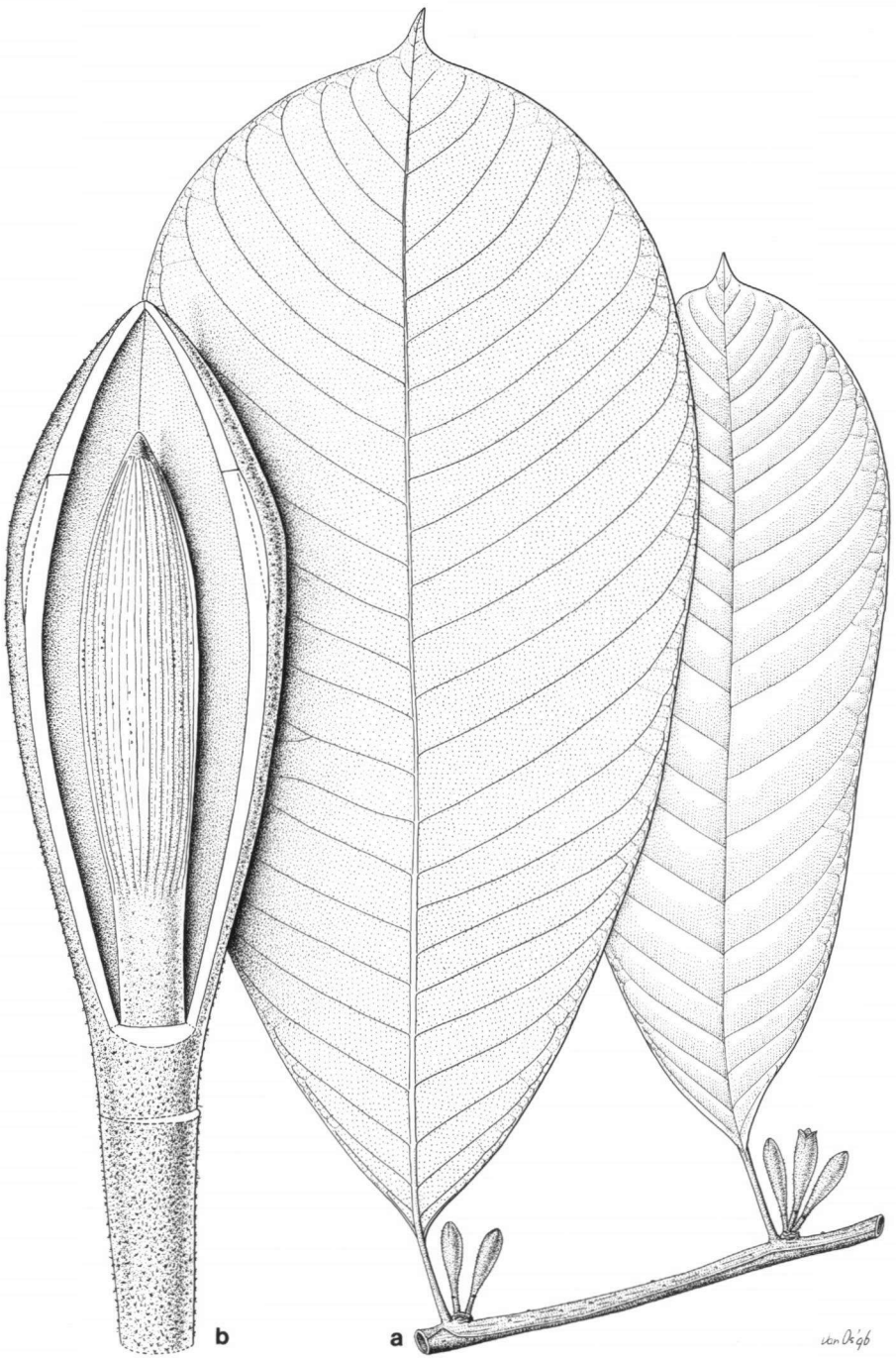

Fig. 3. *Myristica sarcantha* W.J. de Wilde. a. Habit of portion of leafy twig, × 0.5; b. male flower perianth lengthwise opened, bracteole caducous, × 6 (*McDonald & Ismail 3800*, type).

Distribution — Northern parts of Irian Jaya and Papua New Guinea; in lowland forest, 0–400(–1000) m.

Note — This species apparently is an obligate myrmecophyte. Part of the material was included in *M. subalulata* Miq. by Sinclair (1968).

5. Myristica ingrata W.J. de Wilde, Blumea 40 (1995) 290, f. 2c.

a. subsp. **ingrata**; W.J. de Wilde, l.c.: 291.

b. subsp. **velata** W.J. de Wilde, l.c.: 292.

Distribution — Most of New Guinea, in lowland and lower montane forest; also on limestone, at 500–800 m (subsp. *velata*).

Notes — This is an obligate myrmecophyte, with hollow, usually swollen portions in the twigs. Occasional conspicuous irregularly shaped apical swellings look like insect-galls.

The rather small male perianths (6.5–7.5 mm long) are reminiscent of *M. hollrungii* Warb.

6. Myristica sarcantha W.J. de Wilde, *spec. nov.* — Fig. 3

Ramuli cavi formicis incolentes. Flores masculi grandes carnosi, perianthio 15–16 mm longo (4–)5–6 mm lato in alabastro apicaliter triangulari. — Typus: *McDonald & Ismail 3800* (L holo; GH iso), Irian Jaya.

Treelet, 4 m high. *Twigs* moderately stout, 5–6 mm diam. towards the apex, subterete with shallow lines from petiole to petiole, bright brown, partially hollow (see field-notes) but ant-holes not seen, glabrous (glabrescent, but twig apex not seen), smooth (hardly striate), lenticels small, scattered, inconspicuous. *Leaves:* blades membranous, obovate-oblong, 22–32 by 8–15 cm, broadest above the middle, base cuneate, apex broadly rounded with acute-acuminate tip; upper surface drying green-olivaceous, lower surface subglabrous, pale, minutely irregularly papillose and with extremely minute scattered whitish appressed hairs, brown dots absent; midrib slender, almost flat above, nerves 20–22 per side, at an angle of 70–80° with the midrib, flat, lines of interarching nerves slender but distinct; tertiary venation distinct at both surfaces; petiole rather long, 25–30 by 3 mm, brown, glabrous; terminal leaf bud not seen. *Male inflorescences* axillary of leaves, sessile, wart-like, scar-covered, to 5 mm diam., the flowers in subumbels of 2–5, slightly differing in the stage of development, extremely minutely ± scattered mealy pubescent with stellate hairs (less than) 0.1–0.2 mm. *Male flowers* stout; pedicel short, stout, 7–8.5 by 2.5(–3) mm, bracteole caducous (not seen), its scar at about 1/3–1/2 from the apex of the pedicel; mature perianth in bud oblong-fusiform, 15–16 by (4–)5–6 mm, broadest above the middle, acute, base tapered, apical 1/3 portion, i.e. 5(–8) mm, 3-angled with lines of lobe-sutures well-marked, lobes 4–4.5 mm long, at suture 0.6–0.8 mm thick; androecium stout, 12–13 mm long, synandrium oblong, acute, c. 8 by 3 mm, anthers 12 or 13 (i.e. 24–26 thecae), contiguous, sterile apex 0.5–1 mm long; androphore c. 4 by 1.5–2 mm, appearing as glabrous but with very minute (less than 0.1 mm) pale stellate hairs in lower 2/3. *Female flowers* and *fruit* not seen.

Field-notes — Small understorey tree, 4 m tall, branching above and below, lateral branches whorled; trunk straight, cylindrical, 3 cm diam.; lateral branches covered with muricate bodies that attract aggressive ants; flower tubular, tube pale yellow and green, limb segments reflexed.

Distribution — Known only from the type collection, at Sarmi, northern Irian Jaya (West New Guinea). Mixed primary lowland forest, canopy 25–45 m high. Coastal plain, 1–3 km N of Sewan on the Waske River, 2° 4' S, 138° 46' E. Altitude 10–20 m. *McDonald & Ismail 3800*, male flowers June 1993.

Notes — 1. Apparently belonging to the group of ant-inhabited species of *M. subalulata* and readily distinct by its large, robust carnose flowers. Another stout-flowered species is *M. verruculosa*, with flowers larger mainly by a longer pedicel. Taxonomically as well as in general habit *M. sarcantha* is close to *M. fissiflora* (with deeper lobed, less thick-fleshy male perianth, and with the bracteole strictly apically at the pedicel), and also in general habit close to *M. fasciculata* (mature male flowers not known, but immature flowers much different).

2. *Myristica sarcantha* can be inserted in the general key to New Guinean species (De Wilde, 1995: 242) by replacing lead 26b as follows:

26a. (unchanged) ..... **M. ingrata**
b. Flower buds in one inflorescence all of about the same size (same stage of development). Bracteole caducous. Lower leaf surface with lines of interarching of lateral nerves and tertiary veins generally distinct 26-bis
26-bis a. Male perianth stout, carnose, 15–16 mm long, pedicel 7–8 mm, bracteole scar below perianth. (Female flowers and fruit not known.) — Lowland, N Irian Jaya ..... **M. sarcantha**
b. Perianth smaller, pedicel longer with bracteole at the transition of pedicel and perianth. Female flower pedicel c. 10 mm long; fruiting pedicel 10–15 mm. — Lowland, Papua New Guinea, Upper Sepik River (W Sepik) ... **M. fasciculata**

7. Myristica subalulata Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 47; W.J. de Wilde, Blumea 40 (1995) 330.

With five varieties, of which var. *hagensis* W.J. de Wilde is considered as not myrmecophilous.

Distribution — Wide-spread in New Guinea, including Kai and Aru Islands; altitude 0–2100 m.

Note — *Myristica subalulata* Miq. is considered as a true, obligate myrmecophyte, except for var. *hagensis* (see below in the list of non-myrmecophilous species). Almost all herbarium collections possess perforated hollow ant-swellings in the (shallowly) alate twigs.

a. var. **subalulata**; W.J. de Wilde, l.c.: 330, f. 2d. — Fig. 1

Synonyms: ?*Myristica costata* Warb., ?*M. heterophylla* K. Schum., *M. macrophylla* Zipp. ex Miq., *M. myrmecophila* Becc.

Notes — 1. *Myristica costata* Warb. [Bot. Jahrb. 18 (1893) 191; W.J. de Wilde, Blumea 40 (1995) 274 – type *Hellwig 247*, B† from Sattelberg] is doubtful; it was regarded as a synonym of *M. subalulata* Miq. by Sinclair (1968), but as explained by me (l.c.: 274) this is unlikely.

2. *Myristica heterophylla* K. Schum. [in K. Schum. & Hollrung, Fl. Kaiser Wilhelmsland (1889) 45] is a doubtful name. The type material consists of specifically different elements, but the lectotype, *Hollrung 648* (male fl.), designated by Warburg (1897: 489, t. 11) is lost in B and I have not seen the duplicate which is in BO, according to Sinclair (1968: 410), and which he asserts is *M. hollrungii*. Warburg's drawing and description, t. 11, however, depict a plant with hollow, non-alate stem, and an ant-swelling with distinct ant-hole, and reduced leaves in between well-developed leaves; the inflorescence and separate flower can well belong to *M. hollrungii*, but the above given vegetative characters do not, and I cannot imagine a plant with this combination of traits. The reduced leaves are a normal appearance in what I at present accept as *M. subcordata* Blume var. *morindiifolia* (Blume) W.J. de Wilde. The name *M. heterophylla* K. Schum. is an invalid later homonym of *M. heterophylla* Fern.-Vill., 1880, the latter belonging to *Knema*.

3. When one of the sedentary coccids found within the opened ant-cavity of *Polak MP 750* was removed, it appeared that underneath a flock of some 20 minute young ones provided with distinct feet was hidden, the baby creatures deemed to be able to move around; see also Fig. 1.

b. var. **hagensis** W.J. de Wilde, l.c.: 330.
This variety is regarded as non-myrmecophilous (see below, taxon 12).

c. var. **leptantha** W.J. de Wilde, l.c.: 331.

d. var. **paucifructa** W.J. de Wilde, l.c.: 332.

e. var. **pedunculata** W.J. de Wilde, l.c.: 332, f. 2e (once collected).

8. Myristica verruculosa W.J. de Wilde, *spec. nov.* — Fig. 4

Myristicae bialatae affinis, sed foliorum pagina inferiore tomento persistenti denso, perianthii masculi interiore verruculoso differt. — Typus: *Polak MP 1283* (L holo; BO iso), Irian Jaya.

Tree, 15 m high. *Twigs* stout, 4–5 mm diam. towards the apex, subterete with faint lines from petiole to petiole, light brown, partially hollow with incidental ant-holes, without swellings, early glabrescent, at first with minute bright brown tomentum of hairs less than 0.1 mm, older bark striate with scattered lenticels. *Leaves:* blades chartaceous, elliptic-oblong or oblong, broadest at or above the middle, 20–32 by 8–13 cm, base broadly rounded, sometimes shallowly cordate, apex acute or acute-acuminate; the upper surface olivaceous, the lower surface with persistent dense tomentum of pale hairs 0.1 mm or less, not papillose, without dots; midrib flat or slightly raised above, nerves 20–23 per side, flat or sunken above, at an angle of 60–80° with the midrib, line of interarching nerves faint; tertiary veining indistinct; petiole stout, 20–40 by 5 mm, glabrescent, brown as the twigs; terminal leaf bud slender, 15–20 mm, with dense brown stellate hairs 0.1 mm or less. *Inflorescences* axillary of or below the leaves; of the *Knema*-type, i.e. in male simple or forked, to 10 mm long, with a stout peduncle to 5 mm, glabrescent; bracts minute, caducous; *male inflorescences*

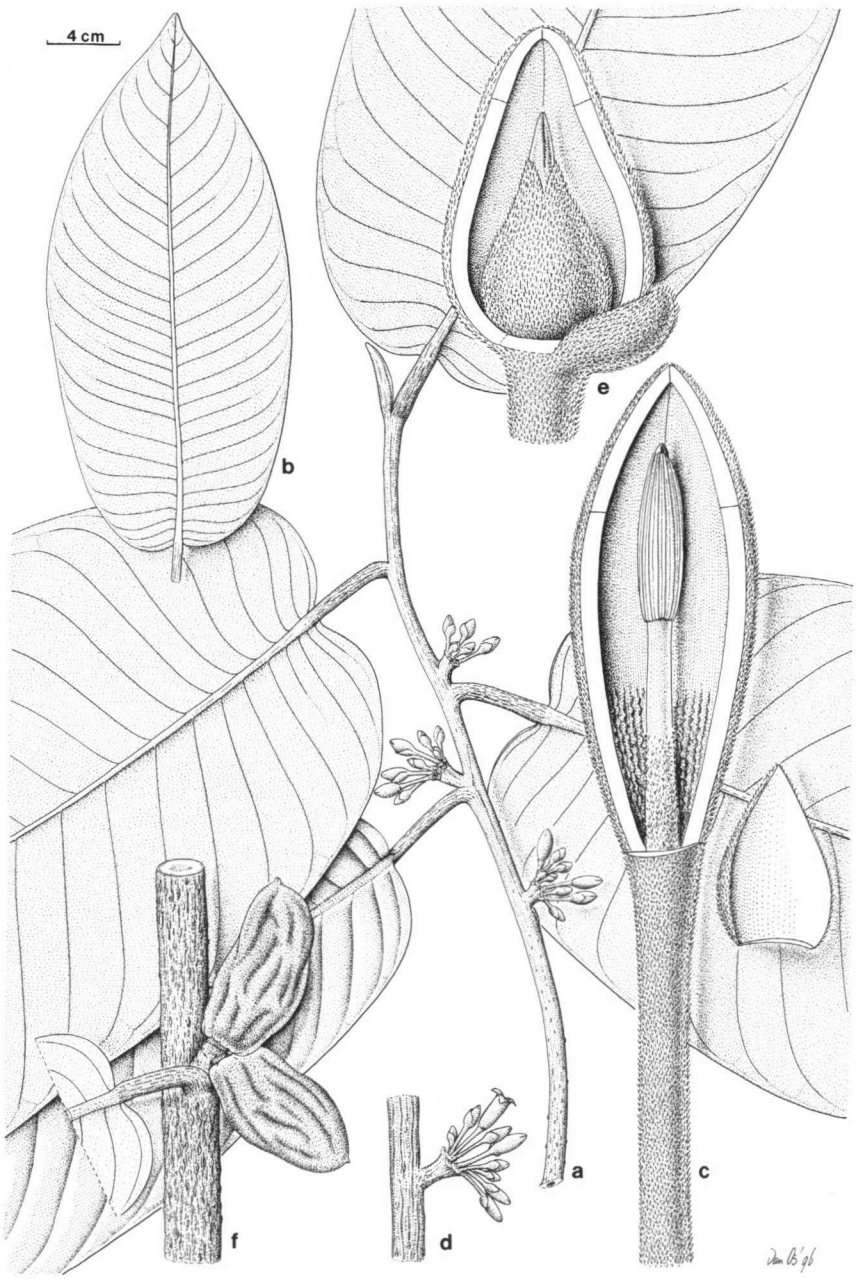

Fig. 4. *Myristica verruculosa* W. J. de Wilde. a. Habit of leafy twig with male inflorescences, × 0.5; b. leaf, × 0.25; c. male flowers, the mature perianth in bud lengthwise opened, (sub)persistent bracteole drawn separately, × 6; d. male inflorescence with one flower blooming, × 0.5; e. female flower, perianth lengthwise opened, × 6; f. portion of twig with infructescence, × 0.5 (a–d: *Polak MP 1283*, type; e, f: *Polak MP 697*).

with clusters of 10(–20) flowers, of different size according to age, minutely yellow brown pubescent with hairs c. 0.1 mm. *Male flowers* stout; pedicel stout, about as long as the perianth, 10–11 by 1.5 mm, bracteole ovate-broad-triangular or rhomboid, acute, 4–4.5 mm, (sub)persistent, inserted apical at the pedicel; mature male perianth in bud oblong, (10–)12 by 4–5 mm, the base somewhat tapered, the apex bluntish to acute, not 3-angular, lobes c. 4 mm long, i.e. splitting the bud for 1/3, ± fleshy, at sutures 0.5(–0.8) mm thick; androecium (8–)10 mm long, synandrium oblong, subacute, 4–5 by 1.5–2 mm, anthers 8–9(?) (i.e. c. 17 thecae), contiguous, sterile apex glabrous, acutish, 0.2–0.3 mm; androphore slender, cylindrical, 5–6 by 0.8 mm, minutely pale pubescent in lower half with hairs less than 0.1 mm. Lower 1/3 of the perianth surface inside conspicuously finely irregularly warted, clearly visible with a lens. *Female flowers* in sessile clusters of 5–10, with perianth buds of various size; tomentum mealy, hairs 0.1–0.2 mm; pedicel 2(–2.5) mm long, mature perianth in bud ovoid(-oblong), narrowed in the apical portion, c. 8 by 4–5 mm, lobes c. 1.5 mm, bracteole oval, slightly hooded, c. 2.5 mm long, (sub)persistent, ovary ovoid, tapering, c. 5 (incl. stigma lobes 1.5 mm) by 3 mm, with tomentum of appressed hairs 0.1 (–0.2) mm. *Infructescences* of clusters of 1–3 fruits; fruits (ovoid-)oblong, base broadly rounded, apex acute, tomentum rusty, of hairs c. 0.5 mm long, 3.5–5 by 2.5 cm, dry pericarp c. 5 mm thick, fruiting pedicel 1–3 mm; seed ellipsoid-oblong, 2.5–3 cm long.

Field-notes — Clear exudate. Leaves pale brown below. Flowers yellow brown, c. 1 cm long.

Distribution — Irian Jaya (West New Guinea): Bombarai Peninsula and Bird's Head, the latter in the ISIR research area, E of Sorong, limestone area at c. 450 m, secondary forest on clay soil.

Vernacular name — Pawiah ksiah.

Notes — 1. *Myristica verruculosa* is related to and much resembling *M. ingrata*, *M. hollrungii*, and *M. subcordata*, and especially morphologically close to *M. bialata*, a species of the Bismarck Archipelago in East New Guinea. The present new species is distinct from all these by the fine warty structure within the perianth. A warty inner perianth, however, is shared with *M. fissiflora* (subsp. *fissiflora*), a species much related, but with deeper cleft male perianth. *Myristica ingrata* is a species with mostly distinct ant-holes in the twigs, and further differing by much smaller flowers and (except var. *velata*) glabrescent lower leaf surface; *M. hollrungii* is a species of swampy areas, equally with smaller flowers and (sub)glabrous leaves; *M. subcordata*, with similar persistent leaf indumentum, has much smaller and more narrow male perianths, with caducous bracteole. *Myristica bialata* has similarly stout male flowers, but differs by having less (5 or 6) anthers, shorter perianth lobes, and the (almost) absence of a warty inner surface; it has a glabrescent lower leaf surface, densely short felty in the present new species.

2. Because of the resemblance in habit of the present species with other species, incomplete or sterile specimens may have been mislaid especially under *M. subcordata* and *M. hollrungii*.

3. This new species can be inserted into the key to New Guinean species of *Myristica* (De Wilde, 1995: 258) by changing leads 163 & 164 as follows:

163a. (unchanged) ..... **M. simulans**
b. Male perianth c. 12 mm long or less, with hairs 0.1–0.5 mm long; androphore about (or nearly) as long as the synandrium, mostly (partly) pubescent. Fruit various 163-bis
163-bis a. Leaves of medium size, i.e. 12–24 cm long. Mature male perianth in bud ellipsoid-oblong, 3–4.5 mm long; bracteole persistent; anthers (3–)5. Fruit variable in size, 2.5–5 cm long; fruiting pedicel 1–3 mm long .... **M. inutilis** (subsp. **papuana**)
b. Leaves medium or large, 12–35 cm long. Mature male perianth in bud much larger. Fruiting pedicel 1–10 mm long 164
164a. Mature male perianth in bud ± narrow, almost tubiform, (6.5–)7–8(–10) mm long; bracteole caducous; anthers 5 or 6. Perianth inside towards base smooth. Fruit (3.5–)4–5.5 cm long, fruiting pedicel 1–10 mm long .. **M. subcordata**
b. Mature male perianth ± oblong, 10–12 mm long; bracteole (sub)persistent; anthers 8 or 9. Perianth inside towards base finely warty. Fruit unknown .... **M. verruculosa**

Collections seen — *Polak MC 697* (female fl., fr.), *Polak MC 1283* (male, type), *Polak NT 11450* (sterile ecological plot-specimen); *de Vogel 9693* (fr.); *Moll BW 13007* (male fl., fr.).

ENUMERATION OF NON-MYRMECOPHILOUS TAXA
(liable to be confused with myrmecophilous taxa)

9. Myristica hollrungii Warb., Mon. Myrist. (1897) 490, t. 19, 1-2; W.J. de Wilde, Blumea 40 (1995) 289.

Synonyms: *Myristica albertsii* Warb., *M. heterophylla* K. Schum. (p.p.), *M. euryocarpa* Warb.

Note — This species sometimes has hollow twigs and usually lined or ridged twigs, but it never seems to be inhabited by ants, and it never has ant-perforations. Superficially it may resemble some forms of *M. subalulata* Miq., with which it is regarded as closely related, as discussed by Sinclair (1968: 411). However, it is quite distinct in its male flowers and fruit.

10. Myristica inutilis A. Gray subsp. **papuana** (Markgr.) W.J. de Wilde, Blumea 40 (1995) 293.

This variable taxon can hardly be taken as myrmecophilous, but specimens can be confused with those of the very variable *M. subcordata* (see below) of which certain specimens may recall myrmecophytes in vegetative habit. Branches of *M. inutilis* are never hollow, nor ridged, and at present the species is somewhat arbitrarily separated on male flower characters.

11. Myristica pachycarpidia W.J. de Wilde, Blumea 40 (1995) 312.

A montane species only known from the type. It has solid twigs which are strongly angled and hence superficially resemble certain myrmecophilous *Myristicas*. *Myristica subcordata* var. *gigacarpa* also is mountainous, but has subterete twigs.

12. Myristica subalulata Miq. var. **hagensis** W.J. de Wilde, Blumea 40 (1995) 330.

This variety was described in order to create some differentiation in the variable *M. subalulata* as accepted by Sinclair (1968). It consists of some collections from the Mt Hagen area (Papua New Guinea, Western Highlands Prov.) which obviously link up with other material of *M. subalulata* but differs by the absence of ant inhabitation and by coriaceous leaves. This variation was briefly discussed by Sinclair (1968: 394).

13. Myristica subcordata Blume, Rumphia 1 (1837) 186; W.J. de Wilde, Blumea 40 (1995) 333.

Distribution — Wide-spread in New Guinea (notably var. *morindiifolia*).

a. var. **subcordata**; W.J. de Wilde, l.c.: 333.

Synonyms: *Myristica fatua* Houtt. var. *subcordata* (Blume) Miq., ?*M. wallacea* Warb. var. *keyensis* Warb.

b. var. **gigacarpa** W.J. de Wilde, l.c.: 333.

Only known from the type and one additional montane collection in Papua New Guinea.

c. var. **morindiifolia** (Blume) W.J. de Wilde, l.c.: 334.

Synonyms: *Myristica morindiifolia* Blume, *M. fatua* var. *morindiifolia* (Blume) J. Sinclair, *M. multinervia* A.C. Sm.

d. var. **rimosa** W.J. de Wilde, *var. nov.*

> Ab *M. subcordatae* Blume varietatibus aliis in ramulis juventis cortice conspicue aspera dense lenticellato verrucoso-fissurata pallenti distincta. — Typus: *de Vogel 9757* (L; iso BO), Irian Jaya, Bird's Head.

Twigs terete, not ridged nor lined, solid, 5–8 mm diam. towards the apex, bark at first blackish brown, soon rather pale and conspicuously rough, flaky and fissured by numerous elongated lenticels. *Leaves:* coriaceous, elliptic-oblong, oblong, or oblong-lanceolate, 17–30 by 5–9.5 cm, broadest at the base or about the middle; nerves 25–35 pairs, flat or sunken above; lower surface with pale yellowish brown dense short-felty indumentum of hairs c. 0.1 mm high; petiole short, 5(–10) by 3–5 mm, dark brown, contrasting with the paler colour of the twigs. *Inflorescences* (female) of the *Knema*-type, sessile, 2- (or 3-)flowered. *Female flower* ± sessile, ovoid-oblong, narrowed towards the apex, with hairs c. 1 mm long. *Fruit* solitary, ellipsoid, 2.5–3.5(–4) by 1.5–2.5 cm, base broadly rounded, top subacute, dry pericarp c. 3 mm thick, with powdery (light) brown tomentum of hairs c. 0.5 mm; fruiting pedicel stout, 1–2 mm long, frequently with the perianth persisting under the fruit, scar of bracteole not seen; seed ellipsoid, 2.5–3 cm.

Distribution — Known only from collections from western Bird's Head, Irian Jaya: *Polak 697; Ridsdale CER 2342*; *de Vogel 9757*; *Schram BW 6099*.

Habitat & Ecology — Forest on sandy or clayey soil, presumably all collections from forest on limestone bedrock; 50–300 m altitude. Fl. & fr. in May.

Note — *Myristica subcordata* is, like *M. inutilis*, accepted as very variable, in general habit as well as in details of flowers and fruits, e.g. in the length of the fruiting

pedicel and length of the hairs of the indumentum. The species has mostly completely solid (sub)terete twigs, and is completely devoid of ant-inhabitation. Stout specimens, especially of var. *morindiifolia*, may in general appearance be confused with those of certain myrmecophytic species. As remarked with the description of var. *gigacarpa*, and the present var. *rimosa*, their taxonomic status is provisional and not at all settled. Of both varieties sufficient material of male flowers is lacking. Both varieties may represent separate species, resembling *M. subcordata*. Var. *rimosa* also may be a variety of *M. verruculosa*.

Myristica subcordata var. *rimosa* is clearly distinct by the rough, flaky and lenticellate-fissured bark of the twigs. The apparently persistent perianth (with hairs about 1 mm long) under the fruit is remarkable.

14. Myristica sulcata Warb., Monogr. Myrist. (1897), t. 19, f. 1-2; J. Sinclair, Gard. Bull. Sing. 23 (1968) 396; W.J. de Wilde, Blumea 40 (1995) 334.

Distribution — Wide-spread in New Guinea.

Habitat & Ecology — In dryland lowland forest.

Note — This species with rather stout, solid, sharply 2-angled twigs may be superficially confused with a myrmecophilous species.

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