ISSN 0374-7859

THE GARDENS' BULLETIN
SINGAPORE

Volume 37
(1984)

A periodical reflecting the interests and
activities of the Botanic Gardens
Singapore

**Published by the Botanic Gardens
Parks and Recreation Department
Ministry of National Development
Singapore 1025**

Printed by Jin Jin Printing Industry Pte Ltd

CONTENTS

Volume 37

PART 1 — 1st June 1984

PART 2 — 1st December 1984

ISSN 0374-7859

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PAGES

Published by the Botanic Gardens
Parks and Recreation Department
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Printed by Amsterdam Type Printers, Singapore

GARDENS' BULLETIN

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The price of the Gardens' Bulletin varies according to the content of each issue. This issue, with the index of volume 36, is priced at Singapore $18.50 cts. excluding postage. Overseas subscribers are requested to make payment in the form of bank drafts or international money orders in Singapore currency payable to the *Commissioner of Parks and Recreation, Singapore.*

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Manuscripts: The Editorial Committee of the Gardens' Bulletin will be glad to receive and consider for publication original research findings and reviews of progress in the fields of botany, horticulture, and allied subjects. Contributions must be original and the material must not have been submitted or, if accepted, be submitted for publication elsewhere.

Two copies of the manuscript should be submitted, typed on one side only with double-line spacings and a margin of at least 4 cm. Do not type all the letters of any word in capitals. Underline only in pencil: with a straight line for italic type face and wavy line for bold type face. Authors should see the layout of other papers recently published in this journal to ensure that papers submitted conform as closely as possible to the accepted pattern. Numerical data should only be included if it is essential to the argument and this can be presented either in the form of tables or diagrams.

Title and authors: The title should give a concise description of the contents of the papers. The name(s) and affiliation(s) of author(s) must be given below the title. Lengthy papers and those of a complex nature must have the contents listed at the beginning of the paper.

Scientific names: The complete scientific name — genus, species, authority, and cultivar where appropriate — must be cited for every organism at time of first mention. The generic name may be abbreviated to the initial thereafter except where intervening references to other genera with the same initial could cause confusion.

Tables: All tables should be numbered and carry headings describing their content. These should be comprehensive without reference to the text.

Abbreviations: Standard chemical symbols may be used in the text (e.g. IAA, IBA, ATP), but the full term should be given on the first mention. Dates should be cited as: 3 May 1976. Units of measurement should be spelled out except when preceeded by a numeral where they should be abbreviated in standard form: g, mg, ml, etc. and not followed by stops.

Literature citations: Citations in the text should take the form: King and Chan (1964). If several papers by the same author in the same year are cited, they should be lettered in sequence (1964a), (1964b), etc. When papers are by three or more authors, they should be cited as e.g., Geesink et al. (1981). All references must be placed in alphabetic order according to the surname of the (first) author and in the following form:

Singh, H. (1967). Sclereids in *Fagraea. Gard. Bull. Sing.* 22, 193-212.

Abbreviations of titles of journals should be those of the World List of Scientific Periodicals (4th Edition) or the Selected Abbreviated Titles of Biological Journals (London: Institute of Biology).

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Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World,* L. Reeve; Ashford, Kent; 242-255.

For literature citations in taxonomic papers the following style is required:

Medinilla alternifolia Bl., Mus. Bot. Lugd.-Bat. I:2 (1849) 19.
Sterculia acuminatissima Merr., Philip. J. Sci. 21 (1922) 524.

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Florae Malesianae Precursores – LVIII, Part Two*
The Genus *Gordonia* (Theaceae) in Malesia

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Department of Botany, National University of Singapore, Singapore

EFFECTIVE-PUBLICATION DATE: 5 SEPT. 1984

Abstract

This is a taxonomic treatment of 21 species of *Gordonia* (of the family Theaceae) found in the Malesian region. Among these, there are two new (*G. borneensis, G. sarawakensis*) and two newly combined (*G. integerrima, G. vulcanica*) species. Besides, two excluded (*G. brevifolia, G. lobbii*) and two doubtful (*lanceifolia, G. sarasini*) ones are briefly mentioned. A complete list of scientific names and their synonyms is presented in an index.

I. INTRODUCTION

The genus *Gordonia* was established by John Ellis in 1771 in honour of James Gordon (1728–1791), an English nurseryman. The type species *Gordonia lasianthus* (L.) Ellis (basinym: *Hypericum lasianthus* L.), is a tree originally from the coastal plain areas along Loblolly Bay in eastern North America.

Gordonia Ellis is a conserved generic name against the earlier name, *Lasianthus* Adanson (1763). In addition, a number of synonyms were proposed by different authors. Some of them perpetuate to this day. The most controversial one is *Laplacea* HBK (1822), which is based on a plant (*Laplacea speciosa* Kunth ex HBK) from Ecuador in South America. The original *Gordonia*, namely *G. lasianthus* Ellis, differs considerably from the type species of *Laplacea*, namely *L. speciosa* HBK. They differ in various aspects of pedicels, bracteoles, sepals, petals, androecia and gynoecia. These differences gradually break down when many more species were subsequently discovered and described. Even in recent literature, several authors (e.g. Melchior, Kobuski) maintain *Laplacea* as a separate genus mainly on the ground of the usually 5 short, free styles; while others (e.g. Burkill, Merrill, Sealy) advocate that these two genera, *Gordonia* and *Laplacea*, should be merged. A formal fusion was made by the present writer (Keng 1980).

For the Asiatic *Gordonia* species, the earliest synonym is *Polyspora* Sweet (1826). It was named after a plant originally described under the name *Camellia axillaris* Roxb. ex Ker. The flowers of this plant are almost sessile, the bracteoles and bracts pass gradually into sepals which protect the rest of the flower parts in bud, the style is stout and 5-fid at the apex. Other notable synonyms are *Antheeischima* and *Closaschima* of Korthals (1842), who tended to think that plants from America and Asia could not be possibly accommodated in the same genus. Korthals' two new genera were based on two Malesian plants, *Gordonia excelsa* Bl. and *G. ovalis* Korth., respectively.

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* Part One: The Genus *Pyrenaria* (Theaceae) in Malesia, *Gard. Bull. Sing.* 33 (1980) 264–289.

Like Korthals, Pitard, (1902) also emphasized the geographic separation between Asia and America, and established the genus *Nabiasodendron* for the Asiatic *Gordonia* species. Besides some external morphological characters, Pitard mentioned some dubious internal anatomical features to stress that the Asiatic species should be classified in a separate genus. For critical discussions of these and other synonyms of *Gordonia*, see Burkill (1917) and Sealy (1958).

On the other hand, the first botanist who referred the Asiatic plants to *Gordonia* is Blume (1825). The Javanese plant was at first described as *Schima excelsa* Bl. in 1823; two years later, it was transferred by himself to *Gordonia*, namely, *G. excelsa* (Bl.) Bl.

II. A GENERAL ACCOUNT OF THE TAXONOMIC CHARACTERS

The Malesian *Gordonia* species are mostly small or medium-sized trees. Some species, however, are lofty trees which can reach 60 m or more in height, while others are shrubs which are usually found in high altitudes (e.g. *G. imbricata* and *G. vulcanica*).

The leaves are alternate, well-spaced, mostly spirally arranged on branchlets. The leaf-bases are acute, attenuate or rounded, sometimes decurrent along the petiole and forming two narrow wings (e.g. *G. multinervis, G. singaporeana* and *G. oblongifolia*), which are especially prominent in young trees and saplings. The nerves are usually visible and often intermingled with smaller, parallel veins and complicately looped and merged near the margin into submarginal veins or reticulations. The secondary veins are invisible in a few species (e.g. *G. imbricata* and *G. ovalis*). The tertiary veins and reticulations, in general, cannot be clearly seen, except after treatment with dilute sodium hydroxide (as seen in some of the illustrations accompanying this paper). The venation is found to be useful in separating some related species and in identifying sterile material of *Gordonia*.

The flowers are borne in leaf-axils, often in the upper axils, usually solitary, rarely 2–3 in a cluster. Each flower is usually subtended by one bract and two bracteoles which are generally caducous. In *G. maingayi*, however, the bracteoles, bracts and sepals, not being clearly differentiated, together form perules subtending the corolla at anthesis. While in most of the other species, the bracteoles, bracts and sepals are ± differentiated, the bract and bracteoles are caducous, only the sepals being present at anthesis. The peduncles vary in length, the flowers are sessile or subsessile in some species.

The differentiation between calyx and the corolla in most species is clear: sepals are 5–6 in number, thick and hairy; petals are also 5-6, generally thick (at least in their lower middle part) and briefly joined at the base into a short corolla-tube and shed together after anthesis. In *G. sarawakensis*, the petals are 8–10 in number, but they are relatively narrow, arranged in one series; whereas in *G. borneensis* and *G. polisana*, the petals are also 8–10 in number, but are very broad, arranged in two distinct series. In the two latter species, the petals of the outer series are smaller and somewhat intermediate between sepals and petals.

The androecium consists of numerous stamens which are in 3–4 whorls, usually briefly fused at the base, sometimes in 5 (or 4) groups. The filaments are glabrous or hairy, or more often the upper part glabrous and the lower, hairy. They are always adnate to the base of the corolla and shed together after anthesis.

The gynoecium consists of a usually hairy, ovoid or subglobose ovary, one (solitary or branched) or several (5, rarely 3 or 4 more) free styles, of which the tip is enlarged into a stigma. Exceptions are found in *G. ovalis* and *G. sarawakensis* in which species the styles are absent and the stigmas lie on top of the ovary. In each ovary-locule, 3–5 ovules are found.

The fruits are capsular, angulate, cylindric-oblong to ellipsoid, rarely broadly ovoid (e.g. *G. borneensis*) or subglobose (e.g. *G. sarawakensis*), dehiscing loculicidally from the top downwards. As they are mostly 5-locular, they thus often dehisce into 5 valves. In those species with ovary-locules other than 5, the number of valves is generally in accordance with that of their ovary-locules; thus 3 (-4) in *G. scortechini*, and 7–8 in *G. sarawakensis*. In the last named species, septicidal lines can be clearly seen in the lower part of the fruit. In fully matured fruits of all *Gordonia* species, the valves break away for most of their length from the stout columella, but remain attached to it at the base for some time and eventually disintegrate.

The seeds are usually ovoid or ellipsoid, always flattened, 2–3 in each locule, with a large obliquely attached apical wing. Superficially they resemble the seeds of some conifers (e.g. *Pinus, Abies* or *Keteleeria*). The embryo is large, slightly bent, surrounded by a thin layer of endosperm.

III. TAXONOMIC TREATMENT

Gordonia Ellis

Gordonia Ellis, Phil. Trans. London 60 (1771) 518, *t. 11* [Type species: *Gordonia lasianthus* (Linn.) Ellis]; Benth. in B. & H. Gen. Pl. 1 (1862) 186 (incl. *Laplacea*); Szyszyl. in E. & P. Pflanzenfam. 3, 6 (1893) 185 (*incl. Haemocharis*); Melchior in E. & P. Pflanzenfam. ed. 2, 21 (1925) 136, *f. 63 (incl. Laplacea*); Burkill, J. Str. Br. Roy. As. Soc. 76 (1917) 133 (*incl. Haemocharis*); Merrill, J. Str. Br. Roy. As. Soc. 86 (1922) 332; Sealy, Rev. Gen. *Camellia* (1958) 8; H. Keng, Gard. Bull. Sing. 33 (1980) 308. *Nom. cons.*

Lasianthus Adans., Fam. 2 (1763) 398 [*non* Jack (1823), *nec* Zucc. *ex* DC (1836)].

Laplacea HBK, Nov. Gen. Sp. 5 (1822) 207, *t. 461.*

Lindleya Nees, Flora 4 (1821) 299.

Haemocharis Salisb. *ex* Martius et Zucc., Nov. Gen. Sp. 1 (1824) 106.

Polyspora Sweet, Hort. Brit. ed. 1 (1826) 61.

Antheeischima Korth., Kruidk. (1842) 137, *t. 27.*

Closaschima Korth. op. cit. 139.

Carria Gardn. Calc. J. Nat. Hist. 7 (1847) 6.

Dipterospermum Griff., Notul. 4 (1854) 564.

Nabiasodendron Pitard, Act. Soc. Linn. Bordeaux 57 (1902) Cpt. Rend. Sc. 54.

Small to medium-sized trees, rarely shrubs. Leaves simple, coriaceous, alternate, spirally or distichously arranged, entire or serrate. Flowers bisexual, axillary, solitary or 2–3 (rarely more) congested in a cluster, shortly pedunculate or subsessile; bracteoles and bracts 2–3 or more; sepals 5–6, unequal; petals 5–6, rarely 9–10, unequal or subequal, usually briefly fused at the base; stamens numerous, in 3 or 4 whorls, shortly connate at the base and often briefly adnate to the corolla, sometimes in 4–5 less distinct fascicles; anthers versatile, on a short or long filament; ovary mostly 5-locular, rarely 8–10 or 3–4 locular; ovules 2–8 (usually 3–5) in each locule, on axile placentation in two vertical rows; styles mostly 5, sometimes more or only 3, fused to varying extent proximally, or sometimes totally free. Fruit a woody capsule, ovoid-cylindric, bluntly angulate, dehiscing loculicidally from apex to base along a persistent central columella. Seeds usually 2–5 in each locule, compressed, with a thin membranous, oblique, unilaterally attached wing; testa soft woody; embryo oblong, straight or slightly oblique; endosperm of a thin layer, enveloping the embryo.

A genus with about seventy species; occurs in SE. Asia and America. Forty or so Asiatic species are found from India, Sri Lanka, Burma, Thailand, Indochina, S. China to Taiwan and southwards to Malesia (the Malay Peninsula, Sumatra, Borneo, Java, the Philippines, Celebes to New Guinea). Thirty or so American species are concentrated in Central America and the West Indies (most of them formerly arranged under the generic names *Haemocharis* or *Laplacea*), with a few species in the northern parts of South America, and only one species (which is the type species) in the southeast of the United States of America.

About 21 species occur in Malesia.

KEY TO THE MALESIAN *GORDONIA* SPECIES

1. Average leaves very large, generally over 15 cm long
    2. Peduncles of flowers generally less than 0.5 cm long
        3. Leaf-apex usually acuminate; nerves 10–11 pairs; flowers 5–6 cm across (the Malay Peninsula) .... 20. *G. taipingensis*
        3. Leaf-apex usually rounded and mucronate; nerves up to 18 pairs; flowers 3–4 cm across (the Malay Peninsula) .... 12. *G. multinervis*
    2. Peduncles of flowers usually over 1.5 cm long
        4. Petioles conspicuously winged; sepals persistent in fruit
            5. Capsules broadly ovoid, 2–3 cm long (Borneo: Sabah and Kalimantan) .... 2. *G. borneensis*
            5. Capsules cylindric, about 5 cm long (Sumatra) .... 13. *G. oblongifolia*

4. Petioles not winged; sepals caducous in fruit; capsules broadly ovoid, about 5 cm long (Borneo: Sabah) ....4. *G. grandiflora*

1. Average leaves smaller, generally less than 15 cm long

6. Average leaves relatively small, usually less than 9.5 cm long

7. Leaf-apex generally obtuse or rounded, often emarginate; plants often found in montane or lower montane forest

8. Petals mostly 5, rarely 6, in one whorl; leaves thick coriaceous

9. Leaves elliptic, 4.5–9.5 cm long (the Malay Peninsula & Borneo) ....7. *G. imbricata*

9. Leaves ovate or broadly oblong 2–5 cm long; capsules 2.5–3 cm long (Sumatra)...... ....21. *G. vulcanica*

8. Petals 8–10, in two whorls; leaves thin-coriaceous (the Philippines) ......16. *G. polisana*

7. Leaf-apex mostly acute or acuminate, pointed or blunt and rarely rounded; plants generally found in lowland or at medium altitudes

10. Ovary 3- (rarely 4-) locular, the 3 (rarely 4) styles free; flowers very small (1.5–1.8 cm across) (the Malay Peninsula) ....18. *G. scortechinii*

10. Ovary 5- (rarely 4-) locular; styles fused together into a column, sometimes branched above; flowers various

11. Number of bracteoles, bracts and sepals rather large (around or over 10) and less clearly differentiated, together forming overlapping perules surrounding the flowers at anthesis (the Malay Peninsula).................................10. *G. maingayi*

11. Number of bracteoles, bracts and sepals generally less than 8, and usually differentiated; normally bracteoles and bract caducous and only the sepals present at anthesis

12. Leaf-apex generally acuminate and obliquely caudate; capsule cylindric, pointed, 3.5–5 cm long (the Malay Peninsula) ....15. *G. penangensis*

12. Leaf-apex acute or sometimes acuminate, but rarely caudate; capsules usually less than 3 cm long

13. Leaves 3–6 cm wide, often glaucescent beneath; flowers 3–3.5 cm across; styles solitary, with a club-shaped tip (Borneo: Sarawak & Sabah) ....5. *G. havilandi*

13. Leaves generally less than 3 cm wide, not glaucescent below; flowers less than 2.5 cm across; styles either branched or absent

14. Nerves visible; style 1.5–2.5 mm long, 5-branched above (Borneo) ....11. *G. marginata*

14. Nerves nearly invisible; style absent, only 5 tiny protrusions (less than 1 mm long) on top of the ovary representing the stigmas (Sumatra) ....14. *G. ovalis*

6. Average leaves generally between 10 to 14 cm long

15. Petals 7–8, in one series; ovary 8–10 locular, style absent or very short; fruit broadly ovoid or subglobose (Borneo: Sarawak & Sabah)............................17. *G. sarawakensis*

15. Petals 5–6; ovary 5- (rarely 4-) locular; style present; fruit generally ovoid or cylindric

16. Leaf-margin entire, subentire, very rarely serrulate (Java, Bali, Celebes) .... 8. *G. integerrima*

16. Leaf-margin serrate or serrulate

    17. Peduncles of flowers usually less than 0.5 cm long

        18. Leaves subsessile or sessile, the blade usually tapering towards the base and winged; capsules 3 or 5 cm long

            19. Leaves thin-coriaceous; nerves 10–12 pairs; flowers 4–5 cm across (the Malay Peninsula) ....19. *G. singaporeana*

            19. Leaves membranous; nerves 12–18 pairs; flowers 2–3.5 cm across (the Malay Peninsula) ....12. *G. multinervis*

        18. Leaves petiolate, petiole 5–8 mm long; leaf-base not winged; capsules 2 or 2.5 cm long (the Malay Peninsula) ....6. *G. hirtella*

    17. Peduncles of flowers generally 0.5–1 cm long, sometimes longer

        20. Style columnar, the tip enlarged, discoid, shallowly 5- (rarely 4-) lobed

            21. Flowers 2.5–3 cm across; capsule 3.5–4.5 cm long (Sumatra and Java) ....3. *G. excelsa*

            21. Flowers 7–8 cm across; capsules 3–4 cm long (the Philippines) ....9. *G. luzonica*

        20. Style distinctly 5-branched above (Celebes, Lesser Sunda Isls., Moluccas and New Guinea) ....1. *G. amboinensis*

1. Gordonia amboinensis (Miq.) Merr., J. Str. Br. Roy. As. Soc. 86 (1922) 332. Fig. 1

Laplacea amboinensis Miq., Ann. Mus. Bot. Lugd. Bat. 4 (1968) 114 (based on *Lignum mucosum* vel *Caju lapia* Rumph., Herb. Amb. III (1743) 203, *tab.130*).

Haemocharis amboinensis (Miq.) Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 141, 158.

Gordonia rumphii Merr., Interpret. Herb. Amb. (1917) 368.

Gordonia brassii Kobuski, J. Arn. Arb. 21 (1940) 135. **Syn. nov.**

Gordonia papuana Kobuski, op. cit., 136 (*incl.* var. *acuminata* & var. *montana*); W. R. Barker, Brunonia 3 (1980) 8 *f.1.* **Syn. nov.**

Gordonia sp. Kobuski, op. cit., 139 (citing *Brass & Versteegh 13169* from W. Irian).

Tree, to 20 (-25) m tall. Bark grey to brown, smooth or shallowly fissured; inner bark beefy red. Young twigs and buds covered with short silky hairs or glabrous. Leaf-blades thin coriaceous or membranous, lanceolate, narrowly ovate to ovate-elliptic, 7–14 (-20) cm long, 3–5.5 (-8) cm wide, apex bluntly acuminate, sometimes obtuse or retuse, base acute or attenuate; margin shallowly crenate to undulate, or subentire; nerves 9–12 pairs, intermingled with less conspicuous veins and merged and looped into submarginal reticulation; glabrous above, glabrescent and sometimes papillate beneath; petiole 0.5–1 (-1.5) cm long, thickened. Flowers in the upper axils, solitary; peduncle 0.5–1 (-2) cm long, slender. Bracteoles and bracts 2–3, caducous. Sepals 4–5, unequal, deltoid, lunate or broadly ovoid, 4–6 mm long, coriaceous, densely covered with silky hairs externally. Corolla 3–4 cm across, creamy yellow or white; petals 5–6, broadly ovate to subrounded, concave, 1.5–2 cm long, the outer surface sericeous in the central portion and below, glabrous around the margin. Androecium 7–8 mm long, the filaments glabrous, except the base which is covered with short hairs. Gynoecium 5–8 mm long, shortly silky; ovary globose or ovoid, 3–4 mm in diameter; style (4-) 5-branched above. Capsule

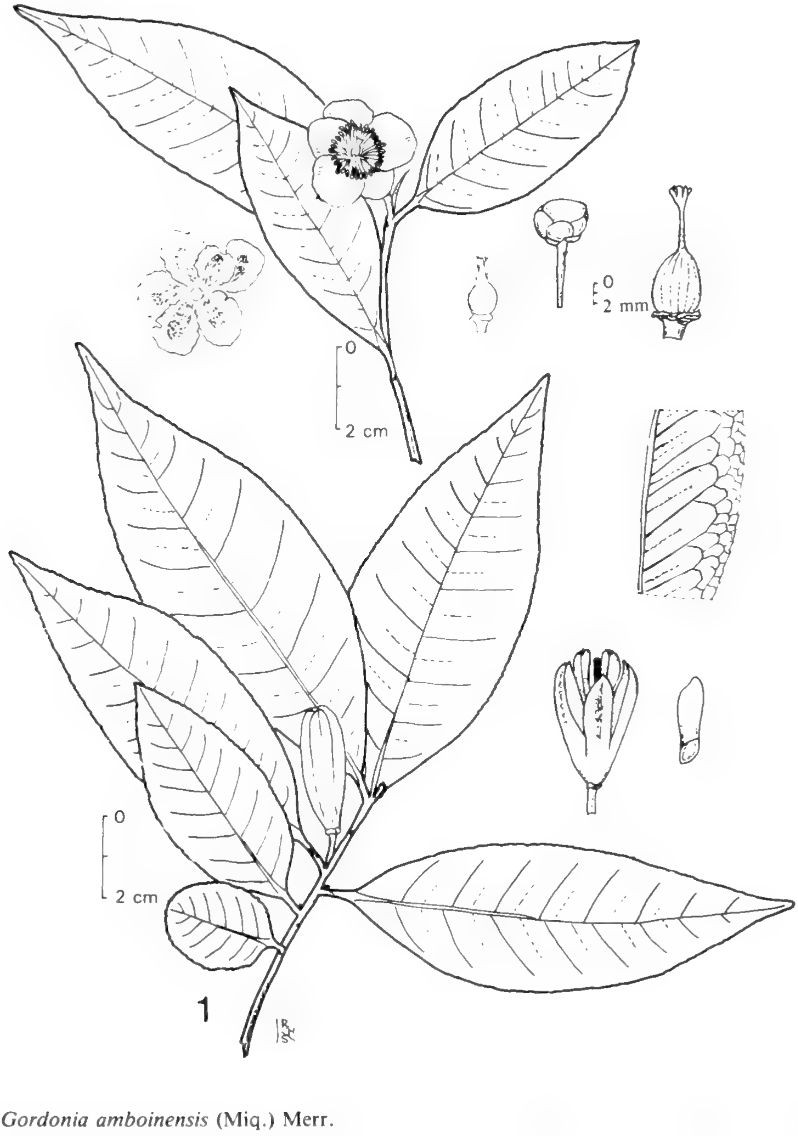

Fig. 1. *Gordonia amboinensis* (Miq.) Merr.
Ambon, *Teysmann H. B. 5587* (Herb. Lugd. Bat. No. *908, 249-227) (lectotype);* Halmahera, *Neth. Ind. For. Serv. 31360* (fr.).

oblong cylindric, 2.5–3 (-3.5) cm long, puberulous, dehiscing into 4 or 5 valves. Seeds about 2 cm long including the wing.

DISTRIBUTION. Malesia (Celebes, Moluccas, Lesser Sunda Isls. and New Guinea) and Bismarck Archipelago (New Britain and New Ireland). (All specimens cited below from L).

Celebes. Minahassa, *Koorders 18910, 18912, 18913, 18914*; Molili, *Neth. Ind. For. Serv. 481.*

Moluccas. G. Sembilan, Halmahera, *Pleyte 341*; Ternate, *Neth. Ind. For. Serv. 24534.* P. Buru, *Neth. Ind. For. Serv. 31360,* Ceram, *Eyma 2214, Kuswata & Soepadmo 240.* Ambon, *Robinson 276* (isotype of *Gordonia rumphii* Merr.); *De Vriese & Teijsmann Herb. Lugd. Bat. No. 908, 251–414; Teysmann H. B. 1970* (*Herb. Lugd. Bat. No. 908, 251–224, & -225*), *H. B. 5587* (*Herb. Lugd. Bat. No. 908,*

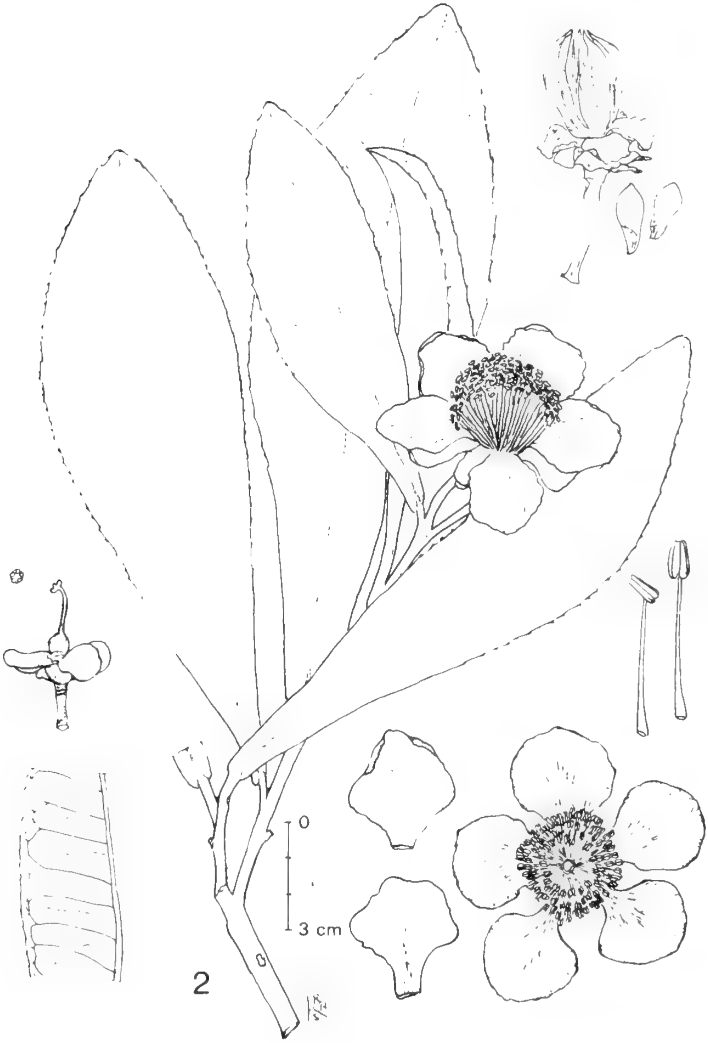

Fig. 2. *Gordonia borneensis* H. Keng **sp. nov.**
Kalimantan, *Kostermans 35063* (fl.); *Kostermans 13627* (fr.).

249-227, lectotype of *Laplacea amboinensis* Miq.)

Lesser Sunda Isls. Bali, Mt. Batukau complex, *Kostermans et al. KK-SS 137, 174.* Flores, near Wae Mao, *Kostermans 838*; Monde Hill, *Schmutz 3552, 3711.*

Irian Jaya (representative specimens only). Sidoarsi Mts., Hollandia D. 3t, *Iwanggin BW 9037*; Sibil Valley, Star Mts., *Kalkman 4285*; near Andai, SW. of Manokwari, *Koster BW 11798*; near Soendei, Isle of Biak, *Moll BW 9721*; Cycloop Mts., Hollandia Dist., *van Royen 3635*; Mt. Tohkiri, Vogelkop Peninsula, *van Royen & Sleumer 7253*; Tobie, Kebar Valley, *Schram BW 7970*; Aisao, Japen Isl., *Schram BW 10584.*

Papua New Guinea (representative specimens only). Arau, Eastern Highlands Dist. *Brass 32063*; Mt. Dayman, Maneau Range, *Brass 23243*; Torricelli Mts., W. Sepik Dist., *Darbyshire 358*; near Lake Birip, Wabag, W. Highlands Dist., *Flenley ANU 2738*; Above Akuna, E. Highlands Dist., *Hartley 11986*; upper Oriomo, Western Dist., *Havel 17246*; Kwa Mountain, Rossel Isl., *Henty NGF 27071*; near Frieda River, W. Sepik Dist., *Henty & Foreman NGF 42579;* Mt. Rawlinson, Morobe Dist., *Hoogland 9262*; Mt. Hunstein, Sepik Dist., *Hoogland & Craven 10951*; near Hagen Station, W. Highlands Dist., *Hoogland & Pullen 5965*; Lake Erobo, S. Highlands Dist., *Powell 2423;* Ingembit, Western Dist., *Ridsdale, Henty & Galore NGF 31943*; Marapuna, Eastern Highlands Dist., *van Royen NGF 15053*; Mt. Kumme, Central Dist., *van Royen NGF 20346, 20416*; Above Kiburu, Southern Highlands Dist., *Schodde 1371*; Mt. Simpson, Milne Bay Dist., *Schodde 5522*; Mt. Pigini; Central Dist., *Stevens LAE 50449*; near Kapiaggo, Western Highlands Dist., Vandenberg, *Womersley & Galore NGF 39995*; near Nondugl, Eastern Highlands Dist., *Womersley 4860.*

ECOLOGY. From lowland rain or swamp-forest to lower montane or montane moss forests, in *Eucalyptus-Gironniera, Castanopsis-Quercus*, or *Nothofagus* forests; on sandy or clay soil, also on limestone ridge and in disturbed areas and grassland. Altitudes 50–2000 m. Fl.: Apr.–Nov., fr.: Jun.–Jan. (few collections only).

VERNACULAR NAMES: *adikelp* (Japen), *alimp* (Tagoba), *bado* (Motus), *baif* (Gab-gab), *benelemonde* (Hattam), *bwabwa* (Wafu), *dapiri* (Mid. Waria), *dimi* (Kiwai), *iniaili* (Je), *kawal-gugn* (Mini), *kerkebo* (Flores), *kimkaroo* (Tehid), *la* (Enga), *kilimdan* (Sepit), *koka kaber* (Knambiadi), *kuku* (Kutub), *La* (Enga), *naningning* (New Britain), *oytungo* (Aseki), *reik* (W. Biak), *sjioe* (Andjai), *tawan* (Wipi), *timor* (Mendi), *toani* (Ormoe), *tokoi* (Manikiong), *totona Rombo* (Garumaia), *tugera* (Waskuk).

NOTE. Kobuski (1940) examined 8 specimens of *Gordonia* from New Guinea then available to him and recognised 4 entities — one uncertain species and two new ones of which one consisted of two varieties. Barker (1980) in a recent revision correctly pointed out that there is only one homogeneous species in New Guinea, showing little or no evidence of polymorphism.

When the New Guinea material was compared with those from Moluccas, Celebes and the Lesser Sunda Islands, they were found to agree in leaf, flower and fruit characters. I therefore adopt *Gordonia amboinensis* (Miq.) Merr. as the name for this widely distributed species.

Regarding the field notes of numerous collectors, the following two are noteworthy: on *Brass 23243* was stated that the flowers are 6–6.5 cm in diameter; this appears much larger than the usual size (3–4 cm in diameter). *Schram BW 10584* indicated the flowers are pink; all the others are recorded as white, creamy white or creamy. Some specimens from Flores (e.g. *Schmutz 3711*) have much smaller capsules (less than 2 cm long) which are probably immature or from trees growing on extremely poor soil. They also may represent a new entity.

Gordonia amboinensis is closely allied to *G. excelsa*. The two are quite similar in shape and venation of their leaves. However, they can be differentiated by their shape and size of the flowers and geographically they are more or less demarcated.

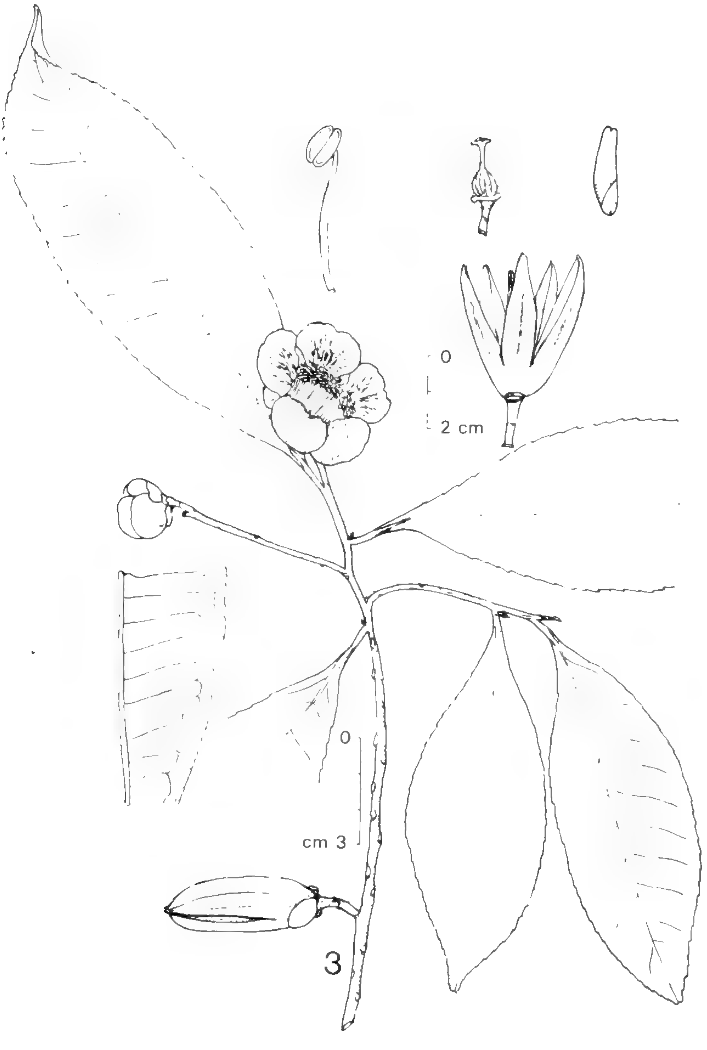

Fig. 3. *Gordonia excelsa* (Bl.) Bl.
Java, Cult. in Hort. Bog. *No. 161* (*Anno* 1901); *Koorders 14735* (fr.).

2. Gordonia borneensis H. Keng, sp. nov.

Fig. 2

Arbor 20–30 m alta. Folia angusto-elliptica, angusto-obovata vel oblanceolata, 18–25 (-30) cm longa, apice acuta vel cuspidata, basi attenuata vel cuneata, coriacea tenui, nervis lateralibus 20–22, petiolo 3–5 mm longo. Flores flavi, axillares, solitarii, 6–7.5 cm diametro; bracteae 2, caducuae; sepala 5, subrotundata, 1–1.2 cm longa; petala circa 10, 1.5–3.5 cm longa. Gynoecium 2.5–3.5 cm longum; styli ad apicem discoideum. Capsula obovoidea, 2–3 cm longa, valvis 5.– Typus: E. Kalimantan, *Kostermans 7084*, in L.

A tree, 20–30 m tall. Bark greyish brown, smooth, or minutely fissured; young branches stout, glabrescent. Leaf-blades thin coriaceous, narrowly elliptic, narrowly obovate or oblanceolate, apex acute or obliquely cuspidate, base attenuate or cuneate and narrowly winged, 18–25 (-30) cm long, 6.5–7.5 (-10) cm wide; margin finely crenulate-serrulate for the most part, subentire or entire near the base; side veins 20–22 pairs, further intermingled with less distinct and smaller ones in between and intricately interlooped near the margin; glabrous on both surfaces, thinly puberulous on the midrib beneath; petiole 2–5 mm long, thickened. Flowers solitary, in upper leaf-axils, sometimes several together on the branch tips; peduncle 1.5–2.5 cm long, often elongate and much thickened after anthesis. Bracts 2, a short distance below the calyx, caducous. Sepals 5, suborbicular, 1–1.2 cm long coriaceous, silky-hairy externally. Corolla 6–7.5 cm across, yellow to bright yellow (*fide* Kostermans); petals about 10, in 2 series, sericeous externally, petals of the outer series thicker (thin coriaceous) and smaller (1.5–2 cm long), broadly oblong or sub-rounded, somewhat intermediate between sepals and the inner petals; petals of the inner series thinner (membranous) and larger (2.5–3.5 cm long), broadly ovate or broadly oblong, apex often notched, base sometimes abruptly narrowed, 2.5–3.5 cm long. Androecium 1.2–1.5 cm long; stamens numerous, in 3–4 whorls, connate below, the filaments glabrous. Gynoecium 2.5–3.5 cm long; style 1, 1.5–2 cm long, the tip discoid, shallowly 5-lobed into stigmas; ovary ovoid, 1.–1.5 cm long, densely covered with yellowish brown hair. Capsule obovoid, 5-angulate, 2–3 cm long; calyx persistent. Seeds about 2 cm long including the wing.

DISTRIBUTION. Malesia (Brunei, Sabah and Kalimantan).

Brunei. Kuala Sebatu, *Ashton BRUN 354* (BO, L, SING).

Sabah. Monsapol F. R., Sipitang, *Aban Gibot SAN 65950* (L); Kalabakan, Tawau, *Bakar SAN 24974* (BO, L, SING); Benawood, Tawau, *Felilis & Sumbing SAN 88140, 88418* (SAN); Sandakan, *J. Singh SAN 53427* (L, SING); Ulu Dusun, Sandakan, *Tarodop SAN 87724* (SAN); Beaufort, *Wood & Kapis SAN 16984* (BO, L, SAN, SING).

Kalimantan. Tg. Bangko, near mouth of Sg. Mahakam, *Kostermans 7084* (L, holotype; BO, isotype); Sangkulirang, Karangan River, *Kostermans 13627* (BO, L); Sg. Tiram Balikpapan, *Kostermans 35063*; Landak, W. Borneo, *Ngabang 6410* (L).

ECOLOGY. In primary forests, on low ridges in sandy soils or on seasonally inundated riverine alluvium. Alt. 20–100 m. Fl. May–Aug.; fr.: Aug–Oct.

VERNACULAR NAMES: *obah* (Sabah), *rawali batu* (Kalimantan).

NOTE. This species differs from *G. grandifolia* Merr. and *G. oblongifolia* Steenis in that the flowers have about 10 petals in two series (instead of 5 petals in one series) and in the much smaller fruits and seeds.

Fig. 4. *Gordonia grandiflora* Merr.
Sabah, *Wood SAN 16185* (fr.); *Meijer SAN 94245* (fl.).

3. **Gordonia excelsa** (Bl.) Bl., Bijdr. (1825) 130; Miq., Fl. Ind. Bat. 2 (1857) 489; Koord. & Val., Med., 's Lands Pl. Tuin (1896) 289 (*incl.* var. *macrocarpa* K. & V.); Koord., Exk. Pl. Jav. 2 (1912) 608; Koord. -Schum. Syst. Verz. fam. 180 (1913) 35; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 155; Merr. Contr. Arn. Arb. 8 (1934) 106; Back. & Bakh. f. Fl. Jav. 1 (1963) 320. Fig. 3

Schima excelsa Bl., Cat. (1823) 80.

Antheeischima excelsa (Bl.) Korth., Kruidk. (1842) 138, *t. 27.*

Gordonia acuminata Choisy in Zoll. Syst. Verz. 2 (1854) 144.

Small or large tree, to 40 m tall. Bark smooth, greyish brown. Young twigs slender, covered with soft yellow hairs or puberulous; old branches glabrescent.

Leaf-blades thin coriaceous or membraneous, elliptic or narrowly elliptic or oblong-lanceolate, apex obtuse or acuminate, base attenuate, (7-) 10–14 (-20) cm long, (2.5-) 3.5–4.5 (-6) cm wide, equal or sometimes slightly bent and unequal-sided; margin remotely serrulate; midrib impressed above and elevated below; nerves 12–15 pairs, connected and merged into submarginal reticulation; glabrous above, appressed pubescent beneath; petiole 0.5–1 cm long, puberulous. Flowers in axils of the upper leaves or subterminal, usually solitary; peduncle 0.5–1 (to 2 cm in fruit) cm long, stout, velutinous. Bract and bracteoles about 3 caducous. Sepals 5–6, unequal, reniform to suborbicular, 7–8 mm long, sericeous. Corolla 2.5–3.5 cm across, white, fragrant; petals 5–6, deltoid-reniform, often concave and notched, 1–1.7 cm long, 1.2–2 cm wide, thin coriaceous, sericeous on both sides except the edge of the inner surface, which is glabrous. Androecium about 1 cm long; filaments nearly glabrous and briefly united below. Gynoecium about 1 cm long; style 1, stout, 5–6 mm long, glabrescent, the tip disk-shaped, shallowly undulate or shortly lobed into 5 stigmas; ovary globose, 4–5 mm across, densely sericeous. Capsule cylindric, 3.5–4.5 (-5) cm long, bluntly angulate, pubescent, dehiscing into 5 valves. Seeds 2–2.5 cm long including the wing.

DISTRIBUTION. Malesia (Sumatra & Java).

Sumatra. Without precise locality, *Forbes 2053* (L). West Coast, *Neth, Ind. For. Serv. 2860, 2878* (L).

Java. G. Loechoer, *Bakhuizen* v/d *Brink 7146* (L); G. Salak, *Blume Herb. Lugd. Bat. 908, 251–415, -421* (lectotype), *-422, -431* (L); without locality, *Houtsoorten van Gedeh* 638 (L), *Junghuhn 73, 83*; Besuki, *Koorders 14735* (holotype of *G. excelsa* Bl. var. *macrocarpa* K. & V.), *20381, 28675, 32342* (L), *Sukari FRI 7525;* Java, *Teysmann s.n. in 1860* (L); Preanger, *Winckel 486* (L) *Wind s.n. in 1918* (L).

ECOLOGY. In primary forests, altitude 600–1700 m . Fl.: Apr.–Nov. fr.: Jun.–Feb.

NOTE. This is the first Asiatic species described under *Gordonia*, a genus previously known only from N. America.

4. **Gordonia grandiflora** Merr., J. Str. Br. Roy. As. Soc. 86 (1922) 331; Masamune, Enum. Phan. Born. (1942) 472. Fig. 4

Small or large tree, 10–28 m tall. Bark greyish brown fissured or scaly. Branchlets stout, glabrescent. Leaf-blades coriaceous, elliptic, narrowly elliptic or obovate, sometimes oblanceolate, 15–25 (-35) cm long, 6.5–8 (-10) cm wide, apex obtuse or abruptly acute, base attenuate, decurrent and narrowly winged or sometimes rounded; margin crenulate; nerves 13–16 pairs; glabrous above, scattered with short hairs beneath; Petiole 3–5 mm long, thickened. Flowers solitary, in upper leaf-axils; peduncles 2–3 cm long, stout. Bracts and sepals not seen. Corolla 8–9 cm across, white; petals 5, membranous, pubescent externally, broadly oblong or obovate, 4–4.5 cm long, narrowed beneath, sometimes notched or bilobed above. Androecium 1.5–2 cm long, the filaments pubescent, connate only at the base and adnate to the corolla. Gynoecium not seen. Fruit (nearly mature) broadly ovoid, about 5 cm long, dehiscing into 5 valves. Seeds about 4 cm long including the wing.

DISTRIBUTION. Malesia (Sabah).

Sabah. Rosab, near Kudat. *P. Castro 972* (A, isotype [photo]); Ranau, Kinabalu National Park, *Aban Gibot SAN 76577, 76605, 76608* (SAN), *Meijer SAN 94245* (SAN); Kota Belud, Kandasan, *Wood & Kapis SAN 16185* (B, SING).

ECOLOGY. In primary forest, on hill side or on dry slopes; alt. 50–1,300 m. Fl.: Sept. & Nov. (2 collections); fr.: Feb. (1 collection).

NOTE. This species, as mentioned in some of the field notes is common in the Kinabalu National Park. However, among the material available, only *Meijer 94245*

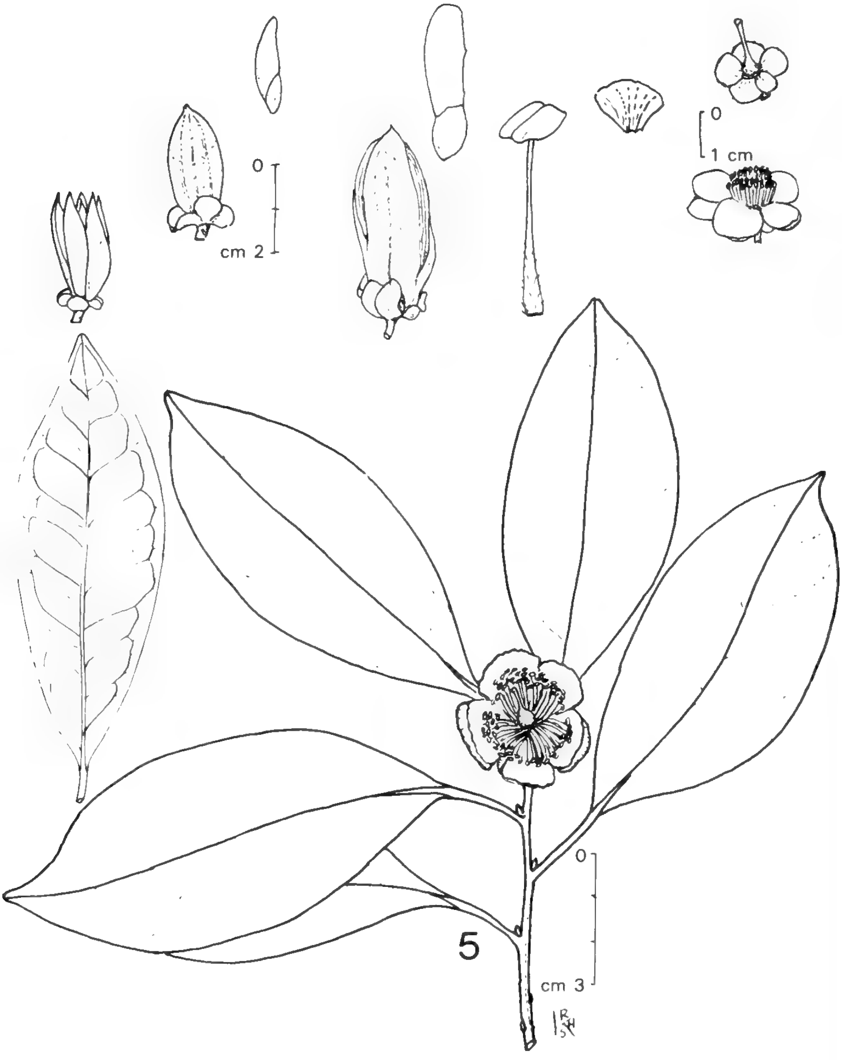

Fig. 5. *Gordonia havilandii* Burk.
Sarawak, *Haviland 1995 (syntype,* fl.); *Rosali S 15184* (fr., immature). Sabah, *Amin G. et al. SAN 93856* (fr., mature).

bears a detached corolla, and *Wood & Kapis 16185* (2 specimens) bears two nearly mature fruits, the others being sterile. A photo of the type (*Castro 972*) was made available through the courtesy of the Director of the Arnold Arboretum, Harvard University.

In Merrill's original description, the sepals are "coriaceous, broadly ovate to orbicular-ovate, rounded, glabrous or slightly pubescent, 1.5–2 cm long and somewhat accrescent in anthesis", the ovary is "pubescent" and the style is "slender, glabrous, up to 2.5 cm long". He also mentioned that the flower is "10–11 cm in diameter". This is larger than in *Meijer 94245*, which is 8–9 cm across.

This species is related to *G. oblongifolia* of Sumatra. Because of the scarcity and imperfection of fertile materials in both species, close comparisons cannot be made at the present.

5. **Gordonia havilandii** Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 157; Merr., op. cit. spec. no. 20 (1921) 389. Fig. 5

Small to medium-sized tree about 25 m tall and 30 cm in diameter. Bark smooth, hoop-marked, mauve brown and grey. Young twigs slender, covered with yellow or black hispid hairs. Older branches greyish brown, glabrescent. Leaf-blades chartaceous or thin coriaceous, elliptic, rarely narrowly or broadly elliptic, obtuse or acuminate, occasionally cuspidate, base cuneate or attenuate, 7–10 (-12) cm long, 3–6 cm wide, symmetrical or sometimes slightly unequal; margin entire or nearly so; midrib impressed above, tomentose and glaucescent beneath; nerves 9–10 pairs, less conspicuous above; petiole slender, 1–1.5 cm long, puberulent. Flowers subterminal and in upper axils, solitary or 2–3 together; peduncles 2–3 mm long, hispid. Bracteoles and bracts 2–3 silvery puberulous, orbiculate-deltoid, 2–3 mm long. Sepals 5–6 suborbicular, 7–8 mm long leathery, sericeous externally. Corolla 3–3.5 cm across, yellow or pale yellow; petals 5–6, suborbicular to reniform, 0.8–1.2 cm long, thin leathery, concave, sericeous externally. Androecium 6–7 mm long, the filaments thinly sericeous in the lower part, and united at the base. Gynoecium about 1 cm long; style 1, 6–7 mm long, glabrescent; stigmas 5, very short; ovary globose, 3–4 mm across, densely sericeous. Capsule cylindric, 2.5–4.5 cm long, 1.2–2 cm across, pointed, bluntly 5 angled, thinly strigose; calyx persistent. Seeds about 2–4 cm long including the narrow wing.

DISTRIBUTION. Malesia (Borneo, known only from Sarawak and Sabah).

Sarawak. Mt. Serapi, alt. 900–1000 m, *Haviland 67* (SING, holotype), *1995* (L, SING, syntype); Burgoh Range, near Summit, *Anderson et al. S 29323* (L); Ulu Kenyana, Mukoh, *Ashton S 195492* (SING); Mt. Meroyang, Ulu Lundu, *Ashton S 18861* (L); Semengoh F. R., *Banyeng & Benang S. 25490* (L, SING), *Banyeng & Jugah S 26882* (L), *Rosli S 15184* (L); Mt. Santubong, *Chew 1386* (L, SING); Bt. Lambir, Miri, *Dan bin Hj. Bakar 3090* (L); Sg. Belaban, Lawas, *Ilias S 26319* (L).

Sabah. Telupid, Sandakan, *Aban Gibot & Joseph SAN 94036*; Kiabau, Beluran, *Amin G. et al. SAN 39856*; Sg. Korang, Lamag, *Madani SAN 76315*; Tongod, *Sundaling SAN 90348* (all in SAN).

ECOLOGY. In heath or fagaceous forests, from lowland to the summit of sandstone hills; alt. 15–1850 m. Fl.: Aug.–Nov., fr.: Dec, Mar. & Aug.

VERNACULAR NAME: *linggai.*

NOTE. This species can be recognized by the elliptic leaves with a tomentose and glaucescent undersurface.

6. **Gordonia hirtella** Ridl., J. Str. Br. Roy. As. Soc. 73 (1916) 142; Burk., op. cit., 149, *f.* 7; Ridl., Fl. Mal. Pen. 1 (1922) 204; H. Keng in Ng, Tr. Fl. Mal. 3 (1978) 285. Fig. 6

Tree, 20 m high; bole coarsely and shortly fluted. Bark grey, smooth-rugulose. Young branches slender, silky-pubescent. Leaf-blades thin coriaceous, elliptic, elliptic-lanceolate or narrowly ovate; apex acute or acuminate, base cuneate or

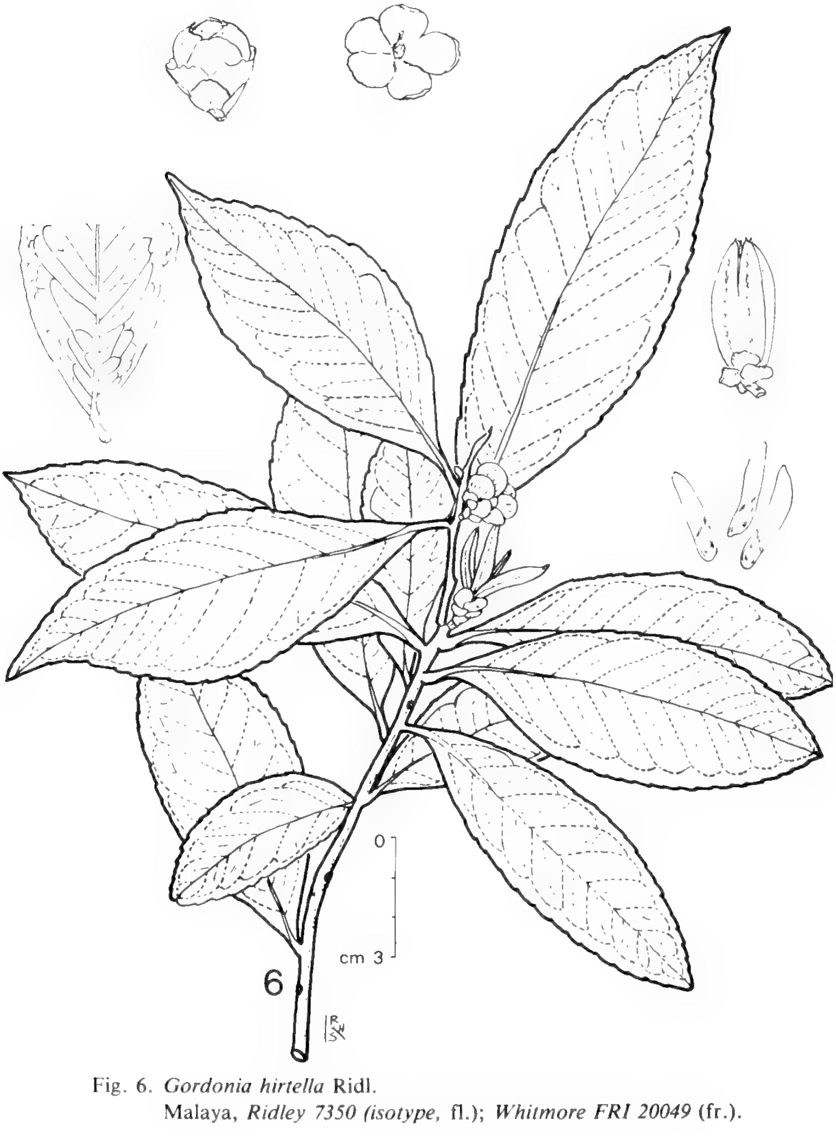

Fig. 6. *Gordonia hirtella* Ridl.
Malaya, *Ridley 7350 (isotype,* fl.); *Whitmore FRI 20049* (fr.).

attenuate, 6–13 (-15) cm long, 2.5–4 (-5) cm wide; margin crenulate-serrate or subentire; nerves and reticulations barely visible above, indistinct below; shining dark green and glabrescent on the upper surface, light green, strigose on and around the midrib especially near the base on the lower surface; petiole 3–6 mm long, densely hispid. Flowers subterminal or in leaf-axils, usually solitary, densely covered with greyish yellow hairs externally; peduncles subsessile or very short (2–3 mm long), appressed silky. Bracteoles and bracts about 3, 1–2 mm long. Sepals about 5, ovate to broadly orbicular, 3–5 mm long. Corolla 2–2.5 cm across, cream in colour; petals 5, oblong to broadly obovate, 1–1.2 cm long, briefly joined at the base. Androecium 4–5 mm long, the filaments connate below and adnate to the corolla tube. Gynoecium 5–6 mm long, the ovary densely covered with greyish yellow hairs, the style and its branches glabrescent. Capsule 2–2.5 cm long, 5-valved, puberulous; sepals persistent. Seeds 1.5–2 cm long including the wing.

DISTRIBUTION. Malesia (the Malay Peninsula)

The Malay Peninsula, Perak, Batu Puteh, *Wray 1116* (syntype, SING). Selangor, Bt. Kutu, *Ridley 7350* (isotype, SING); Bt. Etam, *Kelsall 1848* (SING). Pahang, Sg. Telom Ridge, *Whitmore FRI 20049* (L).

ECOLOGY. In forests and on ridges; alt. 400–1000 m. Fl.: June, fr.: May.

NOTE. Burkill (l.c.) stated that this species "occurs on the central chain of mountains of the Malay Peninsula from Gunong Batu Puteh in Perak to the west of Tapah . . . through Bukit Kutu in Selangor . . . to Bukit Etam . . . on the Selangor Negri Sembilan boundary". Apart from the specimens cited by Ridley and Burkill, which were all collected near the end of the last century, the only single recent collection referable to this species was the collection made by Whitmore from Sg. Telom ridge in NW. Pahang.

7. Gordonia imbricata King, J. As. Soc. Bengal 59, 2 (1890) 204, Ann. Roy. Gard. Calc. 5 (1896) 148, *pl. 179*; Burk., op. cit., 157, *f. 15*; Ridl. Fl. Mal. Pen. 1 (1922) 203; H. Keng in Ng, op. cit., 285. Fig. 7

Low shrub or stout tree, to 15 m tall. Bark brown, finely cracked. Young twigs stout, glabrescent or thinly covered with scattered pilose hairs; older branches often finely fissured. Leaf-blades coriaceous or thick coriaceous, narrowly elliptic to oblanceolate or elliptic; apex obtuse or rounded, sometimes shallowly retuse, base cuneate, 4.5–9.5 (-12) cm long, 2–4 (-5) cm wide; margin remotely undulate or entire, sometimes revolute; midrib sulcate above; nerves about 10–12 pairs, barely visible above, and obscure beneath; drying green; glabrous above, brownish, verruculous and subglaucous beneath; petiole stout, 0.5–1.5 (-2) cm long, puberulous. Flowers axillary or subterminal, solitary or 2–4 and congested near the tip; peduncle absent or very short (1–2 mm long, stout). Bracteoles, bracts and sepals forming an involucre about 1–1.5 cm high, densely woolly externally, and increasing in size from the lower bracteoles (deltoid, 2–3 mm long) to the upper sepals (broadly ovoid to suborbicular, 8–10 mm long). Corolla 2.5–3.5 cm across, white to butter yellow (*fide* Whitmore); petals 5, suborbicular to reinform, 1.2–1.7 cm long, for the most chartaceous and glabrous except the lower portion which is coriaceous and woolly and similar to the sepals. Androecium 8–10 mm long, the filaments velutinous and connate below, Gynoecium 8–9 mm long; style thick, columnar, 2–3 mm long, briefly 5-branched near the tip, glabrous except the lower portion; ovary globose, 5–6 mm long and wide, densely covered with golden velutinous hairs. Capsule cylindric, 4–5 cm long, strigose, dehiscing into 5 valves; sepals persistent until the dehiscence of the capsule. Seed 3–3.5 cm long including the wing.

DISTRIBUTION. Malesia (the Malay Peninsula and Borneo (Sabah)).

The Malay Peninsula. Perak, G. Kerbau, *Robinson s.n.* in June 1913, *Scortechini 402 b* (SING, duplicate of type). Kelantan, G. Stong, *Symington 37695* (SING); Gua Ninik, *Henderson SFN 19745* (SING); G. Rabong, *Soepadmo & Mahmud 1063* (L). Pahang, G. Tahan, *Kloss 12108, 12296* (SING),

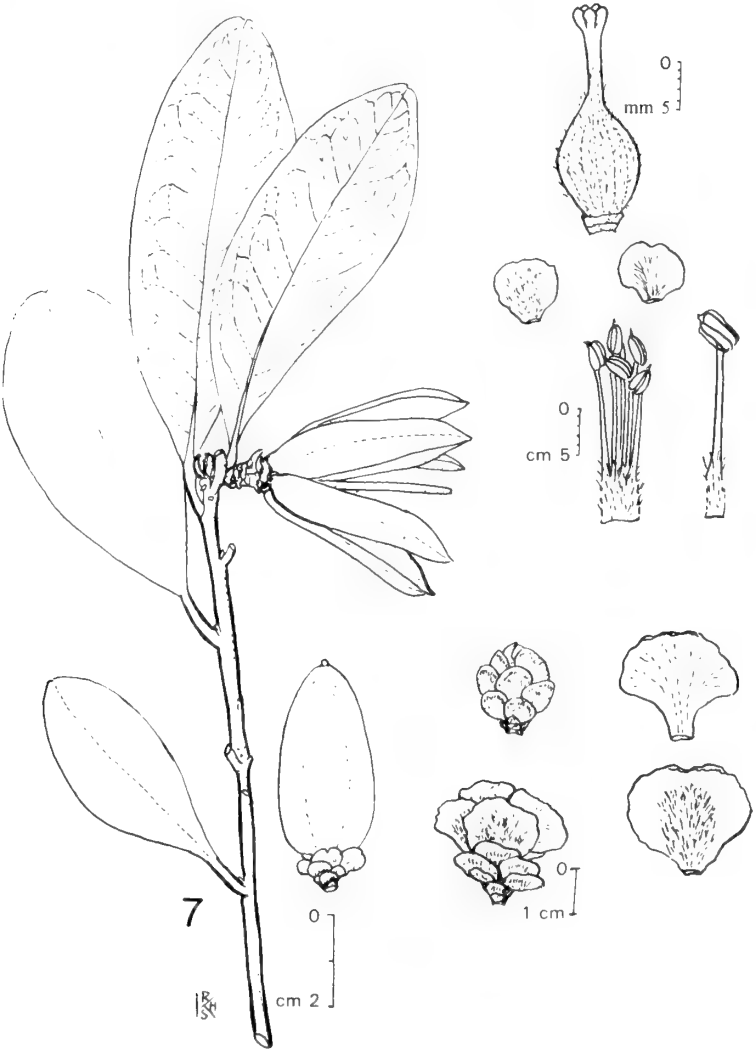

Fig. 7. *Gordonia imbricata* King
Malaya, *Ng KFN 98043* (fr.); *Whitmore KFN 8727* (fl.).

Ridley 16021, 16263 (SING), *Md. Haniff & Md. Nur 7885* (SING), *Seimund 566* (SING), *Holttum 20707* (SING), *Corner s.n.* in Sept. 1937 (L); Cameron Highlands, *Wyatt-Smith KFN 94594* (L); G. Rapis, *Symington & Kiah 28909* (SING). Trengganu, G. Tabu, *Md. Shah et al. 3284* (SING); G. Pandan, *Whitmore FRI 12673* (L), *Kiah SF 33358* (SING). Johore, G. Blumut, *Holttum 10719* (SING), *Md. Shah & Samsuri 2227* (SING), *Ng KFN 98043* (SING, L), *Whitmore KFN 8727* (SING, L), *Suppiah FRI 17839* (SING, L).

Sabah. Mt. Kinabalu, *J. & M. S. Clemens 50720* (L), *Kokawa & Hotta 5628* (SAN), *Hotta 3780* (SAN), *Meijer SAN 29197* (SAN).

ECOLOGY. In lower and upper montane forests, on ridges or in *Leptospermum* scrub. Alt. 1000–2300 m; once recorded at 650 m (*Henderson SFN 19745*). Fl.: Mar.–Sept., fr.: Sept.–Jan.

NOTE. This species is allied to *G. vulcanica* of W. & Central Sumatra. Both species are characterized by the sessile flowers with woolly, imbricate bracteoles, bracts and sepals. Both occur at high elevations. They differ from each other in shape, size and venation of the leaves and in the detailed structures of the flowers and fruit.

Original materials of *G. imbricata* King were collected from the northern Malayan mountains (at about 1700–2200 m). Several recent collections from G. Blumut (at about 1000–1100 m) in S. Johore match well with the original except that the leaves are slightly thinner and the venations clearly visible, and the flowers slightly larger in dimension (3.5 cm vs. 2.5 cm across). It also occurs in Mt. Kinabalu at about 1400–2300 m.

8. Gordonia integerrima [T. & B., Cat. Hort. Bog. (1866) 204. *nom. nud.*] (Miq.) H. Keng, **comb. nov.** Fig. 8

Laplacea integerrima Miq., Mus. Bot. Lugd. Bat. 4 (1869) 113; Back. & Bakh.f., Fl. Java 1 (1963) 321.

Haemocharis integerrima (Miq.) K. & V. Med. 'S Lands Pl. Tuin 16 (1896) 294; Burk. J. Str. Br. Roy. As. Soc. 76 (1917) 151.

Haemocharis serrata K. & V., op. cit., 296, **syn. nov.**

Laplacea serrata (K. & V.) Melch. in E. & P., Pflanzenfam. ed. 2, 21 (1925) 136; Back. & Bakh.f., l.c. **syn. nov.**

A tree, 18–30 m tall. Bark smooth, dark brown. Branches and branchlets terete, glabrous. Leaf-blades thin-coriaceous, narrowly elliptic, or oblong-oblanceolate, apex accuminate, obtuse, rounded or subemarginate, base acute, 7–14 (-16) cm long, 2.5–3.5 (-4.5) cm wide; margin entire, subentire or the upper half (or two-thirds) finely serrulate, nerves (less clearly defined) about 9–11 pairs, anastomosing and twining into submarginal network, glabrous on both surfaces; midrib slightly sunken above, and elevated below; petioles 3–5 mm long, glabrous. Flowers in upper axils, solitary or two to several together; peduncles 2–4 mm long. Bracts 2–3 on the peduncle slightly below the calyx, early caducous. Sepals 5–6, unequal, broadly ovate to reniform, pubescent externally. Corolla 2–3 cm across, white;

petals 5–6, broadly oblong to rounded, concave, briefly joined below, varying from 0.6–1.4 cm long, thin-coriaceous. Silvery hairy on the outer surface except the upper margin which is thin and glabrous. Androecium 5–8 cm long, the filaments shortly united below. Gynoecium 6–8 mm long; style 3–3.5 mm long, the upper half to two-thirds 5-branched, glabrous, the lower half of the style and the ovary densely covered with long yellowish brown hairs; ovary globose, 3–5 mm long and across. Capsule cylindric-ellipsoid, 5-grooved, sparsely pubescent 2.5–3 cm long, dehiscing into 5-valves; sepals persistent.

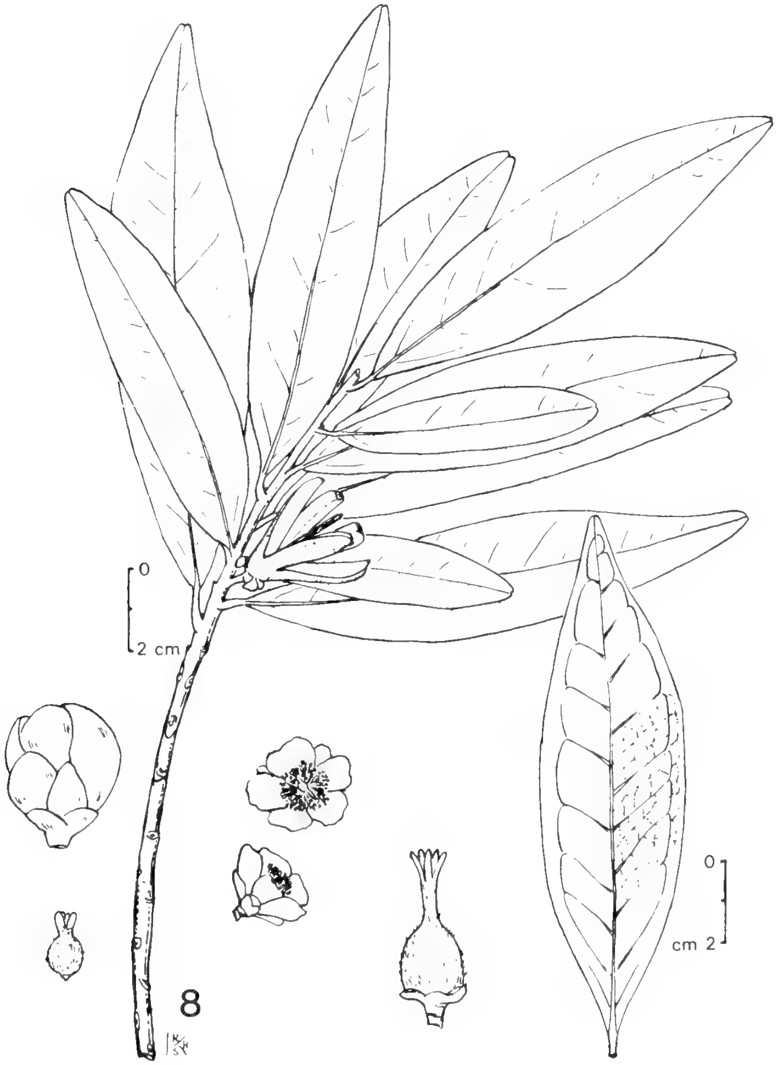

Fig. 8. *Gordonia integerrima* (Miq.) H. Keng **comb. nov.**
Java. *Teysmann s.n.* (Herb. Lugd. Bat. *908, 249-234 & 237)*.

DISTRIBUTION. Malesia (Java, Bali, Celebes).

Java. Locality unknown, *Teysmann s.n.* (*Herb. Lugd. Bat. 908, 249–237*) (lectotype of *Laplacea integerrima* Miq., L); G. Poelasari, Banten, *Koorders 8202* (isotype of *Haemocharis serrata* K. & V., L); Tjibodas, Preanger, *Koorders 10018, 15760, 15761, 24352, 37271* (L); Bandung, *Seekaria 180* (*FRI Ja 7458*) (L).

Bali. Collector unknown, *Herb. Lugd. Bat. 980, 249-283* (L).

Celebes. Minahassa, *Koorders 18099* (L); Menado, *Neth. Ind. For. Serv. 18095* (L), *18100* (SING).

ECOLOGY. In primary forests, alt. 1000–1850 m. Fl.: Jan., Jun. & Oct., fl.: Oct. (one collection).

NOTE. The name *Gordonia integerrima* T. & B. appeared first as a *nomen nudum* in the unpublished Catalogue of the Botanic Gardens, Buitenzorg. This name is thus invalid and without nomenclatural status. Miquel adopted the specific epithet in describing his new species.

An isotype of Koorders & Valeton's '*Haemocharis serrata*' has been studied and found indistinguishable from this species.

9. Gordonia luzonica Vidal, Rev. Pl. Vasc. Filip. (1886) 57; Merr. & Rolfe, Philip. J. Sc. (Bot.) 3 (1908) 114; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 149, *f. 8*; Philip. J. Sc. 15 (1919) 478; Merr., Enum. Philip. 3 (1923) 70. Fig. 9

Gordonia fragrans Merr. Philip. J. Sc. 1 (1906) Suppl. 95.

G. welbornei Elm. Leafl. Philip. Bot. 2 (1908) 500; Burk., J. St. Br. Roy. As. Soc. 76 (1917) 150.

G. benguetica Burk. Philip. J. Sc. 15 (1919) 478; Merr. Enum. Philip. 3 (1923) 70. **Syn. nov.**

?*G. subclavata* Burk. Philip. J. Sc. 15 (1919) 478; Merr., op. cit. 71.

?*G. sp.* Burk., l.c.; Merr., op. cit. 71.

Small to large tree, 10–50 m. tall. Bark thick, greyish, scaling in plates on old trees. Branches spreading; branchlets puberulous. Leaf-blades thin-coriaceous or membranous, elliptic, narrowly obovate or oblanceolate, 5–13 cm long, 2.5–5.5 cm wide, apex acute or obtuse and abruptly acuminate, sometimes rounded, base cuneate or attenuate; the upper half or two-thirds finely serrulate or crenulate, entire near the base; nerves 9–12 pairs, intermingled with less distinct ones; dark green, glabrous above, lighter, more or less puberulose beneath; petiole 2–5 mm long. Flowers subterminal or in upper axils, solitary; peduncles 0.5–1 cm long, stout. Bracts 2–3, caducuous. Sepals 5, broadly ovoid to deltoid, 0.5–1.2 cm long, sericeous externally. Corolla 7–8 cm across, light yellow or creamy white; petals 5, broadly oblong or suborbiculate, 3–3.8 cm long, united below, densely covered with short yellowish hairs throughout the external surface and in the middle basal portion on the internal surface. Androecium 1.2–1.5 cm long, the filaments puberulous. Gynoecium 1.2–1.6 cm long, pubescent; ovary ovoid, 6–8 mm long; style approximately the same length of ovary, rather thick, enlarged at the top, 5-lobed. Capsule broadly cylindric, 3–4 cm long, tapering or nearly rounded above, dehiscing into 5 valves; calyx persistent. Seeds 2.5–3.2 cm long, including the wing.

DISTRIBUTION. Malesia (the Philippines).

Philippines. Luzon, Mt. Mariveles, Bataan, *Borden 809* (SING); Baguio, *Curran 5083* (isotype of *G. benguetica* Burk., SING); Mt. Bulusan, Sorsogon, *Edano & Gutierrez 38465* (L), *Elmer 16373*)L); Llavac, Real, *Lagrimas 521* (L); Apunan, *Meijer 2596* (SING); Panai, Benquet, *Santos 31755* (L, SING); Bontoc to Baguio, *Steenis 17973* (L), Mt. Bulusan, Sorsogon, *Sulit PNH 2754* (L, SING). Mt. Suiro, Biliran Isl., *Sulit PNH 21481* (L). Negros, Dumaguete, Negros oriental, *Elmer 9584* (isotype of

Fig. 9. *Gordonia luzonica* Vidal
Philippines, *Sulit PNH 21481* (fl.); *Lagrimas EPRI 521* (fr.).

G. welborni Elm., L). Mindanao, Mt. Apo, Davao, *Elmer 11217* (L); Kulasihan, Lanao, *Simajon FB 3063* (L).

ECOLOGY. In primary forests and on exposed ridges. Altitude 600–1300 m. Fl.: Feb.–Aug., fr.: Apr.–Dec.

NOTE. Burkill (1919) examined a loan of *Gordonia* specimens (under the name *G. luzonica* Vidal) from the herbarium of the Bureau of Science, Manila, and found five different forms which he called 'species' with a caution that "other authors may perhaps not concede more than varietal rank to one, or possibly even two of them".

Most of the specimens he cited were probably destroyed during the War. At present only one sheet, namely the isotype of *G. benguetica* Burk, is available to me. Burkill emphasizes that in *G. benguetica* the leaves are rounded under the acumen, about one-half as broad as long, and are broadest at the middle. It is in contrast with "*G. luzonica*" of which the leaves are narrowed to the acumen, about ⅓ as broad as long. This does not hold. For example, in *Elmer 11217* (L), the leaves are both acute and rounded at the tip and the length-width ratio varies.

At present, I can only recognise Burkill's *G. polisana* as a good species. As to his *G. subclavata* (characterized by the subclavate capsule, about 4 cm long, with the top domed) and *Gordonia sp.* (characterized by the small entire leaves), I tend to think they are merely variants of *G. luzonica* Vidal.

10. Gordonia maingayi Dyer in Hook.f., Fl. Brit. Ind. 1 (1872) 291; King, J. As. Soc. Bengal 59, 2 (1890) 204, Ann. Bot. Gard. Calc. 5 (1896) 147, *pl. 179A*; Burk., J. Str. Roy. As. Soc. 76 (1917) 147; Ridl., Fl. Mal. Pen. 1 (1922) 204; H. Keng in Ng, Tr. Fl. Mal. 3 (1978) 285. Fig. 10

A small tree, to 13 m tall. Crown dense; bark brownish or light red brown, smooth, finely fissured. Young twigs very slender, densely covered with short yellow-brown hairs; older branches with rough bark glabrescent. Leaf-blades thin-coriaceous, oblanceolate, ovate or narrowly obovate, apex short and bluntly acute, base cuneate or attenuate, (4-) 6–8 cm long, 2–3.5 cm wide; drying yellow-brown; the upper half or two-thirds remotely serrulate, the lower part entire; nerves 5–7 pairs, slightly elevated above, very obscure below; glabrous above, sparsely pubescent beneath; petioles slender, 0.4–1 cm long, pubescent. Flowers subterminal or in upper axils, solitary or sometimes 2–3 together; peduncles very short (1–2 mm long) or almost sessile. Perules (bracteoles, bracts and sepals) persistent at anthesis and forming an involucre about 1–1.5 cm high, densely greyish pubescent externally, increasing in size from the lower bracts (deltoid, 2–3 mm wide) to the upper sepals (suborbiculate, 5–7 mm long and wide). Corolla 1.5–2.2 cm across, white (*fide* van Balgooy) or yellow (*fide* Cockburn); petals obovate to orbicular, concave, 0.6–1 cm long and wide, often emarginate at apex and clawed at base, densely greyish hairy on the external surface except the margin which is usually thinner and glabrous, sparsely pubescent on the internal surface. Androecium 6–7 mm long, the filaments glabrous, briefly connate below. Gynoecium 8–9 mm long; style slender; 4–5 mm long, glabrous; ovary ovoid, 3–4 mm long, ridged, glabrescent. Capsule cylindric, 2.5–3 cm long, 1.2–1.5 cm across, dehiscing into 4, sometimes 5 valves; sepals persistent. Seeds 2–2.5 cm long including the wing.

DISTRIBUTION. Malesia (the Malay Peninsula).

Malay Peninsula. Perak, *Scortechini 1982* (L, SING), *Wray 3766* (SING); Kuala Kangsar, *Kochummen FRI 2461* (L); Bintang Hijau F. R., *Chan FRI 13328* (L, SING); nr. Fort Tapong, *Whitmore FRI 15749* (L); G. Babu, *Selvaraj FRI 6555* (L). Trengganu, Bt. Jebak Puyoh, Ulu Besut, *Cockburn FRI 8335* (L). Negri Sembilan, Nilai Jindaram Estate, *Md. Shah 70* (SING). Pahang, Sg. Telom, Bt. Cheraya, *Sohadi FRI 14731* (L, SING); Taman Negara, *van Balgooy 2577* (L). Kelantan, G. Babong, *Soepadmo & Mahmud 1172* (L). Malacca, *A. C. Maingay 192* (L, isotype).

VERNACULAR NAMES: *titup, titup tiup, tiup, damak.*

ECOLOGY. In primary forest and dipterocarp forest, on ridge-top or on hill side; alt. 300–400 m. Fl.: Apr.–May, fr.: July–Jan.

11. **Gordonia marginata** (Korth.) Endl. *ex* Walp., Repert. 5 (1845) 134; Merr., J. Str. Br. Roy. As. Soc. spec. no. (1921) 390; Masamune, Enum. Phan. Born. (1942). 472. Fig. 11

Closaschima marginata Korth., Kruidk. (1842) 141 (*incl.* var. *dasyophthalma* Korth.); Walp., op. cit. 1 (1842) 375.

Laplacea marginata (Korth.) Choisy, Mém. Soc, Phys. Hist. Nat. Genève 14 (1855) 148; Miq., Fl. Ind. Bat. 2 (1857) 490.

Haemocharis marginata (Korth.) O. Ktze, Rev. Gen. Pl. (1891) 62; Burk., op. cit., 153.

Tree, 25–40 m tall, buttressed. Bark grey, smooth, scaling off in large pieces; living bark beefy red, sap wood reddish white. Young twigs reddish brown, glabrous. Leaf-blades thin coriaceous, obovate or narrowly obovate, sometimes rhomboid, obtuse or slightly emarginate, base cuneate, 4–7 (-9) cm long, 2–3 (-3.5) cm wide; margins for the most part undulate or remotely crenulate, entire near the base; nerves 5–7 pairs, slightly impressed above, inconspicuous below, glabrous on both surfaces, except the lower pilose midrib; petioles stout, 2–3 mm long. Flowers in upper axils or subterminal, solitary or 2–3 in clusters; peduncles very short, 1–3 mm long; bracteoles, bracts and sepals forming an involucre about 5–8 mm high, silvery puberulous on the back, increasing in size from the lower bracts (broadly ovate, 1–1.5 mm long) to the upper sepals (broadly ovate or subrounded, 4–5 mm long). Corolla 2–2.5 cm across, pale yellow; petals 5, obcordate to subrounded, 8–10 mm long, membranous, silky externally except the margins which are thinner and glabrous; petals briefly joined at the base and adnate to the filaments. Androecium 4–5 mm long, the filaments united below. Gynoecium 4–6 mm long; columnar, 1.5–2.5 mm long, ridged, the upper portion separating into 5 branches each bearing a terminal stigma; ovary ovoid, velutinous, tapering above into the style. Capsule ellipsoid-cylindric, 2–2.5 cm long, 5-grooved, velutinous along the grooves; sepals persistent. Seeds 1–1.4 cm long including the wing.

DISTRIBUTION. SE. Borneo (Kalimantan).

SE. Borneo. Without precise locality, *Korthals, s.n.* (several collections, *Herb. Lugd. Bat. 908, 249–245* selected as lectotype of *Closaschima marginata* Korth.); G. Pamatton, Poelau Lampei, *Korthals s.n.*; Martapoera, *Korthal s.n.*; G. Tirin, *Korthals, s.n.* (all from L.); Tanjong Bangko, near the mouth of Mahakam River, alt. 20 m, *Kostermans 7049* (BO, L); West of Samarinda, *Kostermans 6702* (BO, L).

ECOLOGY. Sandy ridges, on loam soil; alt. 30–300 m. Fl. & fr.: Apr.–Aug.

VERNACULAR NAME: *penagit*.

NOTE. Over a dozen specimens collected by Korthals during his Borneo trip (Oct.–Dec. 1836) are deposited in the Leiden Rijksherbarium. They were variously

Fig. 10. *Gordonia maingayi* Dyer
Malaya, *Wray 3766* (fr.); *van Balgooy 2577* (fl.).

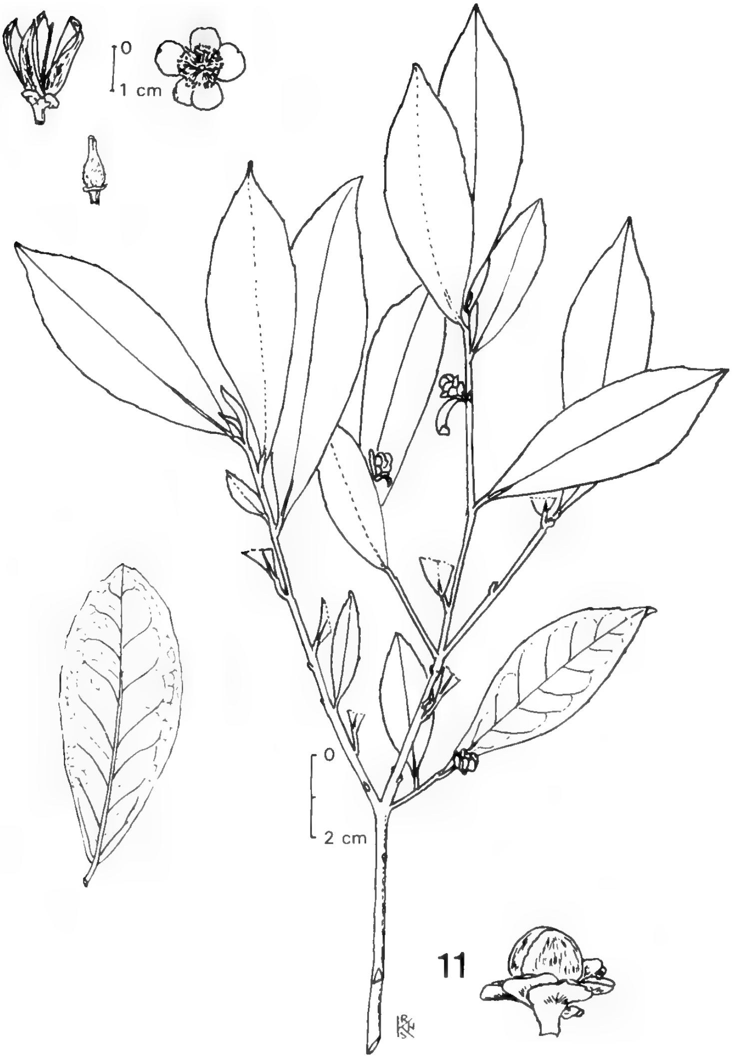

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Fig. 11. *Gordonia marginata* (Korth.) Endl. ex Walp.
Kalimantan, *Korthals s.n.* (Herb. Lugd. Bat. No *925, 250-547); Kostermans 6702* (fl., fr.).

labelled as *Closaschima* (or as *Closaschyma*) *marginata*, *C. obovata, C. lanceolata*, and *C. marginata* var. *dasyopathalma*, all in Korthals' handwriting. Only the first name was published. These specimens bear small flower buds or are sterile. Among them there is only a single fruit (Herb. Lugd. Bat. 908, 249–238). The description presented here is largely based on two collections of Dr. Kostermans.

12. Gordonia multinervis King, J. As. soc. Bengal 59, 2 (1890) 205; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 154, *f. 11*; Ridl., Fl. Mal. Pen. 1 (1922) 203; H. Keng in Ng, Tr. Fl. Mal. 3 (1978) 286. Fig. 12

Gordonia concentricicatrix Burk., op cit., 153, *f. 10 & 11*, op. cit., 78 (1918)

49, pl. 3; Ridl., l.c.; H. Keng, op. cit., 285. **Syn. nov.**

Small to large tree, 10–30 m tall. Bark grey, smooth or reddish brown and with large loose scales in several layers, scallop-marked. Young twigs glabrous except near the tip which is puberulous. Leaf-blades membranous or thin coriaceous, obovate-spathulate, apex rounded, mucronate, or shortly acuminate, base gradually attenuate and often narrowly winged below, varying from 10–15 cm long, 2–5.5 cm wide ('*concentricicatrix*') to 12–20 cm long, 6–8.5 (-10) cm wide ('*multinervis*'), the upper two-thirds crenate, subentire or entire below; glabrous on both surfaces; nerves 8–18 pairs (often with smaller, less conspicuous veins in between), very faint above, barely visible beneath, fused near margin and forming intramarginal reticulations; midrib sulcate above; petiole thickened, 2–5 mm long, glabrescent.

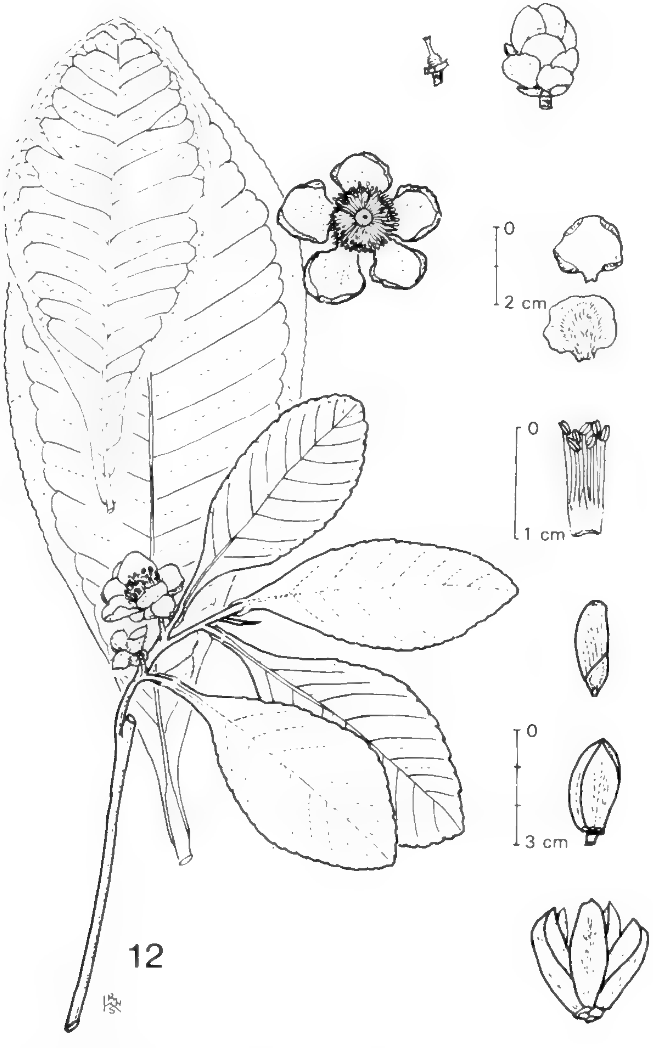

Fig. 12. *Gordonia multinervis* King
Malaya, *Watson CF 878 & Abdul Rawi CF 878* (fl. & fr.); *Scortechini 1968* (large leaf).

Flowers axillary, solitary; peduncles short, 2–5 (-10) mm long, stout. Bracts 2–3, broadly deltoid, 3–5 mm long. Sepals 5–6, broadly ovate to suborbicular, thin coriaceous, about 1 cm long and wide, greyish silky externally. Corolla 2–3.5 cm across, yellow; petals 5, broadly obovate or suborbicular, 1–1.7 cm long and wide, thin coriaceous, greyish silky externally (indistinguishable from sepals from without except by larger size and position) briefly clawed and joined at base, and adnate to the filaments. Androecium 1.2–1.5 cm long, the filaments united below. Gynoecium 1–1.2 cm long; style solitary, columnar, 4–5 mm long, hispid, the tip discoid, 5-lobed into 5 stigmas; ovary ovoid, 3–4 mm long, densely covered with sericeous hairs. Capsule bluntly 5 angulate, 3–4 cm long, 5-valved; sepals persistent. Seeds 2–2.5 cm long including the wing.

DISTRIBUTION. Malesia (the Malay Peninsula).

Malay Peninsula. Kelantan, G. Stong, *Whitmore FRI 12490* (L); Kuala Kerbat, *Whitmore FRI 20244* (L). Perak, *Scortechini 1968* (isotype, SING). Pahang, Chini F.R., *Cockburn FRI 11076* (L). Selangor, Rantau Panjang, *Watson CF 878 & Abdul Rawi CF 878* (Type of *G. concentricicatrix* Burk., SING); Gading F.R., *Loh FRI 13397* (L). Negri Sembilan, G. Angsi, *Loh FRI 17314* (L). Johore, Bukit Tingan Laut, *Corner SFN 37064* (L); Tenggaroh F.R., *Ogata KEP 105152* (L), G. Ledang, *Whitmore FRI 12303* (L). Singapore, Bukit Timah, *Corner SFN 36435* (L); MacRitchie Res., *Sinclair SFN 40231* (L).

ECOLOGY. In lowland forest, on sandstone ridge or on hill side; alt. 10–800 m. Fl.: Apr.–June, fr.: July–Oct.

VERNACULAR NAMES: *kelak merah. samak pulut. samak samak.*

NOTE. This species, as observed by Steenis (Blumea 12 (1964) 319), is closely allied to *G. oblongifolia* of Sumatra; both are characterized by the oblong or obovate leaves with decurrent winged base, by the thin leathery petals with silky outer surface, hardly distinguishable from the sepals before anthesis, and by the single style with an enlarged discoid tip. It can be easily separated from the latter, however, by its smaller leaves with more numerous nerves and more distinct submarginal reticulation and by its much smaller flowers and fruits.

G. concentricicatrix Burk. was described from a small-leaved form of the species. Of this the type specimen is a mixture of two specimens collected by two different persons at the interval of one year but were mounted on one sheet and given the same collection number.

The following two Bornean specimens are probably referable to this species: E. Borneo, Mt. Palimasan alt. 500 m, *Kostermans 13097* (L), and N. Borneo, Beaufort Hill, alt. 350 m, *Lajangah 44532* (L).

13. Gordonia oblongifolia (Miq.) Steenis, Blumea 12 (1964) 319. Fig. 13

Ploiarium? oblongifolium Miq., Fl. Ind. Bat. Suppl. (1861) 483.

Tree, 13 m tall. Branches stout, glabrous. Leaf-blades thin coriaceous, elliptic-oblong, narrowly oblong or oblanceolate-spathulate, apex broadly acute or obtuse, base acute or attenuate, decurrent and narrowly winged, 14–20 (-28) cm long, 6.5–7

(-10) cm wide; margin finely crenulate-serrulate for the most part, nearly entire toward the base; nerves 11–14 pairs, intermingled with less distinct ones and intricately interlocked near the margin; glabrous on both surfaces; petiole 3–5 mm long, thickened. Flowers solitary, in upper leaf-axils, sometimes several together near the top of a top branchlet; peduncle 1.5–2 cm long, very stout. Bracts and bracteoles 2–3, caducous. Sepals 5, broadly ovate, 1.8–2.2 cm long, thick coriaceous, densely sericeous externally, yellowish brown. Corolla unknown. Gynoecium about 1.8 cm long; style about 1.4 cm long, thinly hispid, minutely 5-lobed at the end; ovary ovoid, about 4 mm long, sulcate, densely sericeous. Capsule cylindric, 5-angulate, about 5 cm long; calyx persistent. Seed 3.5 cm long including the wing.

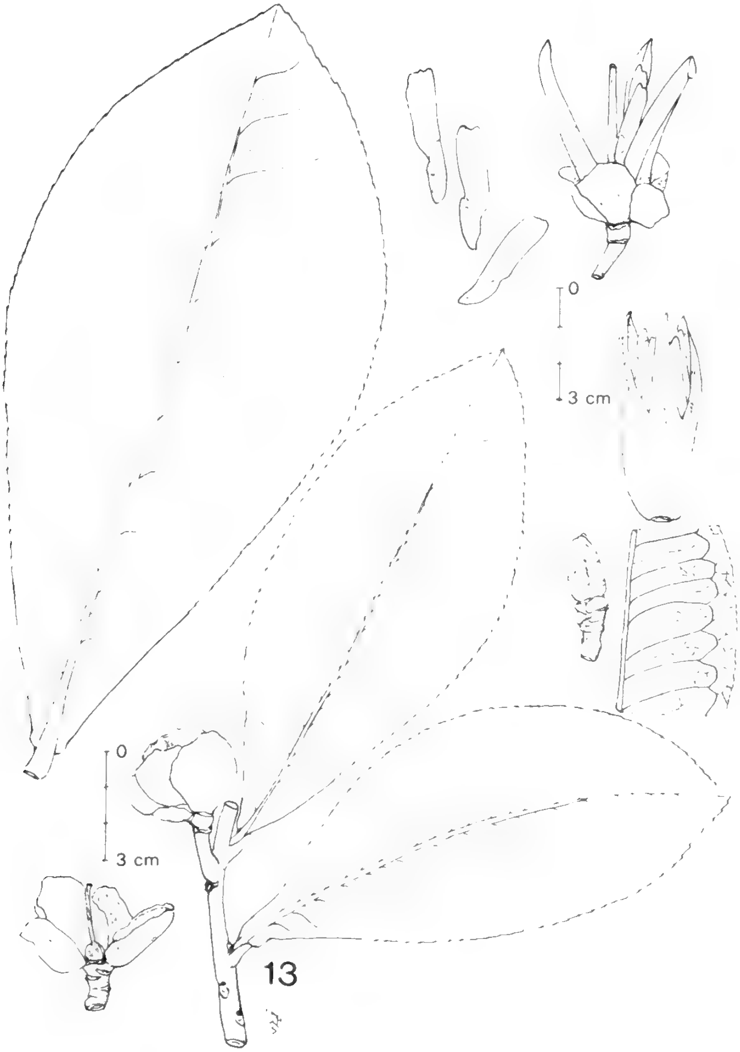

Fig. 13. *Gordonia oblongifolia* (Miq.) Steenis
Sumatra, Neth. Ind. For. Serv. *2794* (fl.), *9571* (fr.).

DISTRIBUTION. Malesia (Central & W. Sumatra).

Sumatra. Benkoelen, Lebong, Neth. Ind. For. Serv. *2794, 9571* (L); Res. Lum, Oud. Agam, *Olivier 16* (B), *Neth. Ind. For. Serv. 2946* (L). Res. Tapanoeli, Sibolga, *Neth. Ind. For. Serv. 3780* (L). Fort de Kock, nr. Bukit Silit, *Teysmann HB 668* (L, type of *Ploiarium oblongifolium* Miq.)

ECOLOGY. In primary forest; alt. 50–1300 m. Fl.: Jan. (one collection), fr.: Dec. (one collection).

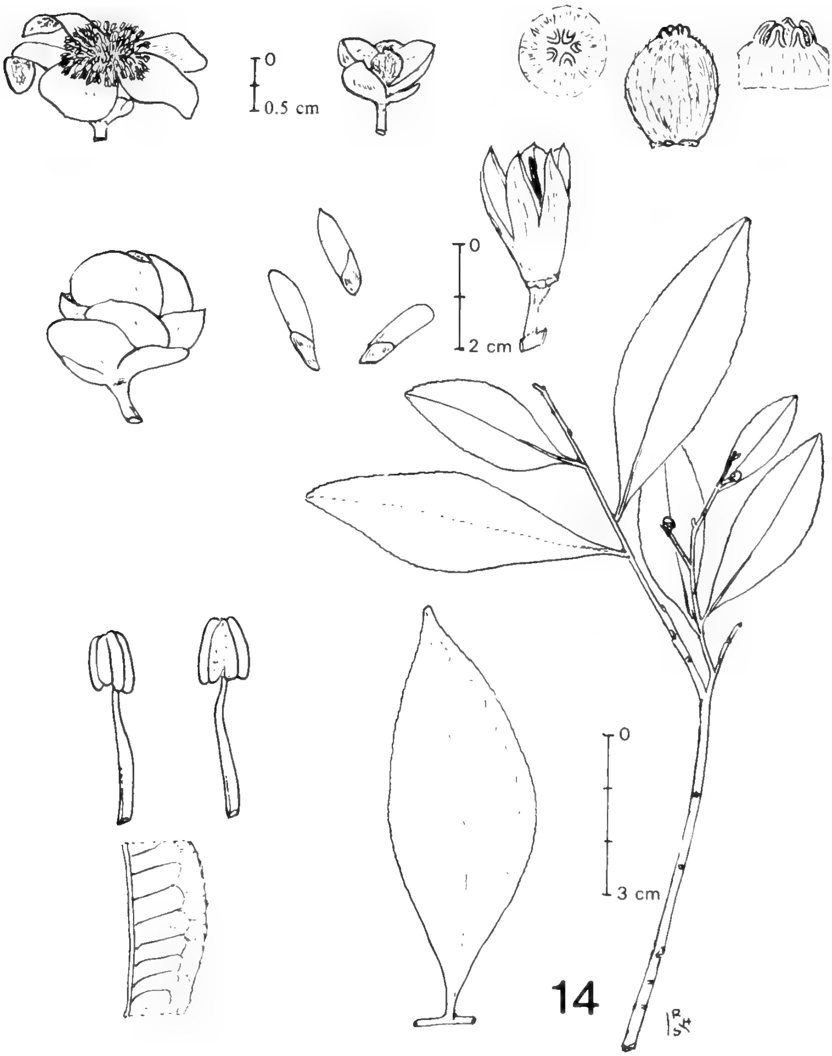

Fig. 14. *Gordonia ovalis* (Korth.) Korth. ex Walp.
Sumatra, *Korthals, s.n.* (Herb. Lugd. Bat. No. *908, 249-324,* fr); *Jacobs 8311* (fl.).

VERNACULAR NAMES: *kajoe patjat, ubar lilim, djirok bantjoh* (Sumatra).

NOTE. The original description of *Ploiarium oblongifolium* Miq. was based on a sterile specimen (*Teysmann HB 668*). Miquel therefore was uncertain about the generic status. In fertile material, van Steenis found the style bearing minute stigmas, and therefore tranferred it to *Gordonia*. A well-preserved fruiting specimen (*Neth. Ind. For. Serv. bb. 9571*) further confirms this transfer.

This species, although with large elliptic-oblong leaves, showy flowers and big fruits, is poorly represented in herbaria. I failed to find any Sumatran specimens collected later than 1925 referable to this plant.

14. Gordonia ovalis (Korth.) ex Walp. Repert. 5 (1845) 134 Fig. 14

Closaschima ovalis Korth., Kruidk. (1842) 140, *t, 28*.

Laplacea ovalis (Korth.) Choisy, Mém. Soc. Phys. Genève 14 (1855) 148; Melch. in E. & P., Pflanzenfam. ed. 2, 21 (1925) 136.

Haemocharis ovalis (Korth.) O. Ktze, Rev. Gen. 1 (1891) 63; Burk. J. Str. Roy. As. Soc. 76 (1917) 158.

Laplacea aromatica Miq., Fl. Ind. Bat. Suppl. (1861) 482, (*incl.* var. *minor*, var. *longifolia*), Mus. Bot. Lugd. Bat. 4 (1869) 114; Melch. in E. & P. Pflanzenfam. ed. 2, 21 (1925) 136. **Syn. nov.**

Haemocharis aromatica (Miq.) Szyszyl. in E. & P. Pflanzenfam. 3, 6 (1893) 185 (*excl.* syn. *L. semierrata* Miq.); Burk., op. cit., 151. **Syn. nov.**

Laplacea subintegerrima Miq. Fl. Ind. Bat. Suppl. (1861) 483. **Syn. nov.**

Haemocharis subintegerrima (Miq.) Burk., op. cit., 155. **Syn. nov.**

Tree, 10–25 m tall. Bark grey, peeling off in pieces. Young branches slender, thinly covered with short silky hairs; older branches puberulent or glabrous. Leaf-blades thin or thick membranous, narrowly elliptic, narrowly ovate or obovate, sometimes slightly asymmetrical; apex acute, acuminate or subcaudate, sometimes obtuse or rounded; base attenuate or cuneate, 4.5–9 (-14.5) cm long, 2–2.5 (-4) cm; wide; margin finely serrulate-crenuate; nerves 10–13 pairs, faint on both surfaces, shining dark green and glabrous above, light green, slightly glaucous and sericeous below; petiole very short, 2–3 mm long. Flowers usually in upper axils, solitary, peduncles 1–3 mm long, sericeous. Bracts and sepals 7–8, silver puberulous externally, increasing in size from the lower bracts (deltoid or reniform, 1–1.2 mm long) to upper sepals (reniform or subrounded, 2–3 mm long). Corolla 1.2–2.5 cm across, white (*fide* Kostermans & Anta); petals usually 5, oblong, broadly oblong to suborbicular, 5–8 mm long, thin coriaceous, silvery puberulous on the external surface except the margins which are thin and glabrous, briefly joined below. Androecium 4–5 mm long, the filaments in several whorls, united below and adnate to the corolla. Gynoecium ovoid to globose, 2–2.5 mm across, sericeous; style absent, only 5 very short, V-shaped protrusions (less than 1 mm long) representing the stigmas; ovary shallowly longitudinally ridged. Capsule 2–2.5 cm long, ovoid or narrowly ovoid, thinly puberulous, dehiscing into 5 valves; sepals caducous fully ripe fruit; seeds 1.5–2 cm long including the narrow wing.

DISTRIBUTION. Malesia (Sumatra).

Sumatra. W. Sumatra, *Korthals s.n. Herb. Lugd. Bat. 908, 249-247, -248, -249, -284, -305, -311, -312, -313, -314, -315, -318, -319, -320, -321, -322* (holotype of *Closaschima ovalis* Korth., L.), *-323, -324, -474* (L); Pariamen, W. Sumatra, *Diepenhorst H.B. 3081* (isotype of *Laplacea aromatica* Miq., L), *2184* (lectotype of *L. aromatica* var. *minor* Miq.), *2492* (lectotype of *L. aromatica* var longifolia Miq., (L). Lampung, NW. of Kota Agung, *Jacobs 8311, 8439* (BO, L). Asahan, *Krukoff 4224, 4235* (BO), *Rahmat Si Boeea 9346* (L). Bangka Lubok Besar, *Kostermans & Anta 540* (BO, L). Palembang, *Neth. Ind. For. Serv. bb. 938, 32002, 31720* (L), *Teysmann H.B. 3969* (holotype of *Laplacea subintegerrima* Miq., L).

ECOLOGY. In primary forest, on 'red' soil. Alt. 20-500 m. Fl.: Apr, May & Sept., fr.: Apr.-May, & July.

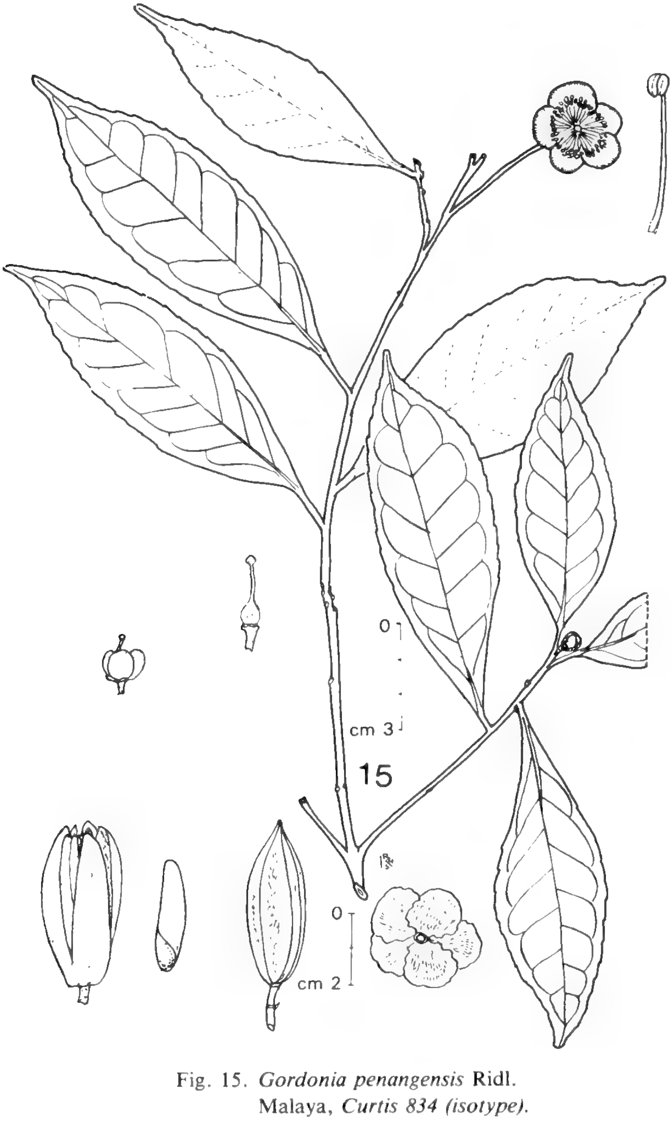

Fig. 15. *Gordonia penangensis* Ridl.
Malaya, *Curtis 834 (isotype).*

VERNACULAR NAME: *palembang putih.*

NOTE. This plant was first collected by P. W. Korthals from the forests of Melintang Mountains (near Padang) between April and May, 1834 during his trip to W. Sumatra. Over a dozen sheets of the same plant (including flowers buds, flowers and a single fruit) are preserved in the Leiden Herbarium to-day. Korthals was probably fascinated by the small flowers with an ovoid ovary totally devoid of styles. In some of these specimens a tiny sheet of paper with hand-written '*Gordonia*' was attached. This was possibly done in the field. Later he described this plant under a new generic name *Closaschima.*

Miquel's *Laplacea aromatica* was based on H. Diepenhorst's collection from Priaman, very near the area where the Korthals' collection was made. Miquel compared his 'new species' with *Laplacea vulcanica* (= *G. vulcanica*) but failed to do so with Korthals' *Closaschima ovalis*, with which it agrees in almost every aspect. Miquel also proposed two new varieties of this species: var. *longifolia* has longer (10–12.5 cm long) lanceolate-oblong leaves, and var. *minor* has smaller, elliptic-lanceolate leaves. The leaves of var. *minor* match closer the type specimens of Korthals.

Szyszylowicz (1893) transferred *Laplacea aromatica* Miq. to *Haemocharis*; at the same time, he cited *L. semiserrata* Miq. as a synonym. This was obviously a mistake, as Miquel never described a species under such a name which is in fact a New World one, namely, *Laplacea semiserrata* Cambess. from Brazil.

There are two distinct forms (which probably warrant infraspecific status) in *Gordonia ovalis*. In one form the leaves are generally smaller (4.5–7 cm long), thin membranous and their leaf-apices usually gradually taper to a blunt point; this includes the type specimens of *Closaschima ovalis* Korthals and *Laplacea aromatica* Miquel, and most specimens were collected from Pariamen-Padang area in the south. In another form the leaves are usually larger (6–9 cm long), thin-coriaceous and their leaf-apices are obtuse or rounded; this includes the type specimens of *Laplacea subintegerrima* Miq. and others from the Palembang area and Bangka Island in the northeast. There are no obvious differences in their flower and fruit structures. In both forms, in the styles are almost totally absent, with five stigmas lying on top of the hairy ovary.

15. Gordonia penangensis Ridl. J. Str. Br. Roy. As. Soc. 73 (1916) 142, Fl. Ml. Pen. 1 (1922) 203; H. Keng in Ng, Tr. Fl. Mal. 3 (1978) 286, *f. 4.* Fig. 15

Gordonia excelsa auct. *non* Blume: King J. As. Soc. Bengal 59, 2 (1890) 203.

A small, slender tree, 10–13 (-20) m tall. Bark smooth, pale grey brown; young twigs very slender, short-silky pubescent, greyish; older branches less hairy, brownish. Leaf-blades thin coriaceous, narrowly elliptic-lanceolate, apex acuminate or more frequently obliquely caudate, base attenuate or cuneate, 6–10 cm long, 2.5–4 cm wide, the upper half or two-thirds remotely serrulate or almost entire; midrib sulcate above and elevated below; nerves about 5–8 pairs, very faint above, barely visible beneath; drying light olive green; glabrous above, somewhat greyish and tomentose below; petiole slender, 0.5–1 cm long, silky, brownish. Flowers solitary, terminal or subterminal on small branches; peduncle 2–3 mm long, silky tomentose. Bracteoles 2, triangular-cordate, 2–3 mm long, caducous. Sepals 5, ovate or suborbicular, thick coriaceous and with thinner and ciliate edge, silvery pubescent at the back, 5–7 mm long and wide. Corolla 2.5–3 cm across, yellowish to golden yellow; petals 5, suborbicular to spathulate, chartaceous, fused below. Androecium 5–6 mm long, the filaments joined into a short tube and briefly adnate to the corolla, more or less in 5 bundles. Gynoecium 9–11 mm long; style solitary, slender glabrescent, 6–7 mm long, the upper portion enlarged into club-shaped stigmas; ovary spherical, 3–4 mm across, woolly. Capsule cylindrical, 3.5–5 cm long, 1.5–2 cm across, glabrescent, 5-valved. Seeds 2.5–3 cm long including the wing.

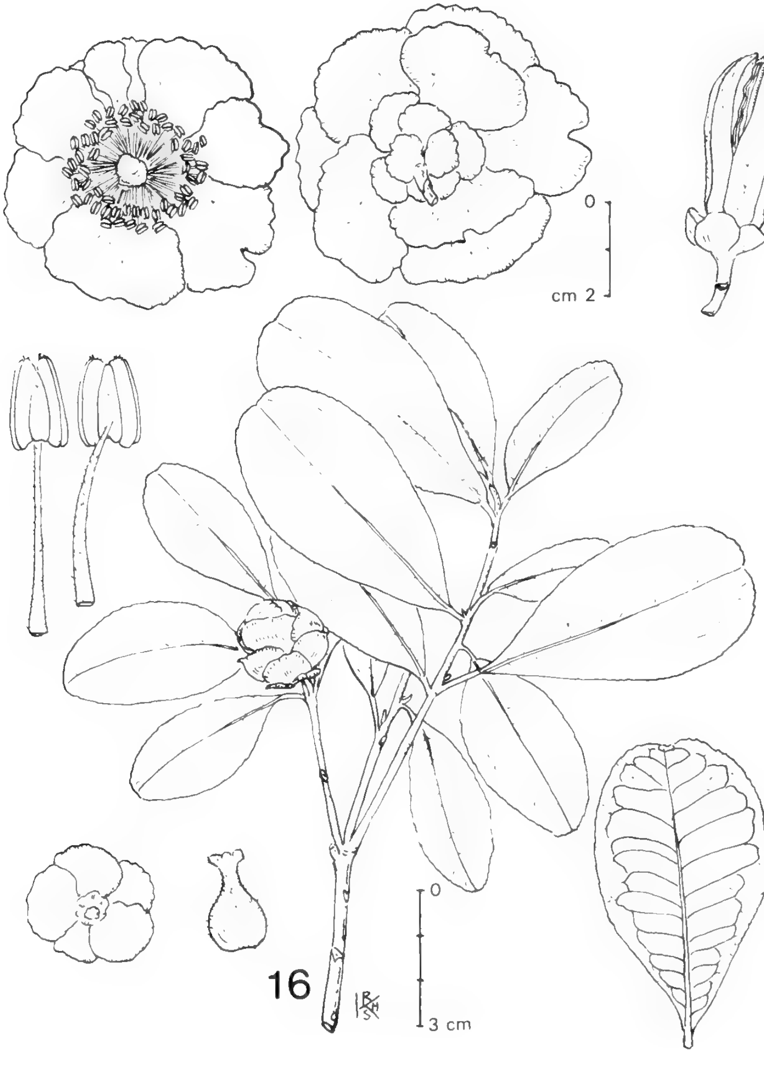

Fig. 16. *Gordonia polisana* Burk.
Philippines, *Celestino 695* (fl.); *Jacobs 7397* (fr.).

DISTRIBUTION. Malesia (the Malay Peninsula).

Malay Peninsula. Penang, Penang Hill, *Curtis 834* (isotype, SING), *Ng FRI 1054* (L). Perak, *Wray s.n.* (SING). Pahang, Cameron Highlands, *Md. Nur SFN 32948* (SING); *Whitmore FRI 15882* (L). Johore, Tg Penawar, *Cockburn FRI 7642* (L); Kota Tinggi, *Stone & Anderson 8714* (L). Singapore, Seletar, *Ridley 6214, 3913* (paratypes, SING); *Sinclair SFN 39585* (L), *Jumali 1048* (SING).

ECOLOGY. In open lowland forests, alt. 20–500 m. Fl.: Feb–May, fr.: May–June.

16. Gordonia polisana Burk., Philip. J. Sc. 15 (1919) 478; Merr., Enum. Philip. 3 (1923) 71. Fig. 16

Shrub or small tree, 8–15 m tall. Branchlets slender, glabrous. Leaf-blades thin-coriaceous, obovate or narrowly obovate, apex obtuse or rounded, often shallowly retuse, base acute or attenuate, 4–7 cm long, 2.5–3.5 cm wide, the upper part remotely crenulate-serrulate, the lower entire, nerves 12–14 pairs, not distinct; glabrous on both surfaces except a few scattered hairs on the midrib beneath; petiole 2–5 mm long. Flowers in upper leaf-axils, solitary; peduncle about 0.5 cm long. Bracteoles about 2. Sepals 5–6, broadly orbiculate or reniform, 0.8–1 cm long, densely yellowish silky externally. Corolla 7–8 (-14?) cm across, white (*fide* Celestino); petals 8–10, in two series, united below, densely covered with short yellowish hairs over the external surface and in the middle-basal portion on the internal. Androecium 1.2–1.5 cm long, the filaments puberulous. Gynoecium about 2 cm long, pubescent; ovary ovoid, about 1.5 cm long; style about 0.5 cm long, very thick and stout, the top enlarged and shallowly lobed into stigmas. Capsule broadly cylindric, 3.5–4 cm long.

DISTRIBUTION. Malesia (endemic to the Philipines; Luzon).

Luzon. Mt. Polis, Ifugao, Mountain Province, *M. Celestino 695* (*PNH 8021*) (L). Mt. Pulog, *Jacobs 7397, 7421* (L).

ECOLOGY. In mossy forest, above stream; alt. 1700–2300 m. Fl. Feb.–Mar. (two collections), fr.: Feb. (one collection).

NOTE. Among the 4 new species described by Burkill from the Philippines, this is undoubtedly the most outstanding. The type specimens (*Alvarez FB 18384* and *Sandkuhl 316*), both collected on Mt. Polis in Bontoc Sub-province, were not available for this study. Among a limited number of Philippino specimens at my disposal, I was only able to identify the above-cited ones as belonging to this species.

Burkill pointed out that (1) the leaves of this plant are rounded under the acumen, broadest above the middle; (2) the flowers are very large, about 9 cm (or according to Sandkuhl, 11–14 cm) in diameter; and (3) the capsule is about 4 cm long, long-tapering above.

The leaves of *Celestino 695* fully agree with Burkill's description. This bears two fully expanded flowers, the larger one measures about 8 cm in diameter. One unusual feature of the flowers, which Burkill failed to mention is that the petals are

8–10 in number and are arranged in 2 series. Petals of the outer series are intermediate between the largest sepals of the calyx and the smaller petals of the inner series.

17. **Gordonia sarawakensis** H. Keng **sp. nov.** Fig. 17

Arbor ca. 30 m alta. Folia angusto-lanceolata vel angusto elliptica, 12–15 cm long, acuminata vel breviter obtusa, basi cuneata, coriacea, nervis lateralibus 20–35 bene intra marginem anastomosantibus, pagina utrinque suborscuris, petiolo 3–5 mm longo. Flores flavi (*fide Banyeng & Benang*), axillares, solitarii, 5–6 cm diametro; bracteae 2–3, decicuae. Sepala coriacea, ovato-rotundata, 1–1.3 cm longa, dorso adpresse pubescentia. Petala late obovata vel lineario-lanceolata, 1.5–2.4 cm longa. Gynoecium 4.5 cm longum; stylo 0; stigmate 8–10. Capsula late ovoidea, 3–3.5 cm longa, valvis 8–10. — Typus, Sarawak, *Banyeng & Benang S25218*, in L.

A large tree, 30 m tall. Bark flaky. Young twigs with scattered short hairs; older branches stout, greyish brown glabrous. Leaf-blades coriaceous, narrowly ovate or narrowly elliptic, acuminate or shortly obtuse, base attenuate, very narrowly winged, 12–15 cm long, 5–6 cm wide; margin crenulate or undulate; midrib elevated beneath; nerves 18–25 pairs (often with lesser ones between) fused near the margin and forming a submarginal vein, faint on both surfaces; drying blade dark green or brown, with scattered short hairs on both surfaces; petiole very thick, 2–3 mm long. Flowers axillary, solitary, peduncle very stout, 4–5 mm long; bracts 2–3, deltoid-caudate, 4–5 mm long, caducous. Sepals 5, broadly ovate or suborbicular, 1–1.3 cm long and wide, thin-coriaceous, greyish silvery externally. Corolla 5–6 cm across yellow (*fide Banyeng & Benang*) or yellowish white (*fide Bujang*); petals 7–8, arranged in one series, varying from broadly obovate or obovate (1.8–2.0 × 1.4–1.8 cm) to narrowly obovate or linear lanceolate (1.8–2.4 × 0.8–1.2 cm), the exposed part in bud thick and silvery hairy externally, other parts thinner and glabrous. Androecium 5 mm long, the filaments glabrous, connate below and adnate to corolla. Gynoecium 4–6 mm long; ovary subglobose, hirsute; style absent or very short; stigmas 8–10, lying on top of the ovary. Capsule broadly ovoid or subglobose, 3–3.5 cm long, 2.5–3 cm across, dehiscing into 8–10 valves; short septicidal lines also developed near the base of the fruit. Seeds 2–2.2 cm long including the wing.

DISTRIBUTION. Malesia (Borneo: Sarawak & Sabah).

Sarawak. Kuching, 12th mile, Penrissen Road, *Banyeng & Benang S 25218* (holotype, L); Semengoh F.R., *Rosli S 14983* (L, SING), *S 15192* (L), *Hj. Bujang S 32444* (L), S 32957 (L, SING), *Galau S 15738* (L), *Zen 10031* (SING).

Sabah. Bukit Hampuan alt. 1300 m., Ranau *Aban Gibot 61804*; G. Lotung Inarat alt. 1700 m. Lamag, *Aban Gibot SAN 83233*; Mt. Silam, Lahad Datu, *Meijer & Anak SAN 37489, Mujin 37816*; along Labuk Road, Sandakan, *Mikil 46699* (all in SAN).

ECOLOGY. In lowland dipterocarp forest, alt. 10–100 m. or in hill forest, alt. 1300–1700 m. Fl.: July–Oct., fr.: Oct.–Nov.

VERNACULAR NAME: *entuyut*.

NOTE. Superficially this species resembles *G. multinervis* King of Malaya, but differs from the latter in detailed structures of the flower and fruit. This species possesses 7–8 petals, more or less arranged in one whorl, (at least as seen in a fully expanded flower); the stamens are comparatively short and fewer in number; the gynoecium is devoid of styles, thus the 8–10 V-shaped stigmas are lying on top of the ovary which is 8–10 locular. The fully developed fruit is a nearly spherical capsule dehiscing loculicidally into 8–10 valves. Short septicidal lines (one each along the dorsal line of the capsule-valves) present near the base of the fruit. The combination of these features makes this species one of the most outstanding in the genus.

At first, all the available specimens referable to this species were collected from the lowland forest near Kuching, Sarawak. Later five specimens were found in a loan from Sabah Forest Department; they match well with the Sarawak material, except *Aban Gibot 61804 & Mujin 37816*, both flowering; in these, a short style (2–3 mm long) is present.

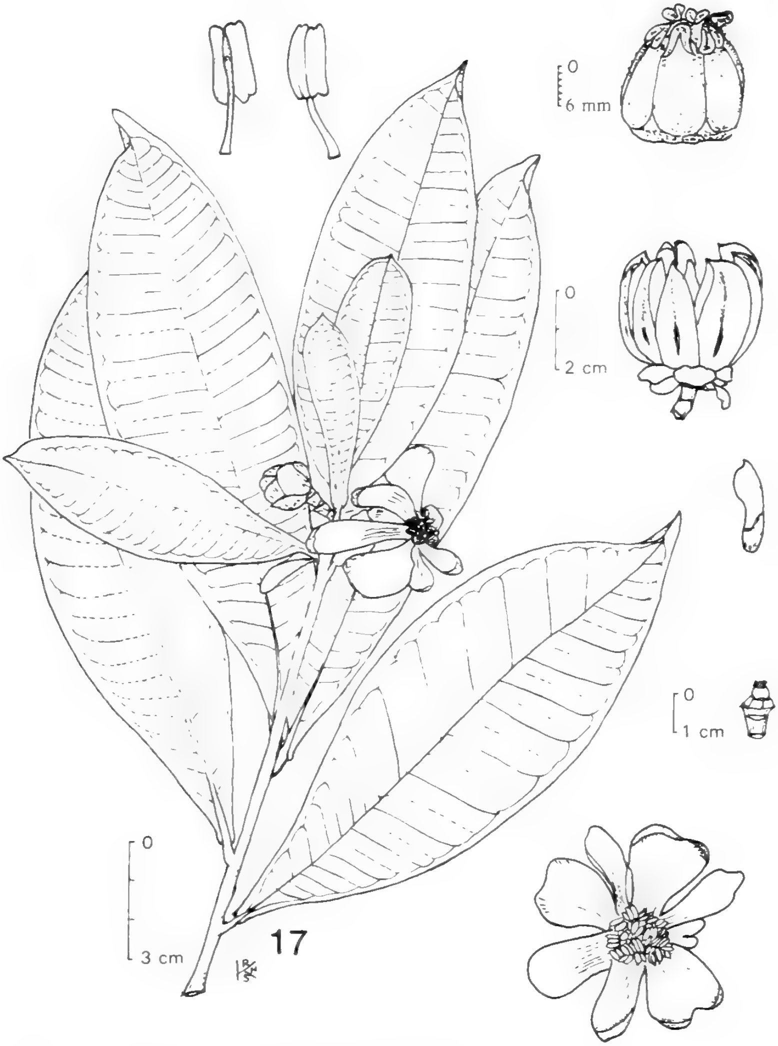

Fig. 17. *Gordonia sarawakensis* H. Keng **sp. nov.**
Sarawak, *Banyeng & Benang S 25218 (holotype)* (fl.); *Galau S 15738* (fr.).

18. Gordonia scortechinii King, J. As. Soc. Bengal 59, 2 (1890) 204; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 158; Ridl., Fl. Mal. Pen. 1 (1922) 204; H. Keng in Ng, Tr. Fl. Mal. 3 (1978) 286. Fig. 18

A tree to 18 m tall; bark smooth, brown. Young twigs slender, dark brown or greyish, puberulent; older branches glabrous. Leaf-blades thin-coriaceous, elliptic or narrowly elliptic, or sometimes narrowly obovate, apex obtuse or bluntly acute, base cuneate or obtuse, 6–9 cm long, 2.5–3.5 cm drying olive green; margin of the upper half or two-thirds remotely undulate or subentire; nerves 6–8 pairs, faint above, almost invisible below; glabrous on both surfaces, shining green above, subglaucous beneath; petiole 3–5 mm long, puberulent. Flowers subterminal and

Fig. 18. *Gordonia scortechinii* King
Malaya, *Scortechini 362 b (isotype)* (fl.); *Chelliah FRI 6545* (fr.).

axillary, solitary; peduncles subsessile or very short (2–3 mm long). Bracteoles 2. Sepals about 5, cordate-deltoid, 2–3 mm long and wide. Corolla 1.5–1.8 cm across, butter yellow; petals 5, ovate or suborbicular, strongly concave, 8–9 mm long and wide, thin-chartaceous, sparsely silvery puberulous externally, briefly joined at base and adnate to the filaments. Androecium 6–8 mm long; the filaments glabrous, briefly united below. Gynoecium 5–6 mm long; styles 3 (or 4?), free to base, spreading; stigmatic surface inside the tip of styles; ovary ovoid densely strigose. Capsule 1.8–2 cm long, glabrous, dehiscing into 3 (or 4?) valves; sepals caducous. Seeds 1.2–1.4 cm long including the wing.

DISTRIBUTION. Endemic to the Malay Peninsula. (Perak, Kelantan Trengganu, Selangor?)

Malay Peninsula. Perak, without locality, *Scortechini 362* b (isotype, SING) Kelantan, *Whitmore FRI 20647* (SAN). Trengganu, Bukit Rauk F.R. Dungun, *S. Chelliah FRI 6545* (L).

ECOLOGY. In hillside primary forest. Fl.: Mar. (one collection), fr.: Nov. (one collection with two specimens).

NOTE. King (l.c) points out that this species superficially resembles *G. maingayi*, but it has smaller flowers with fewer stamens (about 30) and a 3-locular ovary with 3 free styles. Burkill (l.c.) states that this species ''might be described a *G. imbricata* with an admixture of *G. maingayi*. Its branches however are more slender than the first of these two and its flowers are recorded as remarkably small, the stamens being not more than 30.''

For years, only the original collection (*Scortechini 362 b*) was known. During the course of this study, the other specimen which can positively be identified as this species in *Chelliah FRI 6545* from Trengganu. It has a small 3-valved capsule and agrees closely with the type specimen in all aspects of vegetative characters except that the texture of leaves appears slightly thicker. Besides, two other collections possibly also represent this species: (1) Perak, Piah F.R. *Ja'mat FMS 3931* (SING), several small flower buds being present (dissection of one large bud revealed numerous perianth-lobes without any sign of reproductive organs in the centre and is likely to be a gall flower); (2) Selangor, Klang Gates quartz Ridge, *Stone 12094* (L), the small capsules being 4-valved.

19. Gordonia singaporeana Wall. [Cat. no. 1457 (lith. 1829) *nom. nud.; Ridl. J. Str. Br. R. As. Soc. 73 (1916) 141, nom.,* Burk., op. cit., 154, *f. 1, 2, 3, 12, & 13, nom.*] ex Ridl. Fl. Mal. Pen. 1 (1922) 202; Corner. Ways. Tr. 2nd ed. (1952) 629, *pl. 186, f. 236*; H. Keng in Ng, Fl. Mal. 3 (1978) op. cit., 286. Fig. 19

Gordonia grandis King J. As. Soc. Beng. 59, (1890) 203, *non* André (1880).

Gordonia excelsa Bl. var. *sincapuriana* Dyer in Hook. f., Fl. Brit. Ind. 1 (1872) 291.

A tree up to 32 m tall. Bark black, scaly, Young twigs puberulous or glabrous. Leaf-blades thin coriaceous, elliptic or oblong-lanceolate 7–12 (-15) cm long, 2.5–5

(-8) cm wide, apex subrounded or abruptly acuminate, base acute or attenuate, slightly decurrent or not; margin crenulate-serrate or undulate, usually entire near the base; nerves 10–12 pairs, merged and looped near the margin into submarginal reticulations, barely visible above, even less conspicuous below; glabrous on the upper surface, short appressed pubescent beneath; petiole 2–5 mm long, puberulous. Flowers in upper leaf-axils, usually solitary; peduncles 0.3–5 (-0.75) cm long, stout, pubescent. Bracts and bracteoles about 3, caducous. Sepals 5–6, cordate, subrounded or reniform, often notched above, 6–8 mm long, densely covered with greyish hairs externally and also near the base on the inner surface. Corolla 4–5 cm across, cream white, scentless; petals 5–6, broadly oblong or obcordate, 2–2.4 cm long, sericeous on the external surface, scattered puberulous on the internal. Androecium about 1 cm long, the filaments glabrous, connate below.

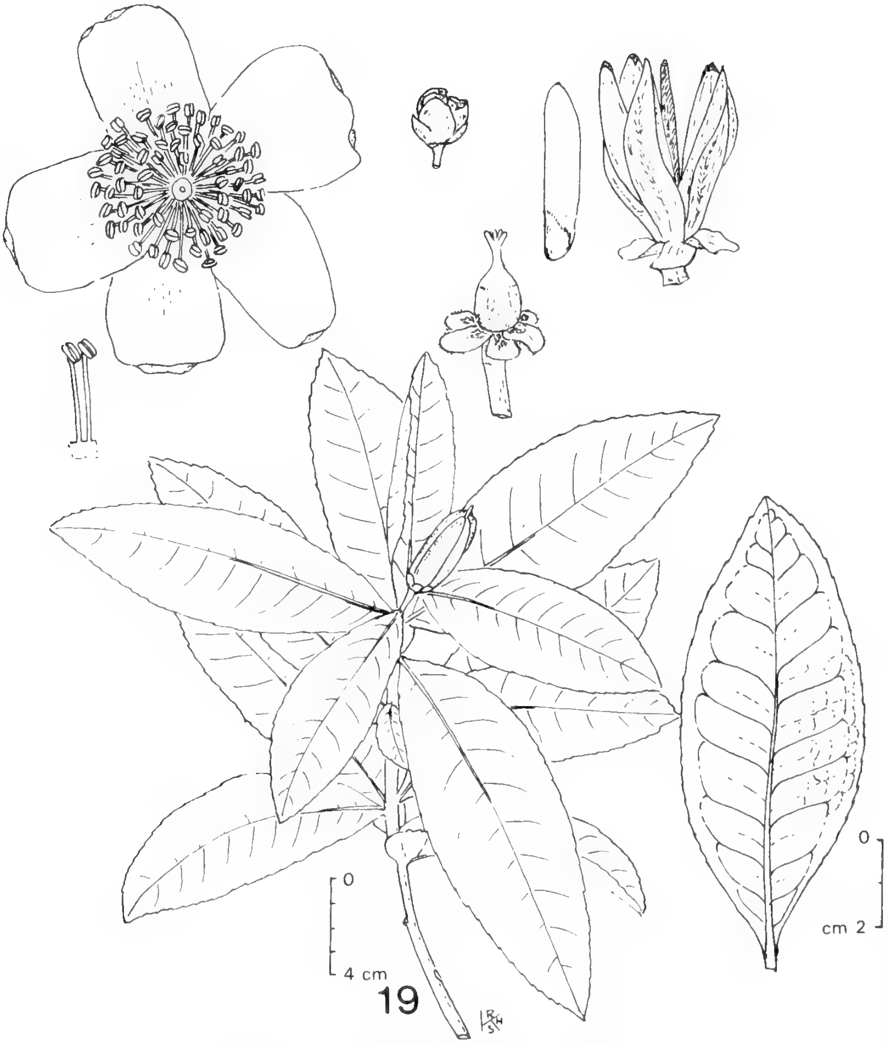

Fig. 19. *Gordonia singaporeana* Wall. ex Ridl.
Singapore, fresh material.

Gynoecium 6–8 mm long, the ovary ovoid, 4–5 mm long, densely covered with long, yellowish grey hairs, tapering above to form a stout style which branches into five for about half its length. Capsule ovoid cylindric, 3–3.5 cm long, dehiscing into 5 valves; seeds 2–2.5 cm long including the wing.

DISTRIBUTION. Malesia (the Malay Peninsula).

Malay Peninsula. Penang, Government Hill, *Burkill 2891, Curtis 2281, Philip CF 1002, Ridley 7963.* Selangor, Fraser's Hill, *Md. Nur 11174, 11454.* Malacca, *Alvins s.n.* in 1886, *Curtis 3488, Derry 976, Maingay 191, 1072, Ridley 976.* Johore, Mawai, *Corner 29253, Ngadiman SFN 34757.* Singapore, *Corner 33564, Ngadiman SFN 35000, 34923, Ridley 1946, 3812, 4564, 4801* (all in SING, except *Maingay 1072, Ridley 976, 481,* L).

ECOLOGY. In primary and mature secondary forests; altitude 50–1300 m. Fl.: May, June & Oct.; fr.: Aug., Nov. & Dec.

VERNACULAR NAMES: *kayu kelat asam, kayu kelat putih, sawak pulot.*

NOTE. Corner (l.c.) observed that this tree is nocturnal, the flowers open at dusk and fall next morning. He also noted that the flowering is seasonal and occurs more than once in a year, perhaps after dry weather.

20. Gordonia taipingensis Burkill, J. Str. Br. Roy. As. Soc. 76 (1917) 148, *f. 6;* Ridl., Fl. Mal. Pen. 1 (1922) 204; H. Keng in Ng, 288. Fig. 20

Small to medium-sized tree, 12–16 (-20) m tall. Young twigs covered with short hairs. Leaf-blades membraneous or thin coriaceous, elliptic to elliptic-oblong, apex acuminate, obtuse or briefly caudate, base cuneate or attenuate, (8-) 13–20 (-30) cm long, (3.5-) 4.5–7.5 cm wide; margin of the upper two-thirds remotely crenulate, entire below; nerves 10–11 pairs on each side, slightly elevated above, faint and inconspicous below; dark green and glabrous above, with scattered strigose hairs on the midrib beneath, otherwise glabrous; petiole 1.5–2 cm long, with scattered short hairs. Flowers axillary, solitary; bracteoles and bracts about 3, caducous; peduncle 0.2–0.5 cm long. Sepals ovate, broadly ovate to suborbicular, 1.2–1.7 cm long and broad, coriaceous, sericeous on both surfaces, but more densely hairy externally. Corolla 5–6 cm across, yellowish; petals 5–6, broadly oblong, suborbicular to reniform, 2.5–3 cm long, the exposed portion of the three outer petals thick and densely sericeous, the covered portion and the two inner petals membranous and puberulous. Androecium 1–1.2 cm long; stamens numerous, in 3 whorls and more or less in 5 bundles, the filaments hairy below, connate briefly with the base of corolla tube. Gynoecium about 1 cm long; ovary globose, densely sericeous, about 6 mm across, the upper tapering into a short style (about 4 mm long) with 5 branches (about 2 mm long). Capsule (immature) ovoid, 2 cm long, subtended by the persistent calyx.

DISTRIBUTION. Malesia (the Malay Peninsula: Perak and Pahang).

Malay Peninsula. Perak, Taiping Hill, *Md. Haniff & Md. Nur SFN 2359* (isotype, SING); Caulfield's Hill, *Md. Haniff & Md. Nur SFN 12734* (SING); Birch's Hill, *Wray 617* (SING). Pahang. Cameron Highlands, *Henderson 11191* (SING).

ECOLOGY. In montane forests, altitude 1200–1700m. Fl.; Feb. & June.

21. Gordonia vulcanica (Korth.) H. Keng, **comb. nov.**

Laplacea vulcanica Korth., Kruidk. (1842) 138, *t. 26*; Miq., Fl. Ind. Bat. 2 (1857) 490.

Haemocharis vulcanica O. Ktze, Rev. Gen. (1891) 62 (as '*vulcania*'); Burk., op. cit., 157.

Gordonia densiflora Ridl. J. Fed. Mal. St. Mus. 8 pt. 4 (1917) 17 **Syn. nov.**

Fig. 21

var. **vulcanica**

A stout shrub, 2–6 m tall, or sometimes a crooked tree to 20 m tall, densely crowned. Young twigs densely covered with yellow or black hispid hairs; older branches stout, less hairy. Leaf-blades coriaceous or thick-coriaceous, ovate or broadly oblong, apex rounded or obtuse, sometimes retuse or emarginate, base rounded or very shallowly cordate, 2.5–5 (-6) cm long, 2–2.5 cm wide; margin of the upper half or two-thirds remotely serrulate or subentire; nerves 5–7 pairs, often slightly impressed above, faint or inconspicuous beneath; drying green and glabrous but often verrucous above, light green and somewhat faintly glaucous below, strigose near and on the midrib especially at the base; petiole stout, 1–3 mm long, sometimes almost sessile, hispid. Flowers in upper axils or subterminal, solitary or 2–3 together; peduncles almost absent or very short, 1–2 mm long, stout. Bracteoles, bracts and sepals 8–10, forming an involucre about 1–1.2 cm high, silvery wooly on the back, and increasing in size from the lower bracteoles (deltoid, 2–3 mm long) to the upper sepals (broadly obovate or suborbicular, 1–1.2 cm long). Corolla 4–5 cm across, creamy white (*fide* de Wilde); petals 5–6, varying from reniform to obcordate, 1.5–2.5 cm long, membranous, tapering below, glabrous except the lower one or two which are silvery puberulous and thickened at the back in the central portion, all petals are briefly joined at the base and adnate to the filaments. Androecium 6–7 mm long, the filaments briefly united below, often in 5 less distinct fascicles. Gynoecium 8–9 mm long; style columnar, 2–3 mm long, ridged, the upper portion separating into 5 free branches; ovary ovoid, 4–5 mm long, strigose or velutinous. Capsule 2.5–3 cm long, puberulous, dehiscing into 5 valves; sepals caducous eventually. Seeds 1.2–1.5 cm long including the wing.

DISTRIBUTION. Malesia (W. & Central Sumatra.)

Sumatra. Without precise locality, *Korthals Herb. Lugd. Bat. 908. 251–803,-804, -815, -824* (lectotype) (L); *Beccari 207* (L). Atjeh, *Jeswiet 6827* (L); G. Losir, Atjeh, *Steenis 8473* (BO), *8493, 8636, 9653* (L), *de Wilde & de Wilde-Duyfjes 15276, 15432, 16141, 16565* (L). Mt. Sinabung, *Lorzing 8182, 13681* (L). G. Singgalang, *Bunnemeijer 2839* (L); Mt Kerintji, *Jacobs 4417* (L); Korinchi Peak, *Robinson & Kloss s.n.* 10 May 1914 (holotype of *Gordonia densiflora* Ridl., SING). Mt Tanggamus, Lampung, *Jacobs 8246* (L).

ECOLOGY. In montane forest, mostly in mossy elfin forests or in dense *Gleichenia* scrubs, sometimes near streams; alt. 2000–3400 m. Fl.: Jan.–May; fr.: April–July.

NOTE. Korthals described this species as having 5 free styles. This was because his description was based on small flower-buds rather than fully developed flowers.

Ridley's *Gordonia densiflora* is clearly a synonym.

var. **buxifolia** (Miq.) H. Keng, **stat. nov.**

Laplacea buxifolia Miq., Fl. Ind. Bat. Suppl. (1861) 482.

Haemocharis buxifolia (Miq.) Szyszyl. in E. & P., Pflanzenfam. 3, 6 (1893) 185; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 158.

It differs from the above in the smaller and narrower (3–4 × 1–1.5 cm, rarely to 6 × 2 cm) leaves with less conspicuous nerves, and in the smaller fruit (1.2–1.4 cm long) (? immature).

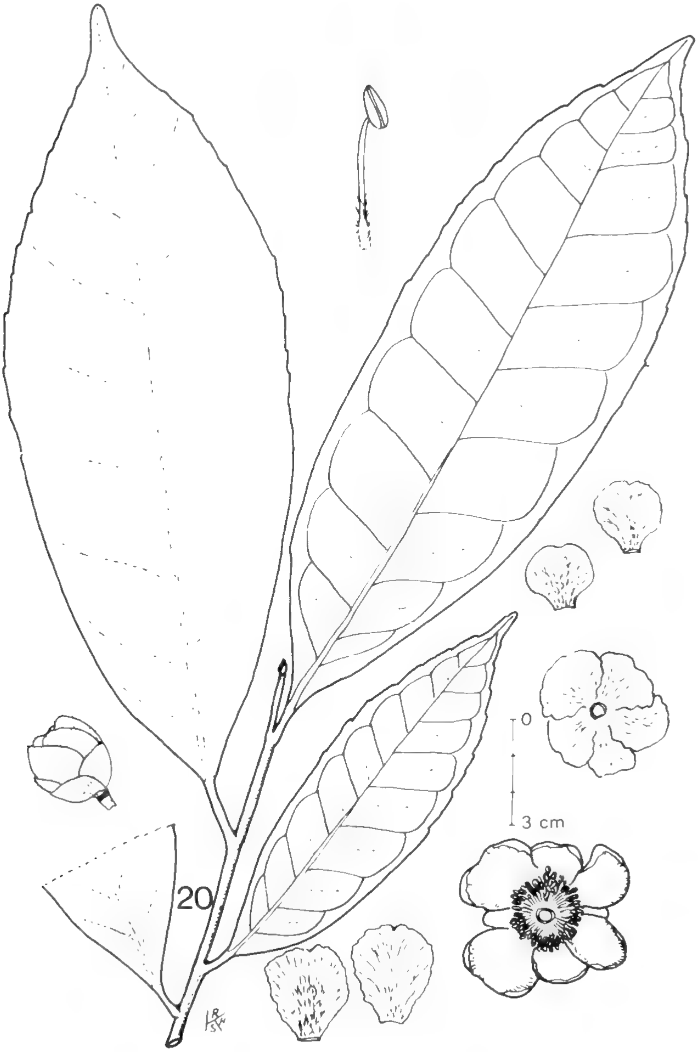

Fig. 20. *Gordonia taipingensis* Burk.
Malaya, *Md. Haniff & Md. Nur SFN 12734* (fl.).

DISTRIBUTION. Malesia (W. Sumatra.)

Sumatra. Paya Kombo, *Herb. Teysmann H. B. 656* (isotype of *Laplacea buxifolia* Miq.); Mt. Sago, near Pajakumbuh, *Meijer 5525;* Taram, Bukit Paku, Pajakumbuh, *Meijer 7171.* Gajo Loeus G. Agosan, *Neth. Ind. For. Serv. bb. 22441* (L).

ECOLOGY. *Meijer 5525* was collected from 1800–2000 m, and *Meijer 7171,* from 600 m. Fr.: July.

NOTE. This variety probably represents merely a diminutive form of the above. The two taxa may have to be merged eventually.

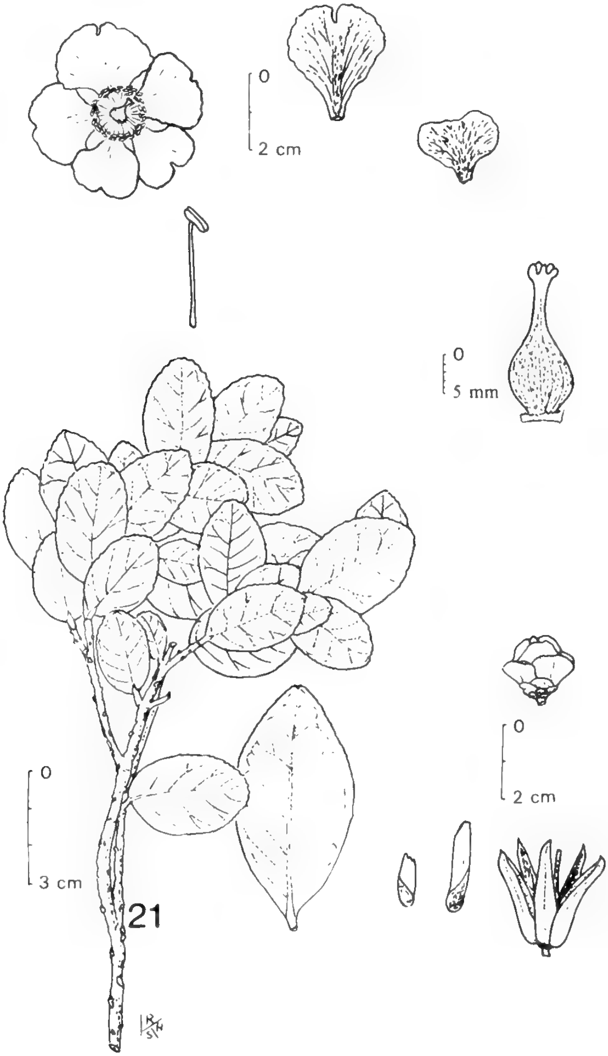

Fig. 21. *Gordonia vulcanica* (Korth.) H. Keng **comb. nov.**
Sumatra, *Steenis 8493* (habit); *de Wilde & de Wilde-Duyfjes 16565* fl & fr).

EXCLUDED AND DOUBTFUL SPECIES

1. *Gordonia brevifolia* Hook.f., Trans. Linn. Soc. 23 (1860) 162; Burk., J. Str. Br. Roy. As. Soc. 76 (1917) 158.
   = *Schima brevifolia* (Hook.f.) Stapf. in Hook. Ic. IV, 3 (1893) *t. 2264*, Trans. Linn. Soc. Bot. 4 (1894) 135.

2. *Gordonia lanceifolia* Burk., op. cit., 150. Fig. 22
   Burkill writes: "*G. lanceifolia*, a new species, comes near to *G. luzonica*. It has leaves of the same outline but more nearly entire, and differently veined. Its

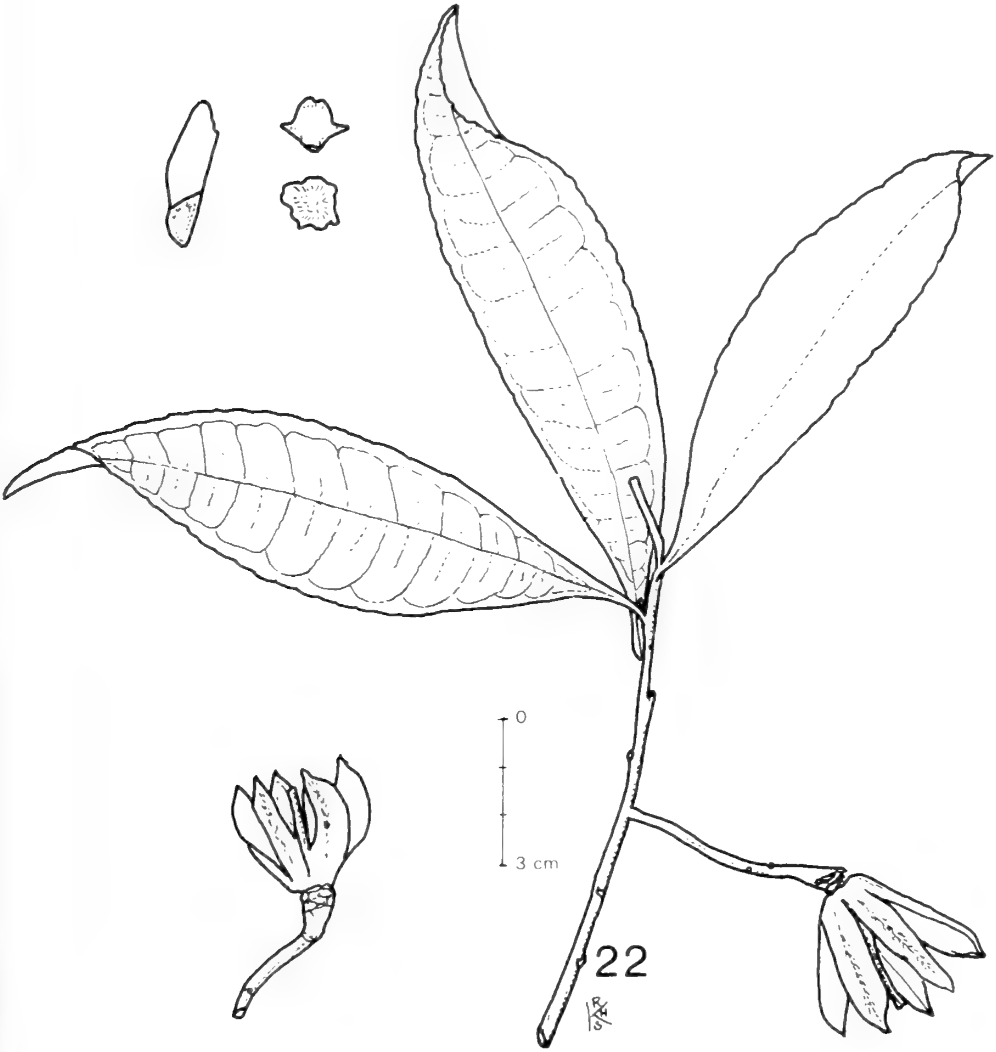

Fig. 22. *Gordonia lanceifolia* Burk.
Sarawak, *Haviland 1010 (holotype)*.

capsule terminate leafless branchlets which may be 4 cm long. It occurs in Borneo near Kuching''. Only a single specimen, the holotype, *Haviland 1010* (SING) was available for this study, which is a fruiting one. A recent (here depicted in figure 22) collection from Sarawak, which is close to or probably referable to this species is: *P. Chai S 32128* (L, SAN), collected from Segan For. Res., Bintulu on Sept. 19, 1972. It differs from the type specimen, however, in the smaller leaves (to 11 vs. to 13 cm long) and fruits (to 2.5 vs. to 3 cm long). There is only a single 5-valved fruit in the type, but over twenty dry capsules in P. Chai's collection, mostly 6-valved, few are 7- or 5-valved.

3. *Gordonia lobbii* Hook. f., Trans. Linn. Soc 23 (1860) 162; Burk., op. cit., 156. This species was based on T. Lobb's collection from Sarawak. Mr L. L. Forman of the Royal Botanic Gardens, Kew, kindly sent me a photo of the type specimen and copied Mr Airy-Shaw's annotation as follows: ''On right, middle —' leaves crenate/ cf. *S. superba* Grdn. et Champ. The word '*Schima*' (Bottom right corner) is in Pierre's hand''. Shaw's note says 'verisim a cl. Pierre scriptum'. The photo appears to confirm J. B. L. Pierre's and H. K. Airy-Shaw's identification that it is a specimen of *Schima*.

4. *Laplacea sarasini* Warb. MS.
Melchior [(in E. & P. Pflanzenfam. ed. 2, 21 (1925) 136)] mentioned this unpublished S. Celebes species in his key to the Malesian *Laplacea*. it differs from other species, according to his key, in the leaves being more or less herbaceous, glabrous, and with an acuminate (or cuspidate) apex. No specimens have been seen. *L. sarasini* is probably a synonym of *G. amboinensis*.

IV. ACKNOWLEDGEMENTS

I am grateful to the Commissioner and staff of the Botanic Gardens, Singapore for the herbarium and library facilities, to the Director and staff of the Rijksherbarium, Leiden, for the loan of the entire collection of *Gordonia*, to the Directors and staff of Herbarium Bogoriense, Bogor, Herbarium of the Forest Department, Sandakan, for the loan of some critical specimens, and to the Directors of the Arnold Arboretum, Cambridge, and Royal Botanic Gardens, Kew, for supplying photographs of the type specimens of *G. grandiflora* Merr. and *G. lobbii* Hook. f., respectively.

I also would like to thank Professor Dr. C.G.G.J. van Steenis for patiently answering my queries and for going through the manuscript of this paper, and for his valuable comments; Dr. Ding Hou for his advice on certain nomenclatural problems and for supplying the xerox and photocopies of literature; and my wife, Mrs. Ro-siu Ling Keng for preparing the illustrations of this paper and for her encouragement.

Index to Scientific Names

Antheeischima excelsa (Bl.) Korth.
= Gordonia excelsa
Closaschima marginata Korth.
= Gordonia marginata
Closaschima ovalis Korth.
= Gordonia ovalis
Gordonia acuminata Choisy
= Gordonia excelsa
Gordonia amboinensis (Miq.) Merr.
Gordonia benguetica Burk.
= Gordonia luzonica
Gordonia borneensis H. Keng
Gordonia brassii Kobuski
= Gordonia amboinensis
Gordonia brevifolia Hook. f.
= Schima wallichii (DC.) Korth. ssp. brevifolia (Hook. f) Bloemb. ex Walp.
Gordonia concentricicatrix Burk.
= Gordonia multinervis
Gordonia densiflora Ridl.
= Gordonia vulcanica
Gordonia excelsa (Bl.) Bl.
Gordonia fragrans Merr.
= Gordonia luzonica
Gordonia grandiflora Merr.
Gordonia grandis King (non André)
= Gordonia singaporeana
Gordonia havilandii Burk.
Gordonia hirtella Ridl.
Gordonia imbricata King
Gordonia integerrima (Miq.) H Keng
Gordonia lanceifolia Burk.
Gordonia lobbii Hook. f.
= Schima wallichi (DC.) Korth. ssp. noronhae Bloemb. var. noronhae Bloemb.
Gordonia luzonica Vidal
Gordonia maingayi Dyer
Gordonia marginata (Korth.) Endl. ex Walp.
Gordonia multinervis King
Gordonia oblongifolia (Miq.) Steenis
Gordonia ovalis (Korth.) Korth.
Gordonia papuana Kobuski
= Gordonia amboinensis
Gordonia penangensis Ridl.
Gordonia polisana Burk.
Gordonia rumphii Merr.
= Gordonia amboinensis
Gordonia sarawakensis H. Keng
Gordonia scortechinii King
Gordonia singaporeana Wall. ex Ridl.
Gordonia subclavata Burk.
? = Gordonia luzonica
Gordonia taipingensis Burk.
Gordonia vulcanica (Korth.) H. Keng
Gordonia vulcanica (Korth.) H. Keng var. buxifolia (Miq.) H. Keng
Gordonia welbornei Elm.
= Gordonia luzonica
Haemocharis amboinensis (Miq.) Burk.
= Gordonia amboinensis
Haemocharis aromatica (Miq.) Szyszyl.
= Gordonia ovalis
Haemocharis buxifolia (Miq.) Szyszyl.
= Gordonia vulcanica var. buxifolia
Haemocharis integerrima (Miq.) K. & V.
= Gordonia integerrima
Haemocharis marginata (Korth.) O.K.
= Gordonia marginata
Haemocharis ovalis (Korth.) O.K.
= Gordonia ovalis
Haemocharis serrata K. & V.
= Gordonia integerrima
Haemocharis subintegerrima (Miq.) Burk.
= Gordonia ovalis
Haemocharis vulcanica (Korth.) O.K.
= Gordonia vulcanica
Laplacea amboinensis Miq.
= Gordonia amboinensis
Laplacea aromatica Miq.
= Gordonia ovalis
Laplacea buxifolia Miq.
= Gordonia vulcanica var. buxifolia
Laplacea integerrima Miq.
= Gordonia integerrima
Laplacea marginata (Korth.) Choisy
= Gordonia marginata
Laplacea ovalis (Korth.) Choisy
= Gordonia ovalis
Laplacea sarasini Warb.
? = Gordonia amboinensis
Laplacea serrata (K. & V.) Melch.
= Gordonia integerrima
Laplacea subintegerrima Miq.
= Gordonia ovalis
Laplacea vulcanica Korth.
= Gordonia vulcanica
Ploiarium ? oblongifolium Miq.
= Gordonia oblongifolia
Schima excelsa Bl.
= Gordonia excelsa

A MONOGRAPH OF *MELIA* IN ASIA AND THE PACIFIC
The history of White Cedar and Persian Lilac

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EFFECTIVE-PUBLICATION DATE: 5 SEPT 1984

Abstract

The wild forms of *Melia* in Asia are described and assigned to one species. The relationship of that taxon to plants cultivated in Asia, Europe, America and Africa is examined and it is concluded that selected forms have been long cultivated in both India and China. Groups of cultivars have been selected from these two centres of domestication and introduced to other warm parts of the world. The widespread Persian Lilac or *mindi kechil* seems to be of Indian stock and to have been widely introduced in America and Africa: mutant forms of it include the Texas Umbrella Tree. The Chinese cultivars are those widely grown in Japan and introduced thence to Europe as *M. japonica*. The whole complex is treated as one species (*M. azedarach*) comprising the wild populations and the two major groups of horticultural cultivars which are set out in a formal revision. All names in *Melia* and its synonyms applied to Asiatic and Pacific plants are identified in an appendix, while the typification of *M. azedarach* is set out in another.

WILD *MELIA* IN ASIA

In the Gunung Leuser Nature Reserve, Aceh, northern Sumatra, grow magnificent specimens of a species of *Melia*. Those collected by W. de Wilde and his wife (15884, 16548 – L!) in the Lau Alas valley in 1975 were noted as being 40 m tall with a diameter at breast height of some 60 cm; the flowers had white petals and the staminal tube was yellow at the apex, turning purple-red as the flower matured; the fruits were some 3 cm long, the twigs stout and heavily clothed with a fulvous stellate indumentum when young, while the leaflets of the bipinnate leaves were strongly acuminate with rather obtuse or even rounded bases and were up to some 6 cm long. These specimens are exceptionally fine examples of a forest species which seems to grow wild throughout the more seasonal forests of Indomalesia, from India, Burma and Malesia (absent from the Malay Peninsula and Borneo) to the Solomon Islands and tropical Australia. In India, it has been known as *M. superba* and *M. robusta*, names based on material collected from trees grown in the Calcutta Botanic Garden from seeds gathered in Soonda (? Carnatic) and 'Malabar' respectively by Andrew Berry, or as *M. composita* and more lately as *M. dubia*. In Burma, it is *M. birmanica*, in Indochina *M. composita* var. *cochinchinensis*; in Java it was described from cultivated material as *M. bogoriensis* while Timorese material has been called *M. candollei* and seems not to differ substantially from *M. azedarach* var. *australasica*, the White Cedar of tropical Australia. The specimens from Java and further east seem to be somewhat more glabrous than those collected in Sumatra, while material from Australia often has distinctly pink or even mauve flowers. Nevertheless this wide distribution with such minor variation is typical of Asiatic Meliaceae of drier forests and other more open vegetation, being very similar to that of *Turraea virens* L. (incl. *T. pubescens* Hell.) for example, while *Cipadessa* *baccifera* (Roth) Miq., which is found only in the western part of the range of those two species, is again absent from the forests of the Malay Peninsula and Borneo.

MELIA IN CULTIVATION

Outside botanic gardens in Malesia, the common *Melia* cultivated is the Persian Lilac or Bead-Tree (fig. 1). It is typical *M. azedarach*, the type species of the genus, and is the only *Melia* to be seen in the Malay Peninsula and Borneo. In the first and in Singapore, it is known as *mindi kechil.* It is one of the most widely cultivated of all tropical trees and differs from the wild trees described above in its variably lobed or serrated leaflets, which are smaller, its relative glabrousness and its large lilac, blue, or occasionally white flowers. As it flowers precociously (even as seedlings sometimes – see van Steenis in *Flora Malesiana* I, 4 (1948) xxi – like a number of other species in cultivation, where this phenomenon is most readily observed), forms of it can be grown in conservatories in temperate countries and in bedding schemes. Selected hardy forms of this plant, which, when fully grown, is straggly and of poor form, may be grown outside in Europe, even in Great Britain where it was probably first cultivated in the sixteenth century.

The source of the European plants was probably Iran or elsewhere in the Middle East, where it has been long known and both its common English name as well as its specific epithet commemorate this. *Azedarach* is a Persian word, or at least a rendering of *āzādraxt* or *āzādiraxt*, which Laufer (*Field Mus. Nat. Hist. Publ.* 201, *Anthrop. ser.* 15, 3 (1919) 583) takes as the name for *Azadirachta indica* A. Juss. (*M. azadirachta* L.), the *neem* tree. The Arab philosopher and physician Avicenna (979–1037) refers to the name, which probably first appeared in a European text in the work of L'Obel (*Nova stirpium adversaria*. . .(1576)) as *Azedaraeth.* It has some medicinal properties but has been widely cultivated in the Mediterranean for shade and as a source of beads for rosaries and so forth, the fruits with a central channel through them when dried being ideally suited to this. Indeed the tree became known there as *arbor sancta* or *arbor pareiso* (i.e. Paradise) a name still common in Spanish-speaking countries. The earliest reference I have found to it is as *(is)zanzaliqu* on a stela of the Assyrian king, Assurnasirpal II, near the doorway of the palace leading to the throne room at Nimrud, the ancient military capital. The inscription is dated ca. 879 B.C. and describes the trees planted: Persian Lilac was one of the 42 species of tree in this Babylonian botanic garden (see D.J. Wiseman in *Iraq* 14 (1952) 24–44 and M. Levey in *Isis* 52 (1961) 94–95). It is very tough and is naturalized in many warm countries, sometimes becoming, as in Madagascar for example, an aggressive pioneer. By contrast, the White Cedar is rarely grown outside the tropics, where a number of selected cultivars are used in forestry and, in Great Britain, where it was introduced in the 1750s, it must be grown under glass.

According to Bailey (*Stand. Cyclop. Hort.* 2 (1933) 2024), *M. azedarach* is widely naturalized in the southern United States. He reports that 'Several forms have been found, a white-flowering and one with the segms. of the lfts. cut in narrow divisions. These forms are not constant, the seedlings frequently reverting to the typical species'. Such may be the forms described from cultivated plants and known as *M. sambucina* and *M. azedarach* var. *incisa* (Java) and var. *acuminatissima* (Sulawesi) and var. *subtripinnata* (Japan), though the last may be a form of the *'tô sendan'* (see below).

A particularly precocious floriferous form has been named *M. floribunda*, though perhaps the most striking of all is that known as the Texas Umbrella Tree, which has a dense flattened crown. Bailey notes, 'The first tree that came to notice is said to have been found near the battlefield of San Jacinto, Texas, but with no record of its intro. there. If the fls. are not crosspollinated with the common sort, the percentage of seedlings which reproduce the exact umbrella shape seldom varies; hence it is supposed by some to be a distinct species'. Linnaeus himself described a variety *sempervirens* from cultivated Sinhalese material grown in Holland, a form which retained its leaves rather more then does the typical plant. However, the text to the plate (see fig. 1) in the *Botanical Magazine* (27 (1807) t. 1066) suggests that even the deciduous form would retain its leaves more effectively under stovehouse rather than greenhouse conditions in Europe. According to Watt (*Dict. Econ. Prod. India* 5 (1891) 221) these Sinhalese plants were brought south from northwest India. An apparently similar form seems to have arisen spontaneously in Argentina (Balozet in *Rev. Bot. App. Agr. Trop.* 33 (1933) 461).

Fig.1. Persian Lilac as long grown in Europe.
Drawing by Sydenham Edwards from material cultivated in a nursery near London at the beginning of the nineteenth century (*Bot. Mag.* 27 (1807) t. 1066).

Melia, as circumscribed by Harms (1940), is an Old World genus*, and all neotropical populations are derived from introduced stock of *M. azedarach*. Of those in the West Indies (*'M. sempervirens'*, though whether they are the form Linnaeus named var. *sempervirens* is not clear), some were brought back to the Old World, much as other Old World plants such as the African *Parkia biglobosa* (Jacq.) R. Br. ex G. Don f. (Leguminosae) were. The *Melia* became naturalized, notably in West Africa. Specimens collected there were duly named *M. angustifolia* and living plants called *M. guineensis*, but there was never any doubt that these were of cultivated origin.

In the nineteenth century, a new source of cultivated *Melia* for European gardens was Japan: the trees were called *M. japonica* and had larger fruits and more entire leaflets. In Japan, they were known as *tô sendan*, i.e., *Melia* from China, and it was soon realized that these, like so many Japanese garden plants, were anciently introduced from China, where they had been long cultivated. The first mention of the plant in Chinese literature is in the ancient Taoist classic *Chuang-tze*, where it is said that the fruit was eaten by a fabulous bird: the text is c. 300 B.C. In Ch'ü Ta-chün's *Kuang-tsung hsin-yu* of 1700, there is an article on *k'u-lian* (*k'u* means bitter as in *k'u-li* (coolie), bitter strength), p. 641, 'It is very easy to grow. In the villages whenever a girl is born they always plant many of them in order to make vessels at the time when they marry. The fruit is bitter and should not be put in the mouth'. He also notes that it was much prized in antiquity and that the flowers were used for making incense, while in the late Ming and Ch'ing periods, the wood was used for patten-making. It was early grown in Japan for it is mentioned several times in the earliest extant anthology of Japanese poetry, the *Manyoshu* of the mid-eighth century.

Forms from China were named *M. toosendan* and plants selected in Japan were named, e.g., var *semperflorens*, f. *albiflora*, but Makino, who described many of these at different ranks and under different specific names, records (*Bot. Mag. Tokyo* 28 (1914) 35) that hybrids between 'subvar. *japonica*' and 'subvar. *toosendan*', which he named subvar. *intermedia*, occur when these forms are grown together.

THE STORY SO FAR

From the foregoing, it can be seen that Persian Lilac in cultivation is extremely variable but that the selected forms which look very different have not lost the capacity to form fertile hybrids. Furthermore, the stocks in Europe and North America seem to have at least two distinct origins: India via the Middle East (and via Sri Lanka and the Netherlands) and China via Japan. White Cedar is a somewhat variable forest tree, tender in Europe and the bulk of specimens referred to it are readily distinguishable from the commonly cultivated forms of Persian Lilac. As Harms noted, however, it would be misleading to infer from this that all specimens can be neatly pigeonholed, for there are specimens of White Cedar with

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* See Pennington in *Flora neotropica* 28 (1981) 25 for fate of names published in *Melia* for native neotropical plants.

little indumentum or with rather serrate leaflets. Fully ripe fruits are rarely gathered and collectors do not always note the colour of the flowers, which changes with time in any case, while young leaves are often gathered with flowers, the mature ones being neglected. Furthermore, I have been quite unable to correlate differences in flower colour, leaf size, shape and indumentum with geography. Indeed, as far as the Asiatic representatives of *Melia* are concerned, then, I cannot but agree with Ramamoorthy (in Saldanha & Nicolson, *Fl. Hassan Dist.* (1976) 395) who notes, 'The taxa of this genus (species, varieties, etc.) apparently intergrade'.

In Africa, the matter is as yet not completely resolved in that there are apparently truly wild trees besides the cultivated Persian Lilac. Those in Angola have been included in *M. dubia*, i.e., White Cedar in the sense of this paper, by Exell and Mendonça, *Consp. Fl. Angol.* 1 (1951) 318. However, the limited material I have seen looks rather different and has been referred to the distinct species *M. volkensii* Guerke (East Africa) and *M. bombolo* Welw. (Angola). These clearly require further study but are something of a sideshow as far as the problem of the taxonomy of the bulk of *Melia* is concerned.

POSSIBLE SYSTEMATIC ARRANGEMENTS

Miquel, who worked on the Japanese cultivars as well as those found in Malesia, wrote (*Ann. Mus. Bot. Lugd. - Bat.* 3 (1868), 'in universum Meliae species nondum ab omni parte satis inter se comparatae novo indigent examine'. Harms, a reluctant 'lumper' elsewhere in Meliaceae, felt (1940, q.v. for detailed references of following works) that there were indeed only two species in Asia and the Pacific, and these were separable only with difficulty: *M. azedarach* (Persian Lilac) and *M. dubia*. The earlier monographer of the family, Casimir de Candolle (*in* DC., *Mon. Phan.* 1 (1878)), in the meantime, had maintained a number of previously described species as distinct and recognized three varieties of *M. azedarach*: var. *glabrior* (Persian Lilac), a superfluous name for the type variety, var. *australasica* (White Cedar) and var. *squamulosa* for forms of the wild tree with a rather heavy indumentum found in mainland Asia and Java. Koorders & Valeton (*in Med. 's Lands Pl. Tuin* 16 (1896)) recognized a number of species in the complex and designated the wild Javanese tree var. *javanica*. Pierre (*Fl. For. Cochinch.* (1897)) had the wild Indo-Chinese tree as var. *glandulosa* and Pellegrin (*in* Lecomte, *Fl. Gén. Indoch.* 1 (1911)) gave the name var. *cochinchinensis* to such a plant.

The cultivated forms have also been variously reduced to varieties, subvarieties or forms, though it would seem that if these are worth recognizing, a cultivar nomenclature would be more appropriate as it is in the provenances used in forestry. Indeed, two extreme types have already been thus designated (see below) but as for any further naming, particularly of the Chinese cultivars, this can be largely left to those who deal with the plants readily available in the trade. The problem from the botanist's standpoint is what to do with White Cedar, given that it is not apparently specifically distinct from the type, which is Persian Lilac (see Appendix II).

Of possible solutions, the simplest would be to amalgamate all the Asiatic plants and those introduced into the rest of the world as *M. azedarach*. This would have the advantage of coping with the intermediate specimens and would leave open the question of the origin of the original 'Indian' material and the Chinese plants. Indeed, with the widespread cultivation of the tree and destruction of the original forest, it may now be quite impossible to reconstruct this history anyway. It would have the disadvantage, however, of throwing together cultivated and wild plants in Asia, where the wild ones are manifestly rather different in form and so forth as well as in value for horticulture. The opposite solution would be to maintain the wild Asiatic trees as one species whilst maintaining the widespread cultivated Persian Lilac as another, as Harms (1940) did. This solution conceals the apparent close relationship of the two 'species' notably in not coping with the rather intermediate position of the Chinese cultivars. In Malesia, it would be convenient to be able to distinguish the truly wild trees from the introduced exotics but as the whole cannot be honestly treated other than as a single species, some intraspecific system is required. With some cultivated plants, it has been found appropriate to name the presumed ancestral populations at the subspecific or varietal level, as in the case of the carrot, sugar beet and teasel for example. In making such a category for the wild plant, in this case, White Cedar, however, the cultivated plants would fall into the nominal variety or subspecies. This is exactly paralleled by the hypothesized state of affairs in the grape vine, *Vitis vinifera* L. (Burtt, *Biol. J. Linn. Soc.* 2 (1970) 233–238)), where Linnaeus is deemed to have made a type variety when actually naming an atypical variant as a variety, while the same plant would be the typical subspecies should an atypical subspecies be described in *V. vinifera*. In *M. azedarach*, such a formal system would be undesirable in any case, as the Chinese and the Indian cultivars would be drawn together in what would be, in effect, a polyphyletic taxon, segregated from the wild forms, to certain groups of which cultivar grouping is more closely allied than to one another.

In view of this, then, it seems preferable to take Burtt's advice and to avoid the artificiality of the formal infraspecific hierarchy and use an informal system, which, in this case, is very straightforward. The whole complex is to be known by its oldest name, *M. azedarach*, even though the type is a cultivated plant. Those cultivated plants which merit recognition as distinct should be given cultivar names by those who deal in the horticultural trade. No name seems to me to have been given at this level to the Persian Lilac in its commonest Indian or 'Japanese' forms, though there are a host of varietal names. The most precocious forms have already been called 'Floribunda', the Texas Umbrella Tree 'Umbraculifera'. Here then, from a botanist's standpoint, the synonyms pertaining to the wild tree are grouped together and those to the horticultural trees are tentatively grouped into Chinese and Indian cultivars.

MELIA L.

Melia L., Sp. Pl. 1 (1753) 384; Pennington, Blumea 22 (1975) 463. – Type: *M. azedarach* L.

Azedarach Mill., Gard. Dict. Abr. ed. 4 (1754) [170]. – Type: not indicated.

Zederachia Heist. ex. Fabr., Enum. Meth. Pl. (1759) 221, *nom. superfl. pro Melia* L.

Antelaea Gaertn., Fruct. Sem. Pl. 1 (1788) 277. – Type: *A. javanica* Gaertn.

Azedara Raf., Fl. Ludov. (1817) 135, *nom. superfl. pro Melia* L.

Azedaraca Raf., Med. Fl. 2 (1830) 199, *nom. superfl. pro Melia* L.

Trees, occasionally flowering precociously as shrublets. *Indumentum* of simple and stellate-tufted hairs. *Leaves* 2(3)-pinnate. *Inflorescence* thyrsoid, axillary. *Flowers* hermaphrodite and male on same tree. *Calyx* 5(6)-lobed to near base, lobes somewhat imbricate. *Petals* 5(6), free, imbricate. *Staminal tube* narrowly cylindrical, slightly expanded at mouth, 10(12)-ribbed, with 10 or 12 truncate, bifid or 4-fid filiform lobes; anthers 10(12), inserted at margin or just within tube, alternating with or opposite lobes. *Disk* small, surrounding base of ovary. *Ovary* 4–8-locular, each locule with 2 superposed ovules; stylehead capitate to coroniform with 4–8 short, erect or incurved stigmatic lobes. *Drupe* 3–8-locular; endocarp thick, bony, deeply dimpled at both ends; loculi 1(2)-seeded. *Seed* oblong, laterally compressed; testa leathery, sometimes slightly swollen and fleshy round hilum; embryo embedded in oily endosperm; cotyledons flat. *Germination* phanerocotylar; eophylls opposite, pinnatisect or trifoliolate. 2n = 28.

One species in Indomalesia with possibly two closely allied ones in south and east tropical Africa. Forms of the Indomalesian species are widely cultivated and naturalized throughout the warm parts of the world.

SYSTEMATIC ARRANGEMENT OF THE COMPLEX OF WILD (ASIATIC) AND CULTIVATED FORMS

Melia azedarach L., Sp. Pl. 1 (1753) 384. – Type: Holland, de Hartecamp, cult. *Hort. Cliff.* 161.1 (BM! lecto; see Appendix II).

Azederach deleteria Medik., Geschl. Malv. (1787) 116.
M. florida Salisb., Prodr. Hort. Chapel Allert. (1796) 317, *nom. superfl.*
Azedara speciosa Raf., Fl. Ludov. (1817) 30, *nom. superfl.*
Azedaraca amena Raf., Med. Fl. 2 (1830) 199, *nom. superfl.*
M. azedarach var. *glabrior* C. DC. in DC., Mon. Phan. 1 (1878) 452, *nom. superfl.* – *Azedarach sempervirens* (L.) O. Ktze var. *glabrior* O. Ktze, Rev. Gen. 1 (1891) 109.
A. vulgaris Gomez de la Maza in Repert. Med.-farm. Havana 5 (1894) 296 (n.v.).

Tree to 40 m, ± deciduous: bole fluted when old, to 60 (180) cm diam. *Bark* grey-brown, smooth, lenticellate, becoming lightly fissured or scaling with age; inner bark yellowish; sapwood whitish, soft; heartwood rusty brown. *Crown* of widely spread but sparsely branched limbs. *Twigs* upturned at ends of drooping branches, smooth, brown, lenticellate, with raised cicatrices. *Leafy twigs* ca. 6–8 mm diam., ± clothed with fulvous stellate hairs. *Leaves* 15–80 cm long with 3–7 pairs of lateral rachides, each with 3–7 leaflets, the most proximal of which sometimes replaced by short rachides with a few pairs of leaflets, ± weakly pubescent but usually subglabrous; petiole 8–30 cm, to 6 mm diam., terete, lenticellate, swollen at base; lateral rachides to 25 cm long, weakly ascendant, articulated with jointed main rachis and weakly swollen there; leaflets 3–6 (–10) × 1–2.5 (–3) cm, ovate or oblong-lanceolate to elliptic, base acute to rounded, apex acuminate, margin entire to variously serrate, costae ca. 7–10 on each side, subsquarrose to weakly ascendant and arcuate, looped at margin; petiolules 3–7 mm. *Thyrses* 10–12 cm, axillary or borne on shoots with terminal bud (see Corner, *Wayside Trees* 1 (1940) 464); primary branches ca. 5–7.5 cm long, weakly ascendant, secondary to 2 cm, bearing fascicles of scented flowers; axes ± mealy pubescent; bracts 3–10 mm long, filiform, pubescent, caducous; bracteoles similar but smaller; pedicels ca. 2–3 mm long. *Calyx* ca. 2 mm diam.; lobes ca. 2 mm long, ovate, stellate- and simple-hairy without, margin ciliate. *Petals* 6–10 × 2 mm, narrowly oblong, white to lilac or bluish, stellate- and simple-hairy without, sometimes simple-hairy within, midvein conspicuous. *Staminal tube* subglabrous without, ± densely simple hairy within, lobes bifid, or 4-fid, sometimes irregularly so; anthers ca. 1.5 mm long, apiculate, ± hairy, inserted opposite lobes. *Disk* obscure and closely enveloping ovary. *Pistil* glabrous; stylehead ca. 0.75 mm diam. *Drupe* 2–4 cm long, 1–2 cm diam., plum-shaped, glabrous, yellow-brown when ripe; endocarp very hard. *Seed* ca. 3.5 × 1.6 mm, oblong, smooth, brown.

Wild trees are known from India, Nepal, Sri Lanka and tropical China south and east through Malesia (Sumatra, Java, Philippines (Luzon, Negros, Mindanao), Lesser Sunda Isls. (Flores, Timor, Wetar), New Guinea to tropical Australia and Solomon Isls. to 1200 m (1800 m in Himalayan tract) in forests, particularly seasonal ones including bamboo thickets (Thailand) and those on limestone, *Tamarindus* woodland and *Eucalyptus* savanna, where it may coppice. Cultivated forms persist and may become naturalized in secondary vegetation in warm parts of the world.

Uses

The wood of different forms of the species has been used for furniture and light construction, notably for ceilings, boats and tea boxes while, during the American Civil War, the trees were a commercial source of alcohol (10% by weight from the fruits). In tropical America, it has been grown in plantation for the production of fibreboard (Pennington in *Flora neotropica* 28 (1981) 24) and is important in the sports goods industries of Pakistan (Amjad & Mohammed in *Pak. J. For.* 1 (1980) 39). If not grown too fast, it is good for paper making (Singh *et al., Ind. For.* 103 (1977) 641). It has been used as fastgrowing coffee-shade and it is alleged that fruit trees grown under it remain relatively free of aphids. Indeed a decoction of the fruits has long been used as an insecticide for plants in India and China and fruits or leaves have been placed with dried fruit, clothing and in books to keep insects away. An extract has also been used as a fish poison.

Although there has been considerable confusion with *neem, Azadirachta indica* A. Juss., *M. azedarach* has been widely attributed with medicinal qualtities. Its root appears as *Cortex Meliae azedarach* in pharmacopoeias, but it is generally held that the bark is most efficacious, particularly as a vermifuge. For details of its action and other medicinal uses, see G.A. Stuart, *Chinese materia medica: vegetable kingdom* (1911) 261 and L.M. Perry, *Medicinal plants of East and Southeast Asia* (1980) 262. So valued are the fruits in the Malay Peninsula, that they have been imported from Szechwan.

The seeds also yield an oil and the trunk a gum but these have been little utilized, though the first is suitable for soap and hair oil (*Wealth of India* 6 (1962) 323 et *seqq.*, *q.v.* for further uses of the tree).

Informal infraspecific classification

The names applied to the wild trees are set out below, followed by those applied to the 'Chinese' and 'Indian Cultivars'.

a. 'Wild' plants, White Cedar

?*Antelaea javanica* Gaertn., Fruct. Sem. Pl. 1 (1788) 277, *t. 58.* - type: 'Java' (Sri Lanka, *König* '120' (L, *teste* Hallier in Réc. Trav. Bot. 15 (1918) 33; lost *teste* Jacobs in Gdns' Bull. Sing. 18 (1961) 74; no duplicates found at BM or TUB).

Melia dubia Cav., Dissert. 7 (1789) 364, *?nom. provis.* (as with *Malpighia dubia* Cav., Dissert. 8 (1789) 413 (= *Heteropterys laurifolia* (L.) A. Juss., Malpighiaceae), it could be argued that this name is not validly published for, like the *Malpighia,* it is placed at the end of the generic account, here with the words, 'Exemplar unicum innominatum vidi in herb. D. de Lamarck, quod fructibus orbatum facile ad Trichiliam aut ad Meliam Linnaei pertinere poterit: itaque ut dubiam speciem hic adiungam quoadusque de fructu constet, et ad debitum genus reducatur'. Elsewhere in the work, where he is uncertain about the disposition of a species, as with *Banisteria sericea* (Dissert. 9 (1790) 429), he uses a '?', which is permissible (Int. Code Art. 34.2). Monographers, however, seem to have considered *M. dubia* valid even though it is so close to the borderline between provisional and valid (J.F. Veldkamp, pers. comm.) - *Azedarach sempervirens* (L.) O. Ktze. var. *dubia* (Cav.) O. Ktze, Rev. Gen. 1 (1891) 110. - Type: (?) Indonesia, (?) Java, *Sonnerat s.n.* (P-LAM! holo).

M. composita Willd., Sp. Pl. 2 (1799) 559. - Type: India, 1785, *Klein* in Hb. Willd. 8086 (B-WILLD!, holo).

M. robusta Roxb., Hort. Beng. (1814) 33, *nom. nud.*: Fl. Ind. ed. Carey 2 (1832) 397. - Type: India, Calcutta, cultivated in Bot. Gard. from seed collected by Berry in Malabar (?CAL; specimen labelled in Roxb.'s hand at G(!); specimen apparently collected from type tree by Carey in 1824 at E(!)).

M. superba Roxb., Hort. Beng. (1814) 33, *nom. nud.*; Fl. Ind. ed. Carey 2 (1832) 396. - *M. argentea* Hiern in Hook.f., Fl. Brit. Ind. 1 (1875) 545, *nom. in synon.*, *sphalm. pro M. superba.* - Type: India, Calcutta, cultivated in Bot. Gard. from seed collected by Berry in Soonda (?CAL; EIC 1254 (K-W!) may be from this tree).

?*M. australis* Sweet, Hort. Brit. ed. 2 (1830) 85, *nom. nud.*; G. Don f., Gen. Syst. 1 (1831) 680. - Type: England, cultivated from material from Australia (?not preserved).

M. candollei A. Juss., Bull. Sci. Nat. Géol. 23 (1830) 239 - Type: Indonesia, Timor, (prob.) *Gaudichaud* (P-JU!, holo; L!, P!).

M. australasica A. Juss., l.c. - *M. azedarach* var. *australasica* (A. Juss.) C. DC. in DC., Mon. Phan. 1 (1878) 452 - *A. sempervirens* (L.) O. Ktze var. *australasica* (A. Juss.) O. Ktze, Rev. Gen. 1 (1891) 110. - Types: Australia, New South Wales, Port Jackson (P-JU!, syn; P!) & d'Entrecasteaux Isls. (P-JU!, syn; P!)

[*M. azedarach* sensu Blanco, Fl. Filip. (1837) 345 ('acedarach'), *non* L., s.s. Cf. Merr., Sp. Blanc. (1918) 209.]

[*M. flaccida* Zipp. ex Span., Linnaea 15 (1841) 182, *nom. in synon.*]

[*M. tomentosa sensu* Miq., Fl. Ind. Bat. 1^2 (1859) 532, *non* Roxb. (1832, i.e., *Chisocheton tomentosus* (Roxb.) Mabb.]

M. birmanica Kurz, J. Asiat. Soc. Bengal 43, 2 (1874) 183. - Type: Burma, Martaban, *Kurz* (?CAL, holo).

M. azedarach var. *squamulosa* C. DC. in DC., Mon. Phan. 1 (1878) 452. - Type: of de Candolle's syntypes, I select Java, *Zollinger* 166 (G-DC!, lecto; L!).

M. bogoriensis Koord. & Val., Med. 's Lands Plant. Tuin 16 (1896) 18. - Type: Indonesia, Java, Bogor, cultivated sub III B 12, 6 Dec. 1895 (BO, holo; L!)

M. azedarach var. *javanica* Koord. & Val. ibid., 15. - Type: of sheets in Koorders's herbarium (BO) labelled 'De hoc specimine agitur in libro . . .' I select Indonesia, Java, Besuki, Curamanis, 17 Oct. 1889, *Koorders 5169β* (BO, lecto; L!)

M. composita var. *cochinchinensis* Pierre, Fl. For. Cochinch. 5 (1897) *t. 356A*. - *M. azedarach* var. *cochinchinensis* (Pierre) Pellegr. in Lecomte, Fl. Gén. Indoch. 1 (1911) 727. - Type: of Pierre's syntypes, I select Vietnam, Pay Ninh, Cai Công, 30 Apr. 1866, *Pierre 1737* (P!, lecto; L!). N.B. The other syntype, *Pierre 3366* (P!, L!), is a cultivated tree apparently referable to one of the 'Indian Cultivars'.

M. azedarach var. *glandulosa* Pierre, op. cit., t. 356B ('*M. composita* var. *biglandulosa*' in *ic.*). - Type: Vietnam, Saigon, cultivated in Bot. Garden, Feb. 1876, *Pierre* 1499 (P!, holo).

Tall forest trees to 40 m. *Leaflets* ± entire, dark above, pale below, when young densely stellate-tomentose like young shoots. *Flowers* sweetly scented, scentless or malodorous. *Petals* white or pale mauve, often pubescent within. *Staminal* tube creamish or pale mauve, darkening to purple with age. *Drupe* to 4 cm long.

Of the fastgrowing forms planted for forestry in the New World, one has been named 'Gigante' (Cozzo, *Rev. For. Argent.* 3 (1959) 127) but it is unclear whether this is intended to be a cultivar name or not, or, indeed, whether it is not more closely allied to forms of Persian Lilac. Other important forestry provenances include 'var. *gigantea'* (Ragonese & Garcia in *IDIA* 385-386 (1980) 110, *nom. non rite publ.*), characterized by its general robustness, hairy anthers and large fruits when compared with Persian Lilac, and treated as two cultivars: 'Gotz' and 'Garrasino INTA, Castelar', both widely planted in Argentina.

b. 'Chinese cultivars', *tô sendan*

?M. japonica G. Don. f., Gen. Syst. 1 (1831) 680. – *?M. azedarach* var. *japonica* (G. Don f.) Mak., Bot. Mag. Tokyo 28 (1914) 34, *nom. superfl.* – Type: England, cultivated from Japanese material (?not preserved).

M. toosendan Sieb. & Zucc., Abh. Akad. Muench. 4^2 (1843) 159. – *M. azedarach* subvar. *toosendan* (Sieb. & Zucc.) Mak., ibid., 35. – *M. japonica* var. *toosendan* (Sieb. & Zucc.) Mak., l.c., *nom. in synon.* – *M. azedarach* var. *toosendan* (Sieb. & Zucc.) Mak., J. Jap. Bot. 5 (1928) 20. – Type: Japan, cultivated from Chinese material, *Siebold s.n.* (?LE, holo; L! M!).

M. japonica Hassk., Cat. Hort. Bog. Alt. (1844) 219, *non* G. Don f. (1831) – *M. javanica* M.J. Roem., Syn. Hesp. (1846) 96. – *M. hasskarlii* K. Koch, Hort. Dendrol. (1853) 72. – Type: Indonesia, Java, cultivated from Japanese material (?BO, holo).

[*M. chinensis* Sieb. ex Miq., Ann Mus. Bot. Lugd.-Bat. 3 (1867) 23, *nom. in synon.*]

M. japonica G. Don f. var. *albicans* C. DC. in DC., Mon. Phan. 1 (1878) 457. – Type: Japan, Nagasaki, cultivated, *Oldham* 159 (B†, holo; N.B. *Oldham* 139 at L!).

M. japonica var. *semperflorens* Mak., Bot. Mag. Tokyo 18 (1904) 67. – *M. azedarach* subvar. *semperflorens* (Mak.) Mak., ibid., 28 (1914) 34. – Type: Japan, Tokyo, cultivated, 20 July 1903, *Makino s.n.* (?MAK, holo).

M. azedarach f. *albiflora* Mak., ibid. – *M. japonica* var. *albiflora* Mak., l.c., *nom. in synon.* – Type: Japan, Tosa, Sakawa, cultivated, *Makino s.n.* (?MAK, holo).

Small trees. *Leaflets* usually almost entire. *Flowers* sweetly scented. *Petals* mauve, pink or blue, occasionally white. *Staminal tube* purple.

This is the form commonly cultivated in Japan, though Indian forms are sometimes grown there, e.g. a white-flowered tree introduced from Lucknow in the 1960s or so (see Hisauchi in *J. Jap. Bot.* 45 (1970) 256). In Malesia it is rarely seen outside Botanic Gardens and has larger fruits than the commonly cultivated Persian Lilac does.

c. 'Indian Cultivars', Persian Lilac, Bead-tree, Chinaberry, *mindi kechil.*

N.B. the cultivars currently recognized as distinct are placed after the main synonymy.

M. azedarach s.s.

M. azedarach var. *sempervirens* L., Sp. Pl. (1753) 384. – *M. sempervirens* (L.) Sw., Prod. Veg. Ind. Occ. (1788) 67. – *Azedarach sempervirens* (L.) O. Ktze, Rev. Gen. 1 (1891) 109. – Type: Holland, de Hartecamp, cultivated, *Hort. Cliff.* 161/1α (BM!, lecto; see Wijnands *Bot. Commelijns* (1983) 145).

M. commelini Medik., Bot. Beobacht. 1782 (1783) 164. – *Azederach commelini* Medik. ex Steud., Nomencl. ed. 2, 1 (1840) 175 'Moench' & 2 (1841) 118, *nom. in synon.* – Type (lecto): Commelijn, Horti Med. Amst. 1 (1697) 147, *t. 76*, drawn from a plant raised from Sinhalese material in Holland.

[*A. odorata* Nor. in Verh. Bat. Genoot. ed. 1 (1791) art. 4,5, *nom. nud.*]

M. arguta DC., Prodr. 1 (1824) 622. – Type: Indonesia, 'Moluccas', ex Herb. Lambert, 1815 (G-DC!).

M. sambucina Bl., Bijdr. (1825) 162. – *M. azedarach* var. *sambucina* (Bl.) Miq. Ann. Mus. Bot. Lugd. – Bat. 4 (1868) 5. – *A. sambucina* (Bl.) O. Ktze, Rev. Gen. 1 (1891) 110. – Type: Indonesia, Java, cultivated, *Blume s.n.* (L! holo; P!).

M. angustifolia Schum. & Thonn. in Schum., Beskr. Guin. Pl. (1827) 214. – Type: Ghana, Elmina, cultivated, *Thonning* 59 (C (microfiche 67: 1, 3, 4!)).

M. guineensis G. Don f. in Loud., Hort. Brit. (1830) 168 & Gen. Syst. 1 (1831) 681. – Type: England, cultivated from seed from 'Guinea' (?not preserved).

?M. bukayun Royle, Illustr. Bot. Himal. (1835) 141, 144. – *M. bukheim* Griff., Itin. Notes (1848) 355, 403. – Type: India, *Royle* (?LIV).

M. cochinchinensis M.J. Roem., Syn. Hesp. (1846) 95. – Type: *M. azedarach sensu* Lour., Fl. Cochinch. (1790) 269.

M. orientalis M.J. Roem., l.c. – Type: *M. sempervirens sensu* Roxb.; EIC 1252E is inscribed *M. sempervirens* in Roxburgh's hand (K-W!; lecto).

[*M. lobata* [Hort. Donat. ex] Planch., Hort. Donat. (1858) 82, *nom. in synon.*]

[*Jacaranda fraxinifolia* [Hort. Donat. ex] Planch., l.c., *nom. in synon.*]

M. azedarach var. *subtripinnata* Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 24. – Types: Japan, *Burger s.n.* (?U), *Keiske s.n.* (L!).

M. azedarach var. *incisa* Miq., ibid., 4 (1868) 5. – Type: Indonesia, Java, cultivated (L (sheet 908. 133-712)!, holo).

M. azedarach var. *acuminatissima* Miq., l.c. – Type: Indonesia, Sulawesi, Amura, cultivated, Dec. 1840, *Forsten s.n.* (L!, holo).

[*M. composita* var. *cochinchinensis* Pierre, Fl. For. Cochinch. 5 (1897) sub *t. 356A, quoad spec. Pierre* 3366].

Small trees. *Leaflets* irregularly serrate, pale green. *Flowers* sweetly scented. *Petals* mauve, pink or blue, occasionally white. *Staminal tube* purple.

Persian Lilac is one of the most widely cultivated of all tropical trees and indeed is so readily grown as to be despised by the discriminating. Good forms with dark, heavily-scented flowers are extremely desirable nevertheless. There is an almost continuous supply of flowers and of fruits, which have long been used for beads (see Hoy & Catling in *Davidsonia* 12 (1981) 65–6 for illus.). The fruits are toxic to man, some 6–8 being considered a fatal dose, and also to pigs, but apparently not to birds, sheep or goats, (For a full account, see J.M. Watt and M.G. Breyer-Brandwijk, *Med. Pois. Pl. S. E. Africa* (1962) 745–751). In Uganda, where it is almost certainly naturalized, it is a particularly valuable source of timber for building poles, as these are reputed to be immune to the attacks of termites (see Styles in *E. Afr. Agric. For. J.* 39 (1974) 416). Two cultivated forms have been given cultivar names:

i. cv. **Floribunda**

See L.H. Bailey Hort., Hortus Third (1976) 724. – *M. floribunda* Carr., Rev. Hort. 44 (1872) 470 *cum tab.* – *M. azedarach* var. *floribunda* (Carr.) Morren, Belg. Hort. 30 (1880) 176 *cum tab.* – Type: France, Paris, cultivated at Jardin des Plantes (?P).

A precocious form, flowering when only a few dm tall and used in bedding schemes (and greenhouse decoration in Europe).

ii. cv. **Umbraculifera,** Texas Umbrella Tree

See L.H. Bailey Hort., Hortus Third (1976) 724. – *M. azedarach* var. *umbraculifera* Knox in Gdner's Monthly 27 (1885) 260 – *M. azedarach* f. *umbraculifera* (Knox) Rehder, Bibliog. Cultivated. Trees, Shrubs (1949) 387. – Type: United States, Texas, trees discussed by Knox (?not preserved).

M. azedarach var. *umbraculiformis* Hort. ex Berck. & Bailey, Cycl. Amer. Hort. 2 (1900) 1001, *t. 1387, ?sphalm. vel mut. pro praec.*

A mutant with a flattened crown of branches. It apparently arose in Texas in the nineteenth century and is widely planted in the southern United States as a street tree.

Acknowledgements

I am indebted to Frank White, Terry Pennington and Brian Styles for their comments on a manuscript version of this paper and to Charlie Jarvis at the British Museum (Natural History) for his help in the tortuous matter of the typification of *M. azedarach*, set out in Apendix II. I am grateful to Professor A.F.L. Beeston and to Mr. R. Dawson for their guidance in the Arabic and Chinese literature respectively. The bulk of the work of this paper was carried out at the Rijksherbarium, Leiden, where I was supported by ZWO*, the Flora Malesiana Foundation and Greshoff's Rumphius Fund.

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* Zuiver Wetenschappelijke Onderzoek (Netherlands Organization for the Advancement of Pure Research).

APPENDIX I

NOMINA DUBIA VEL EXCLUDENDA

Antelaea azadirachta (L.) Adelb., Blumea 6 (1948) 315 = *Azadirachta indica* A. Juss.

A. canescens Cels ex Heynh., Nom. Bot. Hort. 1 (1840) 38 = *sphalm. pro Anthelia ('Anthelea') canescens* Cels, Cat. Cult. Cels Prix Cour. 1842 (1842) 8, i.e., ? *Epipremnum* sp. (Araceae).

Azedarach edulis Nor., Verh. Bat. Gen. 5, ed. 1 (1791) art. 4, 5 *'edule', nom. nud.* = *Sandoricum koetjape* (Burm. f.) Merr.

A. elegans (Seem.) O. Ktze, Rev. Gen. 1 (1891) 110 = *Koelreuteria elegans* (Seem.) A.C. Sm. (Sapindaceae).

A. excelsa (Jack) O. Ktze, l.c. = *Azadirachta excelsa* (Jack) Jacobs.

A. fraxinifolia Moench, Meth. Suppl. (1802) 58, *nom. superfl. pro Melia azadirachta* L., = *Azadirachta indica* A. Juss.

A. nigra Nor., l.c. *'nigrum', nom. nud.* = *Dysoxylum excelsum* Bl. (*fide* Hassk., Cat. Hort. Bog. (1844) 221).

A. ramiflora Nor., l.c. *'ramiflorum', nom. nud.* = *D. parasiticum* (Osb.) Kost.

A. recisa Nor., l.c. *'recisum', nom. nud.* = *Toona sureni* (Bl.) Merr. (Noronâ drawing at BM).

A. tomentosa (Roxb.) O. Ktze, Rev. Gen. 1 (1891) 110 = *Chisocheton tomentosus* (Roxb.) Mabb.

Melia azadirachta L., Sp. Pl. (1753) 385 = *Azadirachta indica* A. Juss.

M. baccata Wall., Cat. (1829) 1256, *nom. nud.* = *seq.*

M. baccifera Roth, Nov. Pl. Sp. (1821) 215 = *Cipadessa baccifera* (Roth) Miq.

M. elegans Seem., Fl. Viti. (1865) 36 = *Koelreuteria elegans.*

M. excelsa Jack, Mal. Misc. 1 (1820) 12 = *A. excelsa.*

M. fraxinifolia Salisb., Prodr. (1796) 317, *nom. superfl. pro M. azadirachta,* = *A. indica.*

M. iloilo Blanco, Fl. Filip. ed. 2 (1845) 241 = *Aglaia* sp. (*A. iloilo* (Blanco) Merr.).

M. indica (A. Juss.) Brandis, For. Fl. Ind. (1874) 67, *nom. superfl. pro M. azadirachta,* = *Azadirachta indica.*

M. integerrima Buch.-Ham. in Trans. Linn. Soc. 17 (1835) 231 = *Trichilia connaroides* (W. & A.) Bentv. (*Heynea trijuga* Roxb. ex Sims). See Mabberley in *Taxon* 26 (1977) 530.

M. koetjape Burm.f., Fl. Ind. (1768) 101 = *S. koetjape.*

M. latifolia Griff., Itin. Notes (1848) 402, *sphalm. pro Melica latifolia* Roxb. ex Hornem., = *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda emend. Mabb. (*T. maxima*), Gramineae. See Mabberley in *Taxon* 33 (1984) 437.

M. montana Herb. Madras ex Wall., Cat. (1832) 214, n. 1256D, *nom. nud.,* = *C. baccifera.*

M. neilgherrica Walp., Rep. 4 (1857) 551, *sphalm. pro Munronia neilgherrica* Wight = *Munronia pinnata* (Wall.) Theob.

Melia parasitica Osb., Dagb. Ostind. Resa (1757) 278 = *D. parasiticum* (Osb.) Kost.

M. parviflora Moon, Cat. Pl. Ceyl. (1824) 35 = *C. baccifera.*

M. pendula Reinw. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 29, *nom. in synon.,* = *Chisocheton patens* Bl.

M. penduliflora Wall., Cat. (1829) n. 1255 = *C. penduliflorus* Planch. ex Hiern.

M. pinnata Stokes, Bot. Mat. Med. 2 (1812) 482, *nom. superfl. pro M. azadirachta,* = *A. indica.*

M. pubescens Reinw. ex Koord. & Val., Bijdr. Boom. Java 3 (1896) 91, *nom. in synon.,* = *Dysoxylum nutans* (Bl.) Miq.

M. pumila Moon, Cat. Pl. Ceyl. (1824) 35 = *Munronia pumila* Wight.

Melia tomentosa Roxb., Hort. Beng. (1814) 90, *nom. nud.*, Fl. Ind. ed. Carey 1 (1832) 394 = *Chisocheton tomentosus.*

APPENDIX II

THE TYPIFICATION OF *MELIA AZEDARACH*

During his stay in coastal Ceylon in the 1670s, the German-born, Dutch botanist and physician, Paul Hermann (1646–1695) collected specimens referable to *Melia azedarach*, the widely cultivated tree known as Persian Lilac, bead-tree or, in the Malay Peninsula, *mindi kechil.* In Hermann's posthumous *Musaeum zeylanicum* (1717), based on the specimens mounted or loose in his book herbarium, is (p. 3) Panukohumba (*Azedarach fructu polypyreno*), mounted in vol. 1, fol. 10, and Kirikohomba (p. 67, *Arbor fraxinifoliis flore caeruleo* CBP, *Azedarach* Dod., i.e., the widespread form of Persian Lilac long known in Europe), unmounted at that time.

Before Linnaeus was to deal with them in his *Flora zeylanica* (1747), based on the Hermann collection, he replaced the long established *Azedarach* by *Melia*, a Greek word for the Manna Ash, *Fraxinus ornus* L. (Oleaceae), which has leaves reminiscent of *Azadirachta indica* A. Juss. (*Melia azadirachta* L.) for they are simply pinnate whereas those of *M azedarach* are doubly so. *Melia* was first published in his *Hortus cliffortianus* (1738, p. 161), where the Persian Lilac is called *Melia foliis decompositis.* As a variety of this he cites another cultivated plant, from Sri Lanka, illustrated in Jan Commelijn's *Horti medici amstelodamensis* 1 (1697) 147, t. 76 and a name quoted by Commelijn, Jacob Breyne's *Azadirachta indica. . .flore albo subcaeruleo purpurascente majore* (*Prodromus fasciculi rariorum plantarum* 2 (1689) 21). Indeed it was Breyne who was the first to separate these two varieties in print, giving the widespread 'Syrian' plant, which he considered to be Avicenna's (i.e. Husain Ibn 'Abd Allah's) *Azadiracht*, the name ending '*. . .flore caeruleo majore*'. In the synonymy of the Ceylon plant, Breyne included *Azedarach floribus albis sempervirens* of Hermann, based on his examination of garden material, Hermann had shown him in the Hortus Botanicus at Leiden, and citing Hermann, *Horti academici Lugduno-batavi catalogus* (1687) 652 but without the synonyms in Hermann's book, for those are referable to *neem, Azadirachta indica*, for it is possible that Hermann mistook the garden material from Sri Lanka, introduced into the Netherlands in the 1680s, for *Azadirachta* which he had collected in Ceylon, his specimen in his book herbarium preserved at Leiden being inscribed *Azedarach floribus albis* (fol. 120). The *neem* was not to be grown in Europe for some decades yet and Breyne seems right, therefore, in having shorn Hermann's garden name of its synonyms.

When Linnaeus gained access to Hermann's main Ceylon herbarium, now preserved at the British Museum (Natural History), he included Panukohumba, the Ceylon plant, and not Kirikohomba, the Persian Lilac, in the typical form of his species (number 162), *Melia foliis duplicato-pinnatis* in *Flora zeylanica.* Another synonym of this typical form is his own *Melia foliis decompositis* from *Hortus cliffortianus* (i.e. the Persian Lilac) as well as Hermann's garden plant, again without synonyms, and the references to Breyne and Commelijn. In this case, the variety of the species is the commonly cultivated Syrian plant in which is included Kirikohomba. By the time of *Species plantarum* (1753), however, Linnaeus seems to have changed his mind yet again, making Commelijn's (and therefore Breyne's and Hermann's garden plant) the atypical variety of the species under the name var. *sempervirens*, which epithet is taken from the cited *Azedarach sempervirens & florens* of Tournefort, who (*Inst.* 1 (1700) 616) included the earlier references too. The typical plant is Persian Lilac, again with the *Hortus cliffortianus* name but the phrase name next to the specific epithet *azedarach* is a new one, indicating a possible rethink of the circumscription by Linnaeus. However, it is written curiously, 'Melia foliis bipinnatis Fl. Zeyl. 162', though that name does not appear in *Flora zeylanica* but may be a mere rephrasing. Had he merely used the *Hortus cliffortianus* reference then the type specimen would clearly be that collected from live plants at George Clifford's garden at de Hartecamp near Haarlem in the Netherlands and now preserved in the British Museum (Natural History). As he did not amend this in later editions, it seems on the face of it that it would be wise to take *Flora zeylanica* into account, particularly as the only specimen in Linnaeus's own herbarium (543/1), although the Persian Lilac, has no indication of its age or origin. The only other *'Melia'* specimens there are (2) *Azadirachta indica* and (3) *?Sandoricum koetjape* (Burm. f.) Merr. Of the materials cited in *Flora zeylanica*, only Hermann's Kirikohomba i.e. the 'Syrian' plant collected by Hermann in Ceylon, was a specimen and it would have seemed to have been wise to select it as lectotype. The var. *sempervirens* is Hermann's plant Panukohumba from Ceylon which was later introduced to the Netherlands and confused by Hermann with *Azadirachta*. Indeed the common name for the latter in Ceylon is still Kohumba. This was identified as var. *sempervirens* by Trimen (*J. Linn. Soc. Bot.* 24 (1888) 141), though Rechinger in *Flora iranica* 133 (1978) 2 has this plant as the type of the species. This lectotypification seems not have taken the complicated history of the cultivated plants into account. Not surprisingly then, the confusing actions of Linnaeus have misled several workers and, sadly, Hermann's unmounted Kirikohomba cannot be found and there is no duplicate at Leiden or in the Sherard or DuBois herbaria at Oxford, both herbaria with a number of Hermann specimens. Of the elements in the protologue of *M. azedarach*, that referring to *Hortus cliffortianus* is supported by specimen 161/1 seen by Linnaeus and I therefore propose that it be the lectotype.

Axillary Buds of Some Tropical Trees

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Abstract

The presence and development of axillary buds are important in shoot and plant growth, especially in trees. As very little information is available on the axillary buds of tropical trees, about 100 local tree species, growing in the Botanic Gardens, Nature Reserves and along waysides, were investigated. The occurrence, morphology and size variations of the axillary buds are discussed.

Introduction

In a growing shoot system, the relationship between the terminal and axillary buds is important in terms of origin, location, number and the relative role of apical dominance. The general information regarding the origin and development of axillary buds is available in the basic reference works on plant development and anatomy (Cutter, 1972; Esau, 1965; Fahn, 1967). While analysing the architecture of tropical trees, Hallé *et al.* (1978) described the developmental variations noticed in the axillary buds of a few dicotyledonous members. The available data on tropical trees is very scanty or almost nil, considering the large number of tropical tree species available in SE. Asia (Corner, 1952). It is said that the axillary buds vary very widely among the species of a genus or sometimes even among the individuals of the same species or, very rarely even within a tree (Hallé *et al*, 1978). It is also well known that the development and the growth behaviour of the apical and lateral buds determine the shape and the architecture of the shoots and eventually of the tree (Koriba, 1958). The present paper summarises the morphological characteristics of the axillary buds of some 100 species of tropical trees, including their occurrence, number, position, prominence and other related characters.

Materials and Methods

Young branches, up to a length of ten nodes, were collected at random from common and easily available trees growing along roadsides, the Botanic Gardens, primary and secondary forests in Singapore. The leaves were removed to expose the buds and these were examined under the binocular microscope to determine their shapes and sizes. The node that was visible, distinctive and nearest to the apex was considered as the first node and the others counted in basipetal order (fig. 1). The relative prominence of the buds at different nodes on the axis was noted. The hundred species studied belong to 31 dicotyledonous families, Podocarpaceae and Gnetaceae.

Observations and Discussions

Buds were present at the axils of most of the species studied except in the case of *Brownea grandiceps* Jacq. and *Plumeria* sp. where they were indistinct or absent.

The unit of study for each species was the shoot with 10 nodes. The relative prominence of buds at different nodes varied. In the majority of them, almost 70%, the buds were present up to the ninth node. Their absence at other nodes could be due to early bud abscission instead of non-formation, since the bud scars were obvious in most of the shoots studied (table 3). The sequential development of buds in relation to the total shoot and individual internodal length should be interesting (Hallé *et al.*, 1978).

In all the standard works referred, very little or no mention was made on the morphology and characteristic features of axillary buds (Goebel, 1900; Corner, 1952; Symonds, 1958; Clowes, 1961; Menninger, 1962; Symington, 1974; Palmer and Pitman, 1972; Bernatzky, 1978; Hallé *et al.*, 1978; Kunkel, 1978; Hora, 1981). It was also revealing that there is no well established terminology to describe the axillary buds, even though other factors that affect shoot growth like mineral nutrition, water availability, soil conditions and others are well considered.

Bud types

Among the tree species studied presently, buds with different sizes and shapes were encountered. They were broadly classified into eight morphological types. The relative shape and outline of the bud was the only criterion used in recognising the eight bud types. The flattened, bulbous, pear-shaped and round ones were somewhat radially symmetrical with almost a circular outline whereas the linear, oblong and triangular ones were somewhat bilaterally symmetrical (fig. 2). All the

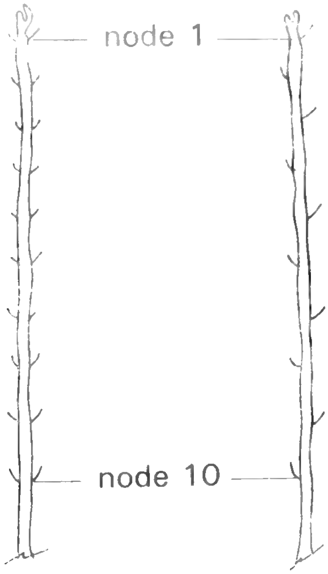

Fig. 1. Young branch with opposite (*left*) and alternate leaf position (*right*) showing the first 10 nodes labelled sequentially (diagrammatic).

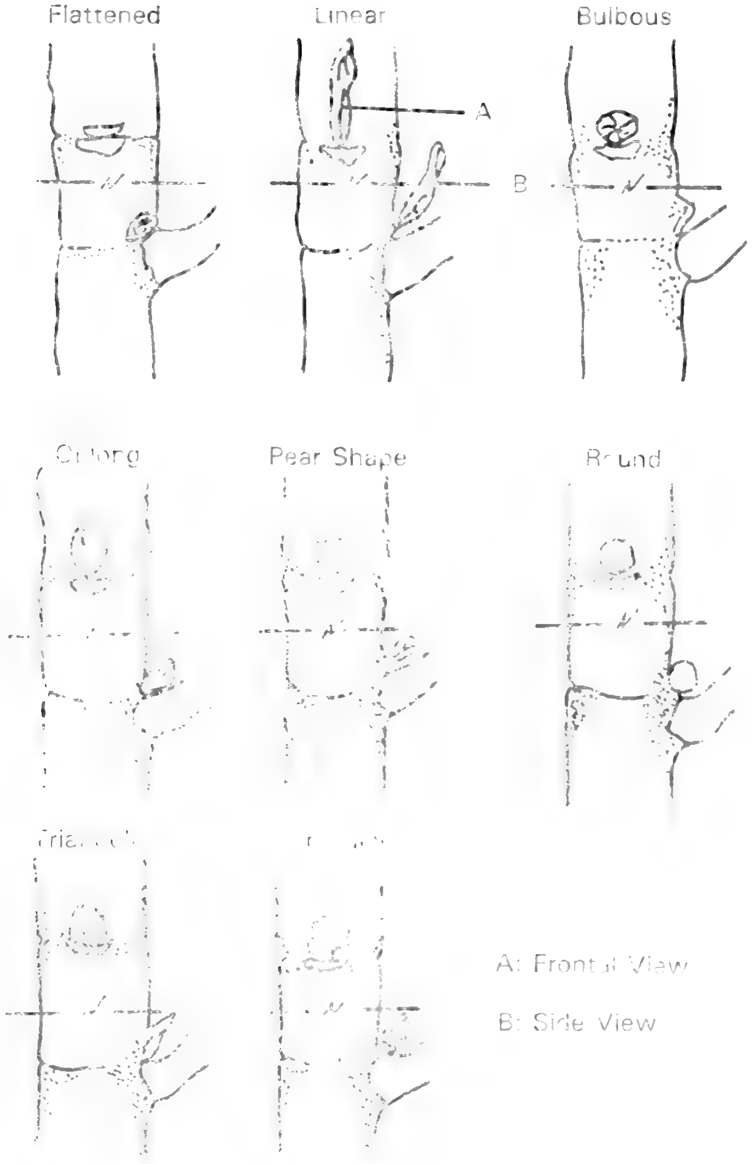

Fig. 2. Diagrammatic representation of the different shapes of axillary buds.

others that did not fit into the above types were grouped under the irregular type. The various types present and the frequency of their occurrence were also noted. The triangular buds (fig. 2; plate 1, h and k) were of most common occurrence, followed by linear (plate 1, b and c), oblong (plate 1, f), bulbous (plate 1, d) and other types. All of them are diagrammatically illustrated in figure 2 and the relative frequencies are shown in table 1.

The bud morphology, quantitative and qualitative aspects are not studied so far in any great detail, especially of tropical trees (Corner, 1952; Opeke, 1982). Lubbock (1899) considered the structure of buds of about 25 temperate trees and shrubs including three Gymnosperms. The buds of each species were described but no bud types were recognised. Greater emphasis was laid on the structures that protect the bud and the bud emergence after wintering. Other papers published occasionally described the buds in individual plants like cotton, sweetgum, bamboos and others (Mannery and Ball, 1959; Kormanik and Brown, 1967; McClure, 1976).

Single and Multiple Buds

In the majority of the trees or woody plants, occurrence of a single axillary bud is common. Of the 100 species presently studied, 17 of them had multiple buds at the nodes (table 2).

The species with multiple buds are grouped in the increasing order of their numbers.

a) Species with 1–2 axillary buds per node

Annona muricata L.
Annona reticulata L.
Annona squamosa L.
Delonix regia (Boj. ex Hk.) Raf.
Gliricidia sepium (Jacq.) Kunth ex Walp.
Hibiscus tiliaceus L.
Mimusops elengi L.
Lithocarpus urceolaris (Jacq.) Merr.
Samanea saman (Jacq.) Merr.

b) Species with 2–3 axillary buds per node

Jacaranda obtusifolia HBK ssp. *rhombifolia* (Meij.) Gent.

c) Species with 3–4 axillary buds per node

Spathodea campanulata Beauv.
Peltophorum pterocarpum (DC.) Back.
Nephelium lappaceum L.

d) Species with 4–5 axillary buds per node

Tabebuia pallida Miers
Acacia auriculiformis A. Cunn. ex Bth.
Erythrophleum suaveolens (Guill. & Perr.) Bren.
Millettia atropurpurea Bth.

The 100 species examined belonged to 74 genera of 33 families. Four or more genera were included in Bignoniaceae, Dipterocarpaceae, Leguminosae and Myrtaceae and in others, 1, 2, or 3 genera were involved (table 2). The family of Leguminosae had the largest representation with about 16 genera and 23 species. In the members of these families, the shape of the buds varied among the different genera, the different species and sometimes even between the allied species in genera such as *Annona, Cassia, Shorea, Nephelium, Tabebuia* and *Podocarpus.* In contrast, the

Table 1

The shapes of axillary buds in some tropical trees.

Bud Shape	Number of Species
Bulbous	16
Flattened	4
Irregular	2
Linear	18
Oblong	16
Pear	7
Round	5
Triangular	30
Buds indistinct	2
	100

Note. The above observations were made on the first 3 nodes where the shape of the distinct buds was relatively consistent. Owing to age, the buds in the older nodes in many species were either detached or the shapes had changed due to emergence. Plate 1 a to q illustrate some of the shapes described.

buds were of the same shape among the species of *Eugenia, Ficus, Artocarpus* and *Bauhinia.*

Hallé *et al.* (1978) also observed that multiple buds are quite common with tropical woody plants such as *Coffea* sp. The frequency of tropical trees species having multiple buds was however not mentioned. The morphogenetic implication of these buds has so far been little considered, especially by developmental biologists. The buds at each node should be further studied as the differential developmental potential of each number of the multiple bud complex will also influence the ultimate architecture of the tree (Hallé *et al.*, 1978). Some preliminary observations made with some tropical plants showed that the pattern of response by the multiple buds, varied from species to species (Varossieau, 1940; Moens, 1963). In *Coffea*, for example, the distal bud of each leaf pair on orthotropic shoots usually grows out as a precocious branch, the others persist as reserve buds. In the case of Dipterocarps, the dominant axillary buds would often grow in a plagiotropic pattern and in some instances, the axillary buds which may be indistinct, would grow to form orthotropic shoots (Ng, 1976).

The distinct variation in numbers, shapes and sizes of the axillary buds among the species within a genus or, between the genera of a family, may have some taxonomic importance. To-date, the morphological features of axillary buds are seldom or not at all used for either identification or species classification (Goebel, 1900; Corner, 1952; Whitmore, 1972; 1973; Cockburn, 1976; Ng, 1978).

Very often, the identification of plants are confirmed through the study of flower characters. However, as most tropical forest trees flower either rarely or infrequently, confirmation through flower features may be a problem. In fact, some tropical trees do not even flower for years (McClure, 1966; Rao, 1973). Therefore, having at one's disposal an additional vegetative character such as the bud morphology may be immensely useful.

Buds, prior to their emergence, seem to be rigid and uniform in their shapes and other morphological characteristics. They may not be so variable as the leaves in sizes and shapes. Stace (1980) has already mentioned that vegetative characters such as leaves of higher plants, are often looked upon as risky evidence because often similar morphological features are found in quite unrelated plants. Therefore, as many other vegetative characters as possible should be included to give an accurate identification and, buds also can be used in terms of their shape, size and number.

In some instances, the number of buds varied from node to node on the same axis. In *Tabebuia pallida*, multiple buds were seen at some of the younger nodes, and at the older ones, the buds were indistinct. Where multiple buds were present, they varied in number from 2 to 5, but in some like *Erythrophleum suaveolens*, five buds were present consistently at most leaf axils. The arrangement of buds varied among the species with multiple buds. Clustered arrangement of buds was seen in *Tabebuia pallida* and in *Erythrophleum suaveolens*; the buds were arranged in basipetal order. The sizes of the multiple buds within a single axil differed greatly and the largest of the lot was dominant. It developed into a shoot when conditions favoured. The smaller ones remained either dormant or frizzled and dropped off.

Regarding their conspicuousness, the buds decreased in prominence in the lower nodes and this was the general pattern for the majority of the species studied (table 3). In most species the buds became detached following leaf abscission and a few species were exceptional like *Bixa orellana* L. and *Michelia alba* DC. where the buds were prominent even at the older nodes.

The largest axillary bud measured up to 1 cm in length was in *Erythrophleum suaveolens* and the smallest, about 0.1 mm, found in *Fagraea fragrans* Roxb., was barely visible even under the binocular microscope. The larger buds were found in the younger leaf axils and this perhaps was due to the vigorous meristematic tissue subtending the bud and the dominant nature of the younger bud itself. In *Peltophorum pterocarpum* and *Fagraea fragrans* the dominant buds at nodes 1, 2 or 3 gave rise to lateral branches.

Apart from shape and size, the buds varied with regard to the number of scale leaves that covered each bud, but on an average, 4–5 bud scales were present in most of them. The bud scales were smooth in certain species as in *Eugenia grandis* Wight

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Plate 1. *(facing page):*

a, lateral view of a flattened bud of *Pterocarpus indicus* Willd.; *b*, frontal view of a linear bud of *Coccoloba uvifera; c*, lateral view of a linear bud of *Michelia champaca* L.; *d*, frontal view of a bulbous bud of *Mangifera indica* L.; *e*, lateral view of a bulbous bud of *Eugenia grandis; f*, lateral view of oblong to triangular buds of *Cinnamomum iners* Reinw. ex Bl.; *g*, frontal view of a pear-like bud of *Samanea saman; h*, frontal view of a triangular bud of *Bixa orellana.*

Scale: 1 division = 1mm.

Plate 1

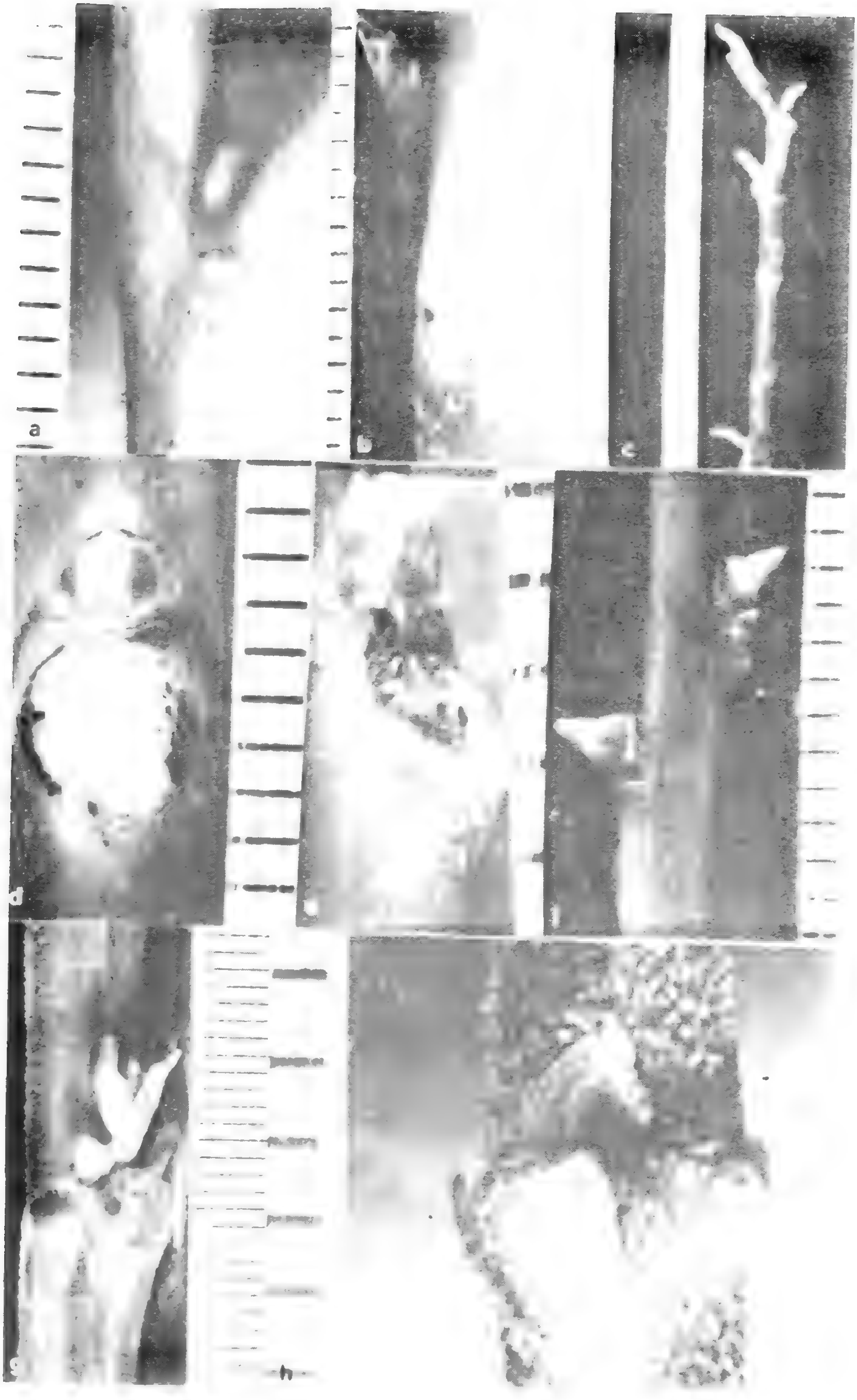
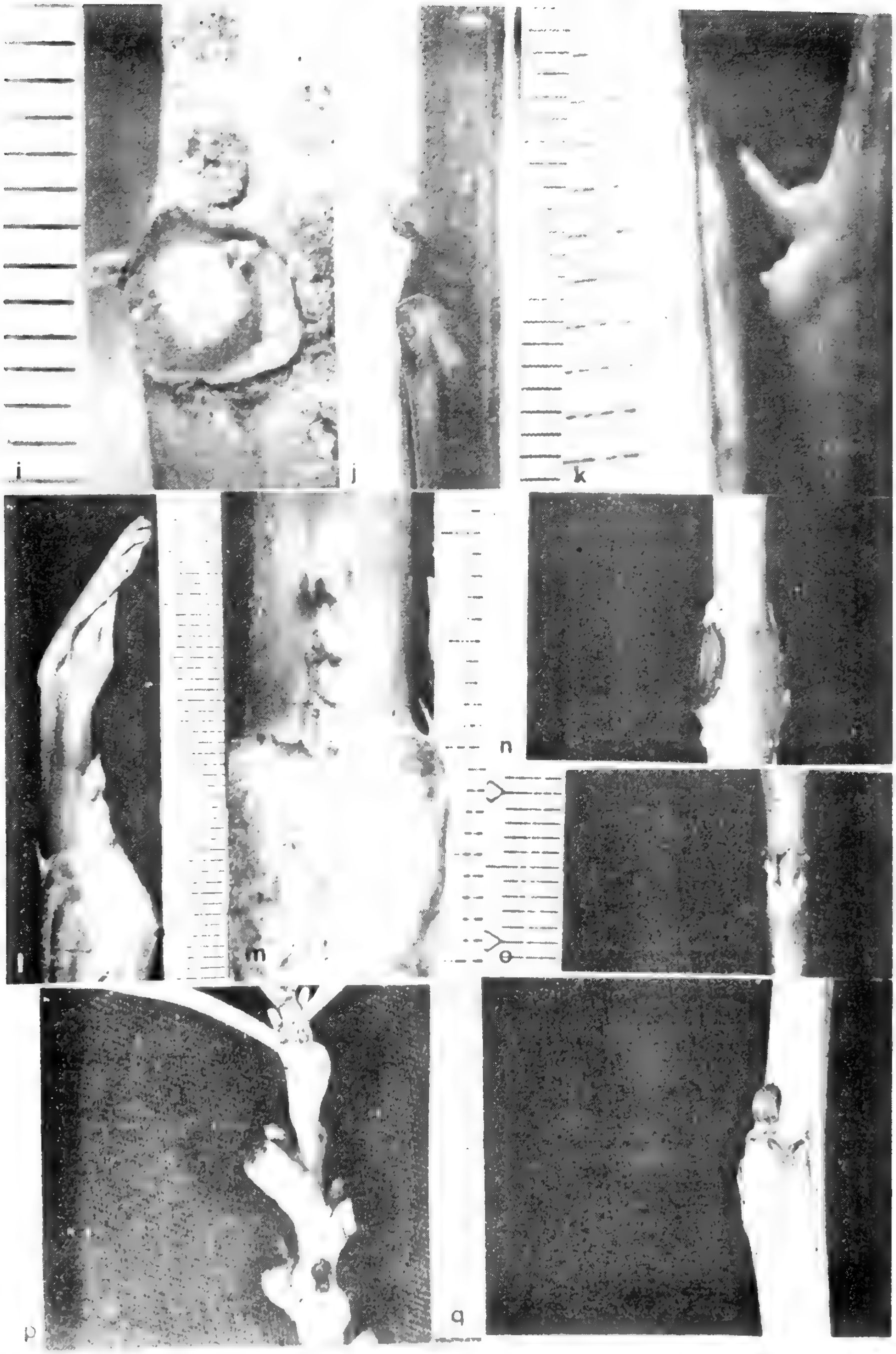


Plate 1 *cont.*



(plate 1d) or covered with hairs as in *Muntingia calabura* L. Most of the buds were brown in colour and some had the same colour as the bark of the tree. Some buds were distinctly pink as in *Coccoloba uvifera* (L.) L. (plate 1b), and covered by very broad stipules.

The architecture and form of a tree is heavily influenced by the growth response of axillary buds (Corner, 1952; Hallé *et al*, 1978; Koriba, 1958). The geometry of the arrangement of the buds and the manner of the response determine the ultimate form of the tree. In monopodial trees, the axillary buds are normally arranged in regular whorls around the orthotropic shoot and the uniform response and growth of these buds give rise to the monopodial pattern of branching. In contrast with the monopodial trees, the response of the axillary buds of sympodial trees varies tremendously. Hallé *et al*, (1978) stated that the pattern of the nodes on which the axillary buds are located, is extremely complex and diverse, thus resulting in a variable response. Furthermore, the distribution and the kinds of lateral or axillary buds can vary widely on the different parts of one plant. Because of these variations, different patterns of branching are observed in sympodial trees (Koriba, 1958).

Buds are also of great value in vegetative propagation as they can serve as starting units for mass propagation. De Fossard (1980) had shown that when nodes of *Eucalyptus ficifolia* F. Muell. were cultured in culture media containing 5 μM IBA and 2 μM BAP, several shoots were obtained. As a result, young nodal segments containing the axillary buds were used widely as explants to induce multiple shoot formation *in vitro* condition for many species of trees (Hutchinson, 1981; Lee and Rao, 1981; Mascarenhas *et al*, 1981). It will therefore be beneficial for further studies to be carried out to determine whether there is any correlation between the prominence or the morphology of these buds and the ease with which they develop into multiple shoots.

Plate 1. *cont. (facing page)*:

i, frontal view of a rounded bud of *Erythrina variegata* L.; *j*, lateral view of an irregular bud of *Nephelium lappaceum; k*, lateral view of a triangular bud of *Citrus microcarpa* Bunge; notice the sharp thorn structure enclosing the axillary bud; *l, m*, lateral and frontal view of multiple buds of *Erythrophleum suaveolens; n*, lateral view of multiple buds of *Gliricidia sepium;* buds were mainly pear-shaped; *o*, frontal view of multiple buds of *Acacia auriculiformis;* buds were linear to triangular in shape; *p*, lateral view of multiple buds of *Peltophorum pterocarpum;* buds were mainly linear to pear-shaped; notice the leader bud being he largest of the 3 to 4 buds present; *q*, lateral view of multiple buds of *Millettia atropurpurea;* buds were oblong to triangular in shape; notice the larger leader bud of the 2 present.

Scale: 1 division = 1mm.

Table 2

Number, shape and sizes of the axillary buds in the different taxa.

* The numbers are mentioned for those taxa which had multiple buds. All others had a single bud at each leaf axil.

\+ The sizes given for each species in this table refer to the smallest and the largest buds (length of) the buds only), distinct at the nodes 1 to 10. All measurements were made only on buds before emergence. Mean lengths of the buds were derived from nodes 1 to 4. Buds were somewhat indistinct in certain species at subsequent nodes. Hence measurements were variable, e.g. *Tabebuia pallida.*

Family/Species	Shape	Sizes (mm) +	Mean (mm)
Anacardiaceae			
1. *Anacardium occidentale* L.	bulbous	0.5–1.0	0.7 ± 0.2
2. *Mangifera indica* L.	bulbous	0.5–1.0	0.8 ± 0.2
3. *Rhus succedanea* L.	triangular	2.0–3.0	2.5 ± 0.5
Annonaceae			
4. *Annona muricata* (1–2)*	linear	1.0–4.0	2.4 ± 1.3
5. *Annona reticulata* (1–2)*	oblong	1.0–2.0	1.5 ± 0.5
6. *Annona squamosa* (1–2)*	irregular	1.0–2.0	1.5 ± 0.5
7. *Polyalthia longifolia* (Sonn.) Thw.	linear	4.0–8.0	5.8 ± 1.7
Apocynaceae			
8. *Ervatamia dichotoma* (Roxb.) Burk.	round	0.1–0.5	0.2 ± 0.1
9. *Plumeria acuminata* W.T. Ait.	–	–	–
Bignoniaceae			
10. *Jacaranda* (2–3)*	linear to oblong	1.0–5.0	3.6 ± 1.8
11. *Spathodea campanulata* (3–4)*	linear to triangular	1.0–5.0	3.4 ± 1.7
12. *Tabebuia pallida* (4–5)*	irregular to linear	1.0–3.0	1.6 ± 0.9
13. *Tabebuia rosea* (Bertol.) DC.	bulbous	0.5–1.0	0.7 ± 0.3
14. *Tabebuia spectabilis* (Planch. & Lindl. ex Planch.) Nichols.	round	0.5–2.0	1.5 ± 0.7
Bixaceae			
15. *Bixa orellana*	triangular	1.0–3.0	2.2 ± 0.8
16. *Cochlospermum religiosum* (L.) Alston	linear	1.0–4.0	1.7 ± 1.3
Capparidaceae			
17. *Crataeva religiosa* Forst. f.	triangular	2.0–4.0	3.1 ± 0.9
18. *Cratoxylon formosum* (Jack) Dyer	triangular	1.0–4.0	2.1 ± 1.0
19. *Cratoxylon pruniflorum* Kurz	bulbous	1.0–3.0	1.8 ± 0.9
Celastraceae			
20. *Elaeodendron quadrangulatum* Reiss.	oblong	1.0–2.0	1.4 ± 0.5
Combretaceae			
21. *Terminalia catappa* L.	triangular	3.0–6.0	4.2 ± 1.3

Table 2 *Continued*

Family/Species	Shape	Sizes (mm) +	Mean (mm)
Dipterocarpaceae			
22. *Dryobalanops aromatica* Gaertn. f.	triangular	1.0–3.0	1.6 ± 0.8
23. *Hopea mengarawan* Miq.	bulbous	0.1–0.5	0.3 ± 0.1
24. *Shorea curtisii* Dyer ex King	bulbous	0.1–0.5	0.3 ± 0.2
25. *Shorea leprosula* Miq.	triangular	0.5–1.5	0.3 ± 0.1
26. *Shorea sumatrana* (V. Sl. ex Foxw.) Sym.	oblong	4.0–6.0	5.3 ± 1.0
27. *Vatica pallida* Dyer	triangular	0.1–1.0	0.6 ± 0.4
Ebenaceae			
28. *Diospyros discolor* Willd.	triangular	2.0–4.0	3.1 ± 1.1
Euphorbiaceae			
29. *Antidesma bunius* (L.) Spreng.	triangular	0.5–1.0	0.6 ± 0.3
30. *Elateriospermum tapos* Bl.	bulbous	0.1–0.5	0.4 ± 0.2
31. *Macaranga triloba* (Bl.) M.A.	pear	3.0–6.0	4.4 ± 1.5
Fagaceae			
32. *Lithocarpus urceolaris* (1–2)*	pear	1.0–2.0	1.4 ± 0.5
Gnetaceae			
33. *Gnetum gnemon* L.	flattened	0.5–1.0	0.8 ± 0.2
Guttiferae			
34. *Calophyllum inophyllum* L.	triangular	1.0–2.0	1.7 ± 0.5
Lauraceae			
35. *Cinnamomum iners* Reinw. ex Bl.	oblong to triangular	2.0–3.0	2.6 ± 0.5
Leguminosae			
36. *Acacia auriculiformis* (2–5)*	oblong to linear	0.5–2.0	1.3 ± 0.7
37. *Albizzia falcata* (L.) Back.	linear	1.0–7.0	–
38. *Andira inermis* (W. Wight) HBK ex DC.	linear	3.0–4.0	3.7 ± 0.5
39. *Bauhinia acuminata* L.	triangular	4.0–6.0	5.0 ± 1.0
40. *Bauhinia blakeana* Dunn	triangular	4.0–6.0	4.5 ± 0.9
41. *Bauhinia purpurea* L.	pear	2.0–5.0	4.6 ± 1.0
42. *Brownea capitella* Jacq.	linear	2.0–6.0	3.4 ± 2.1
43. *Brownea grandiceps*	–	–	–
44. *Cassia bakeriana* Craib	flattened	1.0–2.0	1.5 ± 0.5
45. *Cassia fistula* L.	triangular	2.0–6.0	4.6 ± 0.8
46. *Cassia multijuga* Rich.	linear	1.0–5.0	3.3 ± 1.6
47. *Cassia* sp. (hort. variety)	triangular	2.0–4.0	3.2 ± 1.0
48. *Cassia spectabilis* DC.	oblong	1.0–3.0	1.9 ± 0.9
49. *Dalbergia oliveri* Gamble & Prain	flattened	1.0–2.0	1.3 ± 0.5
50. *Delonix regia* (2)*	pear	1.0–2.0	1.4 ± 0.5
51. *Erythrophleum suaveolens* (3–5)*	triangular to linear	1.0–10.0	6.9 ± 3.4
52. *Erythrina fusca* Lour.	bulbous to pear	2.0–4.0	3.0 ± 0.8
53. *Erythrina variegata* L.	round to triangular	1.0–3.0	2.3 ± 1.0
54. *Gliricidia sepium* (2)*	pear to round	1.0–3.0	1.9 ± 1.1
55. *Millettia atropurpurea* (3–5)*	oblong	1.0–6.0	4.0 ± 1.9
56. *Peltophorum pterocarpum* (2–4)*	linear	1.0–5.0	3.3 ± 1.9

Table 2 *Continued*

Family/Species	Shape	Sizes (mm) +	Mean (mm)
Leguminosae *cont.*			
57. *Pongamia pinnata* (L.) Pierre	flattened	1.0–2.0	1.4 ± 0.5
58. *Pterocarpus indicus* Willd.	flattened	1.0–3.0	2.3 ± 0.5
59. *Samanea saman* (1–2)*	pear to irregular	1.0–6.0	4.0 ± 2.1
Lecythidaceae			
60. *Barringtonia asiatica* (L.) Kurz	bulbous	2.0–3.0	2.4 ± 0.5
Loganiaceae			
61. *Fagraea fragrans*	bulbous	0.1–0.5	0.4 ± 0.2
Lythraceae			
62. *Lagerstroemia speciosa* (L.) Pers.	linear	2.0–6.0	4.2 ± 1.5
Magnoliaceae			
63. *Michelia champaca* L.	linear	5.0–15.0	10.1 ± 3.0
Malvaceae			
64. *Hibiscus tiliaceus* (1–2)*	oblong	1.0–4.0	2.3 ± 1.4
Meliaceae			
65. *Khaya grandiflora* C. DC.	round to oblong	0–1.0	0.9 ± 0.3
66. *Sandoricum koetjape* (Burm. f) Merr.	round to oblong	1.0–3.0	1.9 ± 0.9
Myrsinaceae			
67. *Ardisia elliptica* Thunb.	round	3.0–6.0	4.5 ± 1.2
Myrtaceae			
68. *Callistemon citrinus* (Curtis) Stapf	triangular	5.0–8.0	6.6 ± 1.5
69. *Eugenia aquea* Burm. f.	bulbous	0.5–1.0	0.7 ± 0.3
70. *Eugenia grandis*	bulbous	0–1.0	0.4 ± 0.4
71. *Eugenia javanica* Lmk	bulbous	0.5–1.0	0.8 ± 0.2
72. *Eugenia longiflora* (Presl.) F. Vill.	bulbous	0.5–2.0	1.3 ± 0.8
73. *Eugenia malaccensis* L.	bulbous	0.5–1.0	0.8 ± 0.2
74. *Eugenia michelii* Lmk	linear	2.0–6.0	3.9 ± 1.7
75. *Melaleuca cajuputi* Powell	pear	4.0–6.0	4.4 ± 0.8
76. *Psidium guajava* L.	oblong	2.0–3.0	2.8 ± 0.4
77. *Rhodamnia cineria* Jack	triangular	2.0–4.0	2.6 ± 0.8
Podocarpaceae			
78. *Podocarpus koordersii* Pilg.	bulbous	1.0–2.0	1.7 ± 0.5
79. *Podocarpus neriifolius* D. Don	round	1.0–3.0	2.0 ± 0.8
80. *Podocarpus polystachyus* R. Br. ex Mirb.	oblong	1.0–2.0	1.4 ± 0.5
Polygonaceae			
81. *Coccoloba uvifera*	triangular to linear	4.0–8.0	5.6 ± 1.6
82. *Triplaris americana* L.	oblong	1.0–3.0	2.3 ± 0.9

Table 2 *Continued*

Family/Species	Shape	Sizes (mm) +	Mean (mm)
Rutaceae			
83. *Atalantia spinosa* (Willd.) Tanaka	linear	1.0–3.0	2.0 ± 1.1
84. *Citrus grandis* (L.) Osb.	triangular	2.0–6.0	3.2 ± 1.5
Salicaceae			
85. *Salix* sp.	linear to triangular	5.0–9.0	5.6 ± 1.7
Sapindaceae			
86. *Arfeuillea arborescens* Pierre	oblong	2.0–3.0	2.6 ± 0.5
87. *Filicium decipiens* (Wright & Ann.) Thw.	oblong	2.0–4.0	3.1 ± 1.0
88. *Nephelium lappaceum* (1–4)*	irregular	1.0–3.0	2.0 ± 1.0
89. *Dimocarpus longan* Lour. var. *malesianus* Leenh.	oblong	1.0–2.0	1.3 ± 0.6
Sapotaceae			
90. *Achras sapota* L.	oblong to irregular	1.0–2.0	1.2 ± 0.4
91. *Mimusops elengi* L. (2)*	triangular	2.0–5.0	3.5 ± 1.3
92. *Palaquium obovatum* (Griff.) Engl.	bulbous	0.5–1.0	0.8 ± 0.2
Saxifragaceae			
93. *Brexia madagascariensis* (Lmk) Thou.	triangular	2.0–4.0	2.8 ± 0.8
Tiliaceae			
94. *Muntingia calabura*	linear	0.5–1.0	0.8 ± 0.2
Urticaceae			
95. *Artocarpus integer* (Thunb.) Merr.	linear	2.0–3.0	2.4 ± 0.5
96. *Artocarpus gomeziana* Wall.	linear	2.0–5.0	3.7 ± 1.4
97. *Artocarpus heterophyllus* Lamk.	oblong	1.0–3.0	1.5 ± 0.8
98. *Ficus benjamina* L.	triangular	2.0–4.0	3.0 ± 1.0
99. *Ficus elastica* Roxb. ex Hornem.	triangular	2.0–6.0	2.8 ± 0.8
100. *Ficus retusa* L.	triangular	1.0–3.0	1.6 ± 0.8

Table 3

The prominence of the axillary buds in relation to their positions at different nodes.

Relative prominence of buds	Number of species exhibiting the pattern of prominence
Buds prominent in all 10 nodes	29
Buds prominent up to 7th to 9th node	39
Buds prominent up to 4th to 6th node	18
Buds prominent only in first 3 nodes	12
Buds not visible	2
	100

Note. All buds above the size of 2mm, which were visible to the naked eye, were classified as prominent.

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Physical Effects of Soil Compaction and Initial Growth of *Acacia pycnantha* (Leguminosae) in a Clay-loam Soil

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Abstract

An ornamental plant, Golden Wattle (*Acacia pycnantha*) was grown in a clay loam subsoil supplemented with adequate amounts of inorganic fertilizer and then compacted by four methods, namely, light finger pressure, rubber hammer, steel bar and machine pressure. Dry matter accumulation and rooting behaviour after four months growth in pots under glasshouse conditions were studied in relation to the degree of soil compaction. Influences of compaction on such physical properties as dry bulk density, penetration resistance, total porosity, oxygen diffusion rate and moisture content were also investigated. Plant growth and soil penetration resistance were significantly related to the level of compaction. Amelioration by addition of a medium-size grade of sand on a 50% volume basis before applying compaction reduced the soil strength substantially and allowed the plant to grow normally.

Introduction

Soil compaction is a problem confronting urban horticulture in the Republic of Singapore. Construction involving standard engineering procedures for building roads and buildings, reclamation from the sea using clayey subsoils that lack organic matter and the effects of recreational activities on school fields and in parks, often lead to excessive soil compaction. In line with the Singapore Government's 'greening' policy, the Parks & Recreation Department is required to establish vegetation in planting holes frequently impounded by compact subsoil, typified by a myriad of adverse physical conditions such as impeded drainage and high soil strength. Consequently, root-bound vegetation is susceptible to root-rot during the wet seasons (Raghavan *et al.*, 1982 and Vigier *et al.*, 1983).

The adverse effects of compaction on soil physical properties have been extensively reviewed (Barley & Greacen, 1967; Cannell, 1977; Drew & Goss, 1973; Greacen & Sands, 1980; Lal & Greenland, 1970 and Ruark *et al.*, 1982).

The subject of this trial, *Acacia pycnantha* Benth., is much valued as an ornamental plant in New Zealand. In addition, its bark is a source of tannins and gum. This plant is deep-rooting and hardy, and can thrive under severe natural conditions (Audus, 1934). The objectives of this glasshouse trial were to study the rooting configuration of Golden Wattle under various levels of soil compaction, to determine the growth limiting levels of soil compaction and to evaluate the ameliorative effects of different levels of two anti-compaction materials, i.e. sand and sewage sludge, incorporated in the potting medium prior to artificial compaction. If the findings prove significant and beneficial, then they could be adapted for practice in Singapore.

Table 1

Summary of treatments.

*Treatment	Soil medium	Mode of compaction
1	Clay loam	Light finger pressure (uncompacted control)
2	Clay loam	Tapping with a rubber hammer
3	Clay loam	Hitting with a steel bar
4	Clay loam	Mechanical pressure of 5 tonnes applied intermittently with a MTS stiff loading frame
5	Pure sand	Hitting with a steel bar
6	Clay loam + sand (80:20 v/v)	Hitting with a steel bar
7	Clay loam + sand (50:50 v/v)	Hitting with a steel bar
8	Clay loam + sludge (80:20 v/v)	Hitting with a steel bar
9	Silty pan material	No treatment — Natural reconstitution back into a hard pan

* There were 6 replicates in each treatment except for treatment 9 which was replicated twice.

Table 2

Effects of compaction on dry bulk density, total porosity, soil strength and plant dry matter.

Treatment	1 (Control)	2	3	4	5	6	7	8
Parameters								
+ Dry bulk density (g cm^{-3})	1.07	1.13	1.29	1.32	1.22	1.31	1.22	1.29
+ Total porosity (%V)	60.7	58.6	52.6	51.4	54.0	51.5	54.8	51.3
Shoot dry weight (g plant^{-1})	1.46a	0.65bc	0.72b	0.07**c	0*	0.38bc	1.44a	0*
+ Root dry weight (g plant^{-1})	0.54	0.27	0.24	0.03	0*	0.15	0.37	0*
Penetration resistance (bar)								
At 0–1 cm	2.46e	21.14d	39.20b	54.80a	—	34.69bc	5.41e	29.76c
At 1–2 cm	3.69e	31.61d	52.52b	>100.00a	—	40.02c	6.74e	32.02d
At approximately 10 cm	5.75g	24.63e	75.54b	>100.00a	—	51.79c	15.48f	47.62d

Treatment 1–8 have reference in Table 1.
+ Average of two measurements.
* Complete mortality.
– Very low, not measured
**Low value due to mortality of 3 plant replicates.
Values in each row if not followed by the same letter are significantly different as judged by the DMR test at $P < 0.05$.

Materials and Methods

The soil compacted in this trial was taken from a buried reddish clay-loam layer at a depth of 5 to 6 m from the surface of Paremata clay. It was collected from a recently excavated area of quarry used for brick and pipe manufacture (Grid. Ref. NZMS1 N160 473462). The undisturbed material had a dry bulk density of 1.44 g cm^{-3}, particle density of 2.72 g cm^{-3}, native moisture content of 23.7% and a natural penetration resistance of 86 bar measured with a Chatillon Guage-R penetrometer. On mechanical analysis, it was found to contain 52% clay, 45% silt and 3% sand-size particles. Its pH was 5.6 and liming was not necessary. For this study, a pan material was also collected from the natural B horizon and this had an innate mechanical impedance of greater than 100 bar, particle density of 2.66 g cm^{-3} and a native moisture content of 12.8%. Mechanical analysis revealed a composition of 9% sand, 53% silt and 38% clay. This material reconstituted rapidly into a pan after initial disintegration for potting.

For anti-compaction purposes, a medium-size grade of sand, containing 3% silt-size and 2% clay-size particles, was collected from the C horizon of a coastal aeolian dune system at Waikanae. It had a natural moisture content of 4.4% and particle density of 2.64 g cm^{-3}. Digested and dried sewage sludge was collected from a nearby treatment plant and pulverized before mixing with the trial material.

The containers used were sections of PVC drain pipes of dimensions 150 × 300 mm (diameter × height) with one end closed by a black perforated planting bag. The composition of potting media and methods of compaction are summarized in table 1. Each medium, in its naturally moist state, was packed layer by layer by one of 4 methods (table 1).

Seeds of *A. pycnantha* were germinated on moistened filter paper. When 5 mm of root had developed, uniform seedlings were selected and implanted into a 1 cm^3 scarified zone in the middle of each pot. The replicates were arranged in randomized blocks. The plants were watered by spraying twice daily according to their growth requirements, and harvested after 4 months.

For treatments 1 to 8 (table 1), in two of the replicate pots an oxygen platinum electrode was inserted to a depth of 3 cm to determine the oxygen diffusion rate (Gradwell, 1972) and for measurements of penetration resistance using a probe of 5 mm in diameter. A second lot of two pots from each set were cored with the core sampler to a depth of 1 to 4 cm in order to determine the amounts of water held at a range of moisture tensions. Equilibrium times for these cores on the tension plates varied as follows: 10 cm for 1 day; 25, 50 and 75 cm for 2 days and 100 cm for 3 days. Dry bulk densities and porosities were determined from the same cores according to Gradwell (1972). The particle densities were determined separately. The remaining two pots per treatment were washed free of soil on a sieve to retain roots. Plant tops were harvested from all replicates of each treatment. Both the root and the shoot were subjected to dry matter determination after 4 months.

Results and Discussions

Results are presented in table 2, plates 1–4 and figures 1 and 2. Where possible, data were analysed with the Duncan Multiple Range Test for significance.

The highest dry bulk density attained by using machine pressure on the clay-loam soil was 1.32 g cm^{-3} (table 2). This value was less than the native value of 1.44 g cm^{-3} measured of the material in situ. A still higher value of 1.60 g cm^{-3} had been recorded for the B horizon of Paremata clay developed naturally over many wet and dry seasons (New Zealand Soil Bureau, 1968). Repeated attempts to establish *A. pycnantha* on a scarified zone on this pan material supplemented with inorganic fertilizer were in vain (plate 1). The inability of the seedling to root in this pan material guided the limits required for maximum dry bulk density in the pot trial.

The soil strength was directly and significantly proportional to the degree of compaction at the 3 depths concerned (table 2). Such a relationship has been confirmed by other researchers (Cannell, 1977 & 1982; Drew & Goss, 1973 & 1974; Eavis, 1972 a&b; Heilman, 1981; Russell & Goss, 1974; Sands & Bowen, 1978 and Zisa *et al.*, 1980) It was noted that the penetration resistance generally increased with depth (table 2). A soil strength of 25–55 bar in the rooting zone (0–10 cm) resulted in a 50% reduction in shoot and/or root growth (table 2). Compaction with the rubber hammer produced values of soil strength similar to those that were measured in the field, 18–19 bar, on one occasion (New Zealand Soil Bureau, 1968). Data on dry bulk density and total porosity were not statistically analysed. However, as expected, dry bulk density increased and total porosity decreased with increasing rate of compaction (table 2). This is in accordance with Baligar *et al.*, (1981) and Boone *et al.*, (1978).

Amount of shoot dry matter from compacted pots differed significantly from those of the control and an inverse relationship occurred between plant growth and the level of compaction (*cf* Mitchell *et al.*, 1981). There was a 10-fold range in the growth at extreme degrees of soil compaction. However, no difference in shoot dry matter was found between the intermediate rates of compaction (table 2). Top growth is shown in Plate 3: A-E. Dry root matter was not statistically analysed but a downward trend with increasing rate of compaction was apparent. Typical development of the root system in straight, compacted and uncompacted clay loam is depicted in Plate 2: a, b, c & f. Plate 2g represents the root system of an *A. pycnantha* developed in an uncompacted garden loam supplemented with inorganic fertilizer. This was kept solely for observation. Plate 2 shows that the root system became less fibrous and ramified with increasing level of compaction, and in the case of machine compaction (plate 2a), root development was highly incompatible with normal plant growth.

Addition of a medium-size grade of sand on a 20%V basis had no mitigating effect on the mechanical impedance of clay loam compacted with the steel bar. The presence of a small amount of coarse material could have actually promoted the compactibility of the fine clay loam. Consequently, plant growth in treatment 6 did not differ from that in straight clay loam soil compacted similarly (table 2 — treatment 3). The ameliorative effects of sand were prominent on a 50%V basis (table 2).

Plate 1. Natural and remoulded pan material.

A, *left*, pots of remoulded and natural pan material (*middle*) from the B horizon of Paremata clay; *B*, *right*, close-up of remoulded material.

Plate 2. Development of root systems in straight and amended clay loam under different levels of compaction.

Right to left, *a*, treatment 4; *b*, treatment 2; *c*, treatment 3; *d*, treatment 6; *e*, treatment 7; *f*, treatment 1 (uncompacted soil); *g*, root system developed in an uncompacted garden loam.

The penetration resistance was reduced to a level similar to that of treatment 1 and was significantly lower than that of treatment 3 (table 2). On adding 50%V sand, the dry bulk density decreased while the total porosity increased as compared with those in treatment 3 (table 2). As a result, plant growth in treatment 7 was of the same order as in treatment 1 (table 2; plates 2, e&f, 3A & 4B). All seedlings established in pure sand died after 4 months (plate 4C). It was thought that the particular grain size of sand used might have given rise to a transient high water table after irrigation, thereby damaging the root system. The cause of total seedling mortality in clay loam amended with digested sludge (plate 4D) was tentatively attributed to a partial/total reduced state in the rooting zone generated by the initial decomposition of the sludge.

The value obtained from the oxygen microelectrode inserted to depths of 3 to 4 cm below the surface were all greater than 2.5 × 10^{-7} g cm^{-2} min^{-1}. A value of

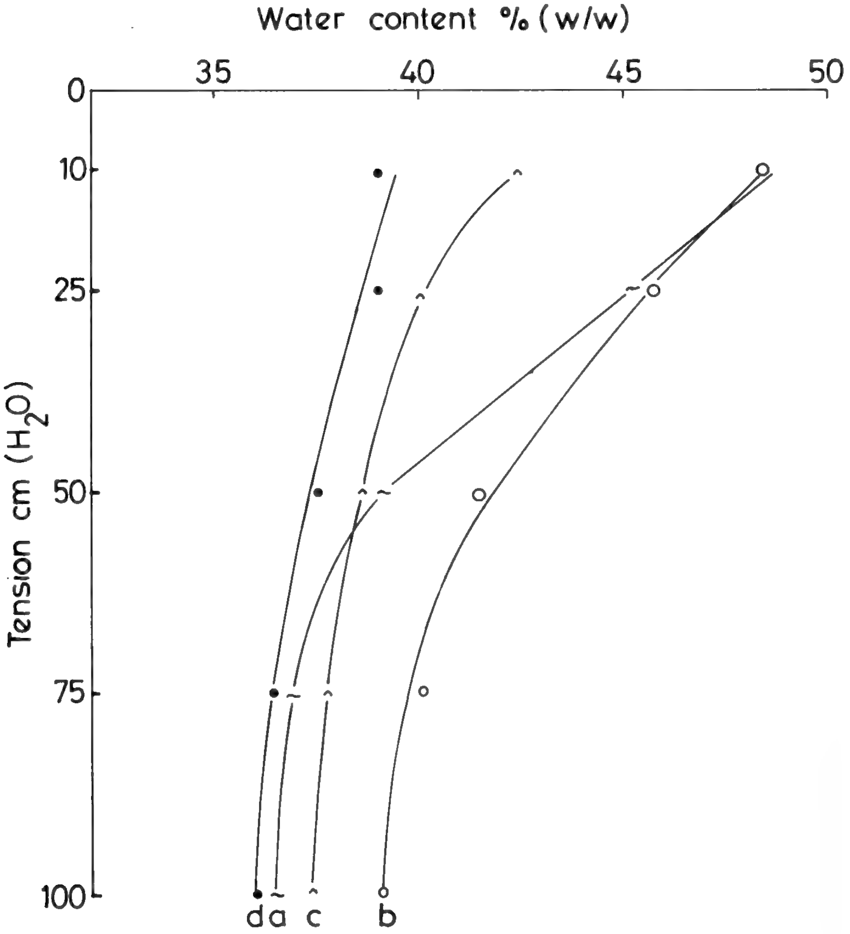

Fig. 1 Water contents of a clay loam compacted by four methods and equilibrated at five moisture tensions.
Soil compacted by: *a*, light finger pressure; *b*, rubber hammer; *c*, steel bar; *d*, mechanical press.

Note. Each point on the graphs is an average of 2 measurements.

1×10^{-7} g cm^{-2} min^{-1} is generally considered adequate for plant growth (Gradwell, 1972). The purely inorganic soil matrix supplemented with inorganic fertilizer had the advantage of not inducing the type of reducing conditions as might be encountered when digested sludge was incorporated in clay soils.

Figure 1 presents pF plots of the average water contents of cores from the compacted clay loam soil after equilibration at five values of moisture tension. Under the weak compaction exerted by finger pressure or rubber hammer, the soil had about 10% more water available at tensions of 10 and 25 cm than in soils compacted by steel bar or by machine compression. At high moisture tensions, above 75 cm, the water contents of the cores were similar for all methods of compaction. Mixing sand with the clay loam had marked influence on the water content of the cores after equilibration at different moisture tensions. Figure 2 shows pF curves of water content against moisture tension for mixtures of clay loam and sand, and clay loam and sludge, when all were compacted with the steel bar. The water contents were all very similar at low moisture tensions. At high moisture tensions, the water contents varied inversely according to the amount of sand that had been added. In other words, addition of sand made water more easily available.

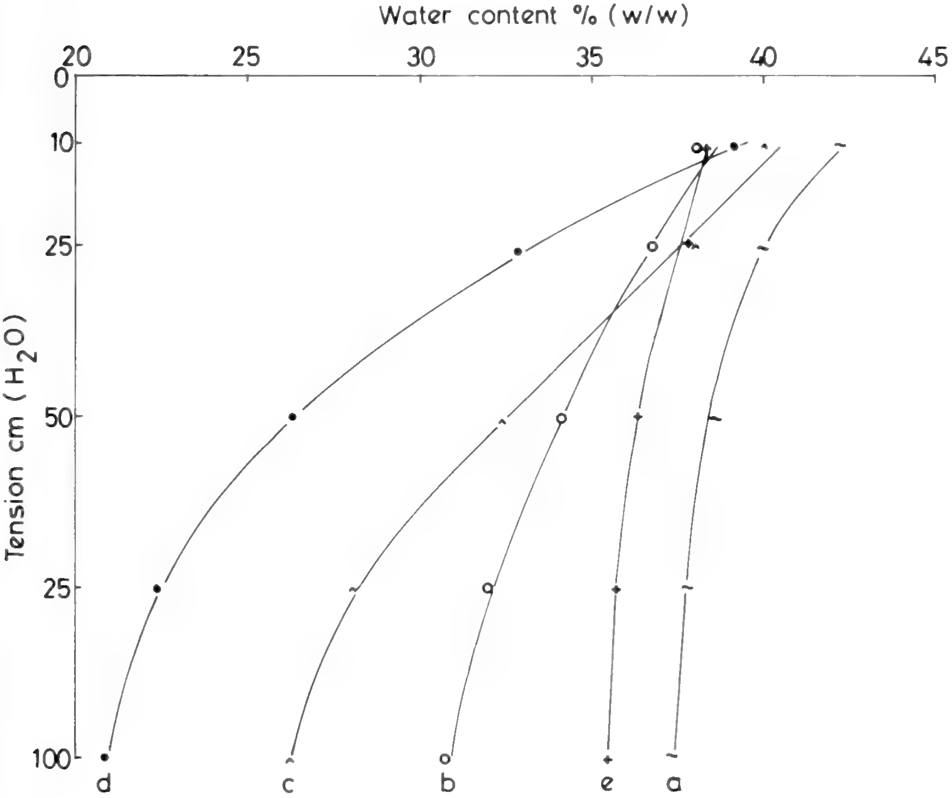

Fig. 2 Water contents of a clay loam ameliorated by sand or sludge and compacted with a steel bar. Composition: *a*, clay loam: *b*, 80% clay loam + 20% medium sand; *c*, 50% clay loam + 50% medium sand; *d*, medium sand; *e*, 80% clay loam + 20% sludge.

Note. Each point on the graphs is an average of 2 measurements.

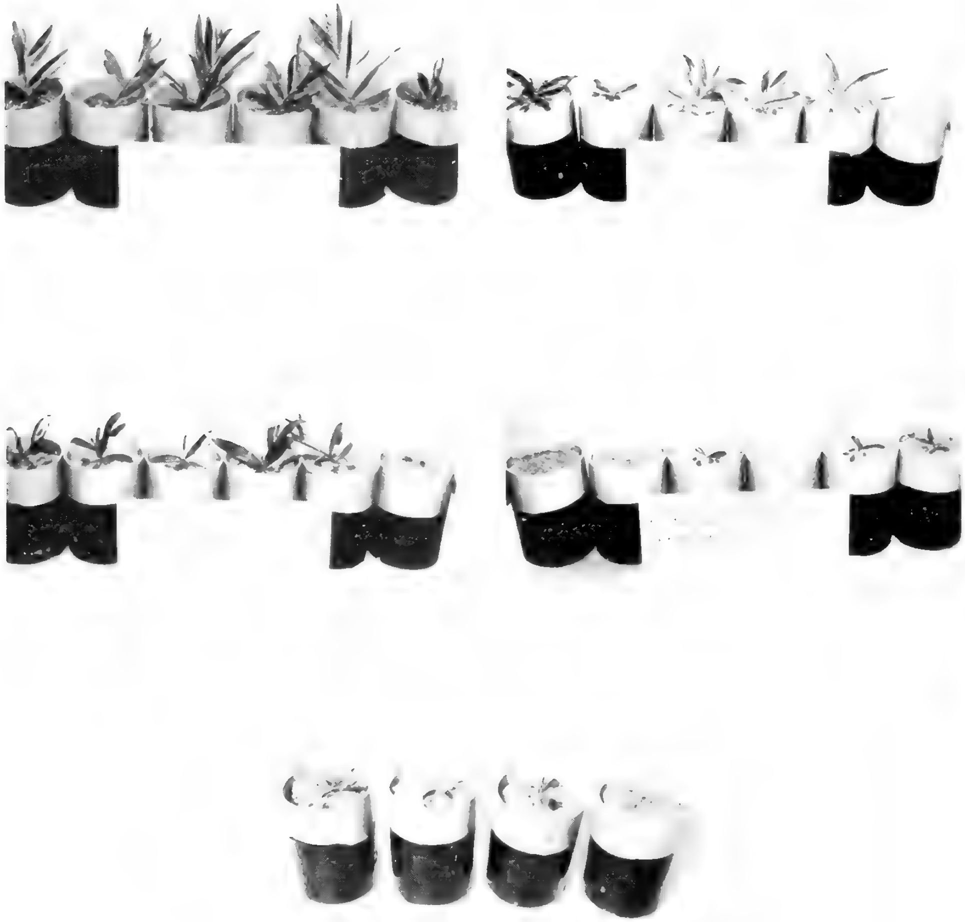

Plate 3. Development of plant top on clay loam under different levels of compaction.
A, *above left*, treatment 1; *B*, *right*, treatment 2; *C*, *middle left*, treatment 3; *D*, *right*, treatment 4; *E*, *below*, comparison of 4 rates of compaction on the development of plant top; *left to right*, treatment 1 (control), treatments 2, 3 and 4.

Plate 4. Development of plant top on clay loam amended with 2 rates of sand, pure sand and clay amended with sludge, all compacted with steel bar.
A, *above left*, treatment 6; *B*, *right*, treatment 7; *C*, *middle left*, treatment 5; *D*, *right*, treatment 8; *E*, *below*, comparison of the ameliorative effects of 2 rates of sand on the development of plant top; *left to right*, treatment 1 (control), treatments 6, 7, and 5.

Conclusions

A. pycnantha seedlings were unable to establish roots on a scarified surface of a pan material from the subsoil of Paremata clay or on the remoulded pan material containing adequate mineral fertilizer.

It was evident that upon compaction, soil strength became the severely limiting physical attribute that controlled the establishment and early growth of *A. pycnantha* in the Paremata clay-loam subsoil. A direct relationship was found between this property and the degree of compaction. Mechanical impedance, derived from machine compaction, represented a limit to penetration by roots. Hence, the growth of *A. pycnantha*, a very hardy plant, could be inimically affected by high degrees of soil compaction.

Alleviation of the dramatic changes in soil strength due to compaction was accomplished by adding a medium-size grade of sand on a 50%V basis prior to compaction; this resulted in normal plant growth.

Acknowledgements

The work reported was carried out at the New Zealand Soil Bureau under a New Zealand-Singapore Colombo Plan Co-sponsorship for the first author. He is grateful to the Soil Bureau staff for their help and discussions during the course of the practical attachment, and Mrs Foong Thai Wu for her assistance with the trial.

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The Embryology of *Garcinia mangostana* L. (Clusiaceae)

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Abstract

The anther is tetrasporangiate. The anther wall is four-layered and the secretory tapetum is binucleate. Most of the pollen mother cells degenerate just before meiosis and a few undergo meiosis. Cytokinesis is simultaneous and tetrads are tetrahedral.

The ovule is anatropous, bitegmic, tenuinucellate and the micropyle is formed by the outer integument only. The embryo sac development is of the *Polygonum* type.

The endosperm is of the Nuclear type. Cell-wall formation proceeds from the periphery towards the centre. The development of the adventive integumentary embryos is irregular and sometimes within the same embryo sac, several embryos may be found. The mature embryo is straight. The seed coat develops from the outer integument. The seed is non-endospermous and shows hypogeal germination and 10% of the germinated seeds give multiple seedlings.

Introduction

The mangosteen (*Garcinia mangostana* L.) commonly known in Malaysia as the "Queen of fruits" is indigenous to the Malay Archipelago (Burkill, 1935) but the present distribution stretches from southern India through the Malesian region to as far as the Philippines. The plant is dioecious, of medium height (5–15 m) and produces a characteristic opaque, yellow latex. It is slow-growing and requires approximately 15 years to bear fruits. In Peninsular Malaya, the mangosteen produces fruits twice a year; between June and August, and October and December. This seasonality can easily be upset by any change in the pattern of the wet and dry seasons. Most individual trees, however produce fruits only once a year, some during the first season and the others during the second. The fruits are usually eaten fresh or they can be made into a pleasant preserve called "halwa manggis".

As early as 1919, Sprecher described the fruits, seeds and the embryogeny of *G. mangostana*. Treub (1911), Puri (1939), Horn (1940) and much later Ha (1978) contributed some information on the flower, fruit and seed development in *Garcinia*. Nevertheless, our knowledge of the embryology on this genus remains fragmentary.

Materials and Methods

Buds, flowers and fruits of *G. mangostana* were collected at regular weekly intervals from the fruit-tree nursery, Ministry of Agriculture, Serdang, West Malaysia. A voucher specimen *KLU 1837* was deposited in the Herbarium, Botany Department of the University of Malaya. The buds and flowers were fixed in formalin-propionic-alcohol (5 c.c. formalin, 5 c.c propionic acid and 90 c.c 50% ethanol). For fruits, the fixing solution used was Craf III (30 c.c. 1% chromic acid, 20 c.c. 10% acetic acid, 10 c.c. 37% formaldehyde and 40 c.c. distilled water) at 0°C, as 50% F.A.A.

hardened them excessively. Customary methods of dehydration and embedding were followed. Much difficulty was encountered in sectioning the fruit tissues because of the bulk and presence of sclerenchyma tissue. To overcome this, the wax blocks, with the tissues exposed, were immersed for a month in a softening solution of Molifex (B.D.H., U.K. Co.) or Bakers solution (36 c.c distilled water, 54 c.c. 95% ethanol, 10 c.c. glycerol). Microtome sections were cut at 12μ and stained in 1% alcoholic (in 50% alcohol) safranin and 0.5% alcoholic (in 95% alcohol) fast green FCF.

Observations and Results

FLORAL AND FRUIT MORPHOLOGY

The flowers about 4 cm wide, borne singly or in pairs, are terminal in position. The four curved sepals are persistent on the fruit and the four fleshy petals are tinged red (fig. 1A-C). The superior ovary is round, capped by the sessile 5–8-lobed stigma. The base of the ovary is surrounded by 14–16 staminodes. Anthesis is in the evening between 4 and 6 pm and after 24 hours the petals drop off whereas the sepals persist on the ripe fruit.

The fruits are approximately 8 cm in diameter and when ripe, have a purplish rind 0.5 cm thick. Within the rind, there are 5–8 fleshy or pulpy segments which, in some, contain a light, brown seed that adheres to the flesh. The texture of the pulp is soft, delicately flavoured and slightly acidic in taste.

The mature seeds are non-endospermous, flattened and of various sizes. They are usually 1.0–1.5 cm long and 0.3–0.5 cm thick.

MICROSPORANGIUM, MICROSPOROGENESIS AND MICROGAMETOPHYTE

The anther is tetrasporangiate with four distinct wall layers within the epidermis *viz.*, the endothecium, two middle layers and the tapetum (fig. 2A-D). The secretory tapetum is initially uninucleate but later becomes binucleate (fig. 2C). It degenerates soon after the formation of microspore tetrads.

In young anthers, the microspore mother cells are well formed and prominent (fig. 2B, 2C). However, as they enter into the meiotic division, their nuclei disintegrate first and then their cytoplasm, causing most of them to degenerate (fig. 2K). A few do undergo reduction division and simultaneous cytokinesis (fig. 2F-J) but the chromosomes stain very faintly and show signs of disintegration. At various stages of meiosis, the microspore mother cells continue to degenerate in large numbers. A few microspore tetrads and single microspores appear normal but the latter were non-viable as shown by their failure to stain in 1% 2, 3, 5-triphenyl tetrazolium chloride.

Simultaneous with the degeneration of the tapetal cells, the epidermis accumulates tanniniferous materials while fibrous thickenings are formed in the endothecium and the middle layers (fig. 2E) and all these persist in the mature flower.

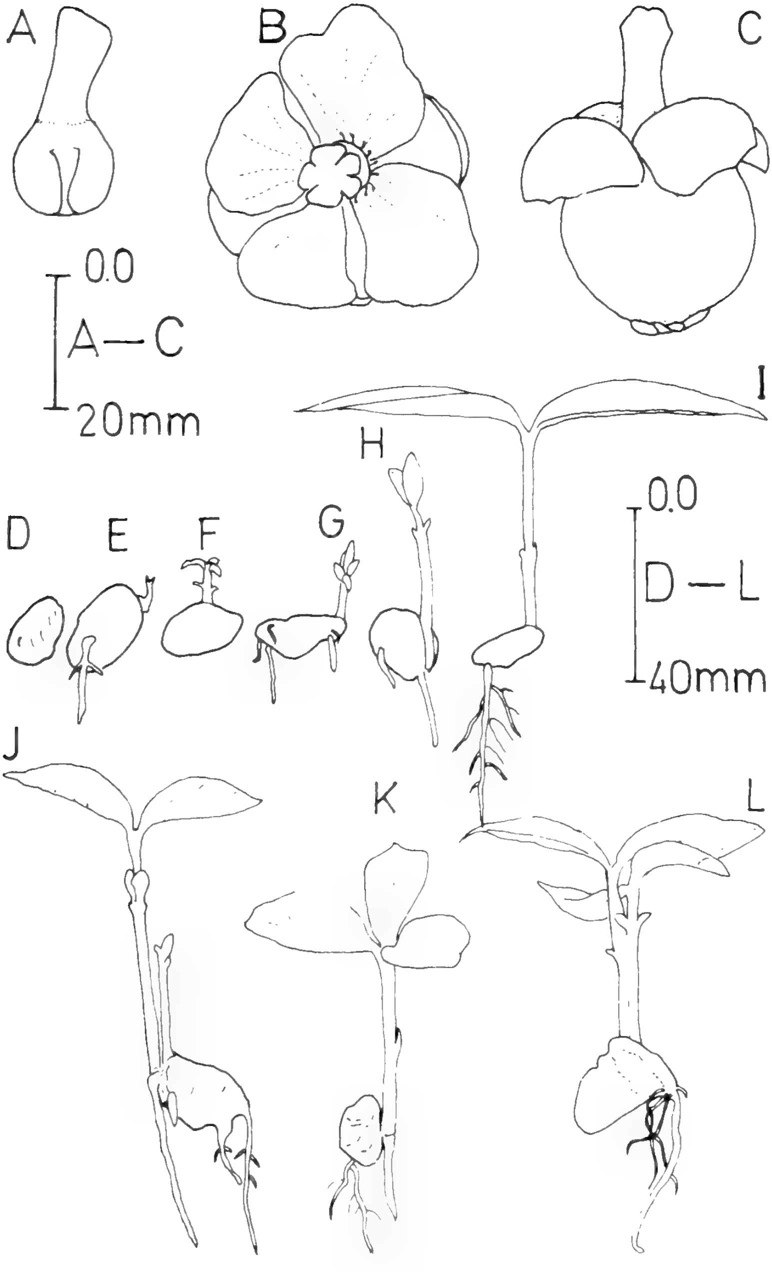

Fig. 1. Flower, fruit and seedling morphology. *A*, flower bud; *B*, flower; *C*, fruit; *D-I*, seed germination; *J*, polyembryonic seedling; *K*, "three-leafed" seedling; *L*, twin seedlings partially fused along the stem.

MEGASPORANGIUM, MEGASPOROGENESIS AND MEGAGAMETOPHYTE

The ovular primordium develops from the placenta. The differentiation of the inner integument is followed by that of the outer (fig. 3A-C). Simultaneously, one of the hypodermal, nucellar cells enlarges to form the archesporial cell (fig. 3A, 3B). The ovule is anatropous, bitegmic, tenuinucellate and the micropyle is formed by the outer integument only (fig. 3K). A short, thick funiculus is present. Only one ovule is present within each loculus.

The archesporial cell enlarges to function directly as the megaspore mother cell (fig. 3A, 3B). At this stage, the outer integument gradually outgrows the inner, enclosing the nucellus to form the micropyle (fig. 3C). Usually only one archesporial cell is produced but sometimes two or three are formed. Following the first meiotic division in the megaspore mother cell, a pair of unequal dyad cells is developed and the pair divides further to form a linear tetrad. At the completion of meiosis, only the chalazal megaspore enlarges further to form the female gametopyte while the other three megaspores degenerate (fig. 3F). The nucleus of the functional megaspore undergoes three successive divisions to form an 8-nucleate embryo sac which is of the *Polygonum* type (fig. 3H-J). The antipodals usually degenerate soon after formation but rarely do they persist even up to the stage when the egg apparatus degenerates (fig. 4A). Approximately 50% of the ovules examined showed degeneration of its embryonic content (fig. 3K). This was observed during various stages of the embryo-sac formation. Often, the multiple archesporial cells differentiate into the megaspore mother cells and further develop into multiple embryo sacs. The development of multiple embryo sacs is not synchronous and frequently, all but one degenerate (fig. 3D-G).

POLLINATION AND FERTILISATION

In the female flower, viable pollen grains are never found and those formed are empty and non-viable. Viable pollen grains are probably produced in the male flower but there is no report of a male *G. mangostana* tree in the Malay Peninsula. Parthenocarpy and apomixis in the species had been suggested by Corner (1952).

In order to confirm this inference, bagging experiments were done. A set of 100 flower buds (diameter 1.5 cm) at similar stages of development was selected and tagged. While 50 were bagged with the anthers removed, the rest were bagged with the anthers intact. Fruit set in the samples bagged with anthers removed versus anthers intact were 20% and 53% respectively. This suggests that cross pollination and fertilisation are not necessary for fruit formation. The removal of anthers from the buds before anthesis also excludes the possibility of self pollination. The percentage of fruit set in flowers with intact stamens is much higher than that with the anthers removed, possibly because of the unavoidable injury while emasculating.

ENDOSPERM

Before the degeneration of the synergids, the two polar nuclei fuse to form a secondary nucleus. The division of this is not followed by wall formation and hence

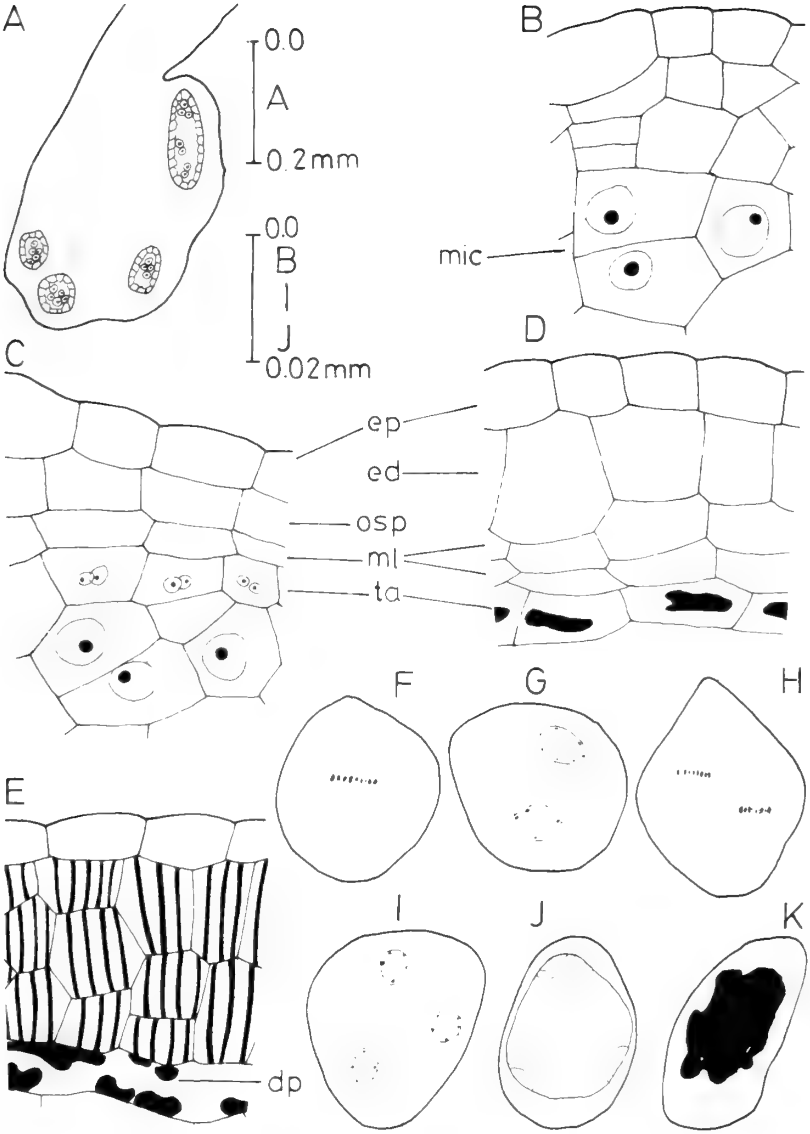

Fig. 2. Microsporangium and microsporogenesis. (*dp*, degenerated microspore mother cell; *ed*, endothecium; *ep*, epidermis; *mic*, microspore mother cell; *ml*, middle layer; *osp*, outer secondary parietal layer; *ta*, tapetum). *A*, tetrasporangiate anther; *B-E*, stages of anther wall development; *F-J*, meiosis in microspore mother cell; *K*, degenerated microspore mother cell.

endosperm formation is of the *ab initio* Nuclear type. The embryo sac enlarges at the expense of the nucellus and the inner integument. Free nuclei increase in number and remain scattered within the enlarging embryo sac (fig. 4B-D). Proceeding from the periphery to the centre, they become cellular when the embryo is in its advanced stage of development. This endosperm is progressively consumed by the developing embryo and in a fully mature seed, only one or two layers of it remain.

EMBRYO

The degeneration of the egg apparatus follows that of the antipodals and the fusion of the polar nuclei. However, one instance of an egg (probably developing into an embryo) surrounded by endosperm nuclei was observed (fig. 4F). An exceptional case of a persistent antipodal, was also observed simulating a developing egg (fig. 4A). As the embryo sac enlarges, the nucellus disintegrates, leaving only one or two layers of cells in the chalazal region. The degeneration of the nucellar tissue is followed by that of the inner integument, leaving only one or two layers of cells at the chalazal region of the embryo sac. When the embryo sac is about 0.4 cm long, the cells of the inner integument will have completely degenerated and the innermost layer of the outer integument becomes meristematic and divides rapidly. Undulations appear along the inner wall of the embryo sac. Cells of the outer integument divide periclinally and anticlinally, producing buds which project into the embryo sac. The divisions in these buds are irregular and buds of different shapes result *vis.*, button-like, linear etc. (fig. 4G-L). In the early stages of development, numerous integumentary buds are formed, but as development proceeds only a few of these attain maturity. Both the linear and button-shaped 'proembryos' eventually form broad-based, irregularly shaped embryos (fig. 4P). The developing embryos apparently obtain nutrients mainly from the integument and the nuclear endosperm.

The two cotyledons of mature embryos differ in size and shape. The epidermal cells of the cotyledons are small and their nuclei prominent while all the other layers have large and vacuolated cells with their nuclei peripheral. Polyembryony occurs when more than one bud matures within an embryo sac. In 50% of the ovules examined, the content of the embryo sac degenerates but the development of seed coat and ovary wall proceeds normally (fig. 3K). This produces seedless fleshy segments.

SEED COAT

In a mature ovule, the inner and outer integuments are respectively two layers and five to six layers thick (fig. 4M). At the time when the outer integument becomes meristematic, the outer epidermis of the outer integument accumulates tannin (fig. 4N). As development proceeds, more tannin is deposited in the cells of the outer integument. At the mature embryo stage, the enlarged embryo-sac cavity is lined by one or two layers of parenchyma cells while the rest of the cells of the outer integument are interspersed with tanniniferous cells (fig. 4O).

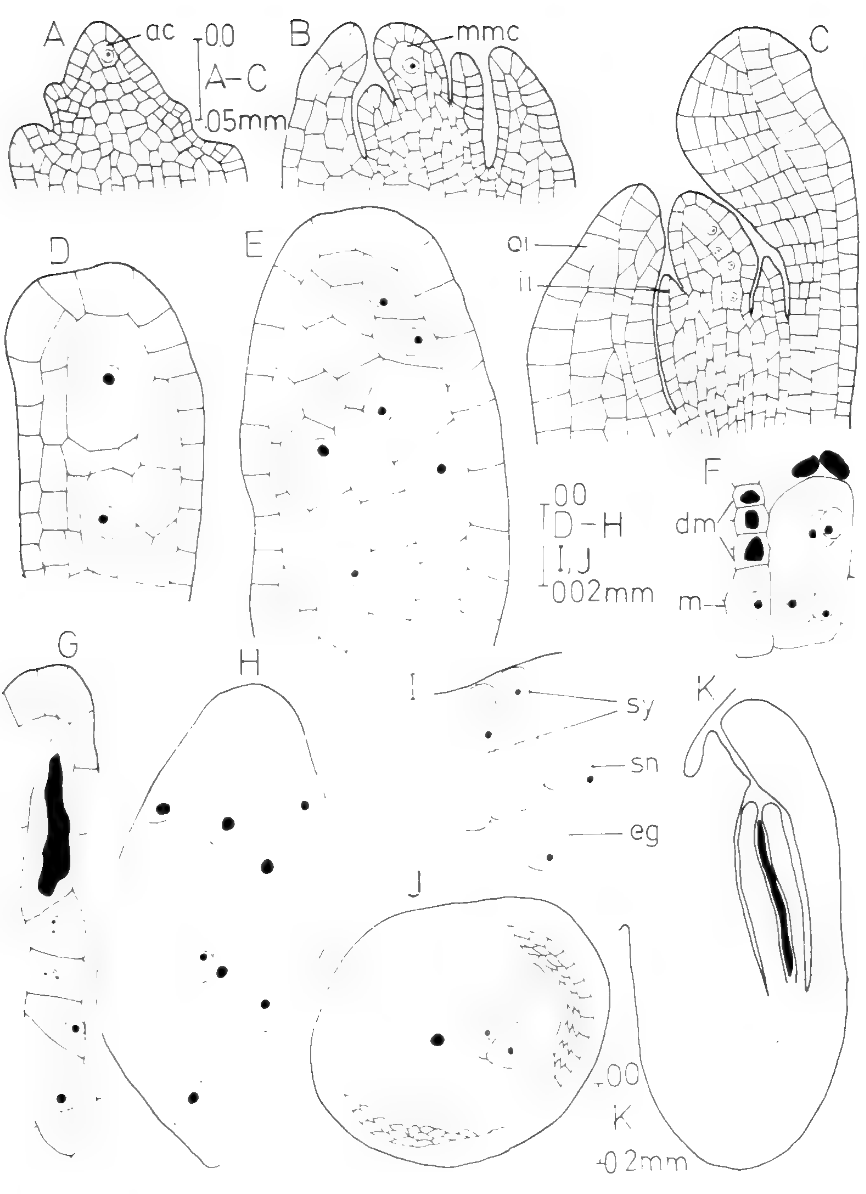

Fig. 3. Megasporangium, megasporogenesis and megagametophyte (*ac*, archesporium; *dm*, degenerating megaspore; *eg*, egg; *ii*, inner integument, *m*, megaspore; *mmc* megaspore mother cell; *oi*, outer integument; *sn*, secondary endosperm nucleus; *sy*, synergid). *A-C*, development of integuments; *D-G*, development of twin embryo sacs within an ovule; *H*, a developing embryo sac; *I*, egg apparatus with secondary endosperm nucleus; *J*, *t.s.* embryo sac showing the egg, one synergid and secondary endosperm nucleus; *K*, degeneration of embryonic content within an ovule.

FRUITS AND SEEDS

When the fruit fully mature, the diameter varies from 5 to 7 cm. The number of segments (5–8) within it corresponds to the number of stigmatic lobes of the flower. The fleshy segment may enclose a seed or it may be seedless. A random count of fifty fruits showed that the ratio of seeded to seedless segments was 1:2.

The seeds are of various sizes ranging from 0.5 to 2.0 cm in width. They are brown, flattened, have no endosperm and traversing its surface is a network of vascular bundles.

SEED GERMINATION

Seed germination is hypogeal and the incubation period is one week. The viability of fresh seed is very high, showing an average of 91% germination. During germination, the testa splits, one small root emerges from one end of the seed a few days before the appearance of the plumule at the opposite end (fig. 1D-G). The erect shoot system grows to about 4.0 cm before unfolding its first pair of leaves (fig. 1H-I). Normally, only one seedling germinates from each seed but in approximately 10% of the seeds germinated, polyembryony occurs and commonly, two or three, as many as even four seedlings per seed have been observed. All these seedlings arise from different positions of the seed and possess their own separate root systems (fig. 1J). Occasionally, the two to three shoots may arise from the same point of the seed and then they share one root system. This occurs as a result of the development of lateral buds in the shoot as can be seen from the longitudinal section of the multiple shoots which shows that the vascular bundles of the shoots are branches of the main vascular bundle of the hypocotyl (fig. 4Q).

Fasciation is another common phenomenon among the seedlings. Often two seedlings are partially fused along the stem or the two shoot systems are completely fused except at the apices (fig. 1L). Sometimes, a seedling may have three leaves at a node owing to incomplete leaf separation (fig. 1K).

Discussion

In *G. mangostana*, so far, in Malaya only trees with female flowers are known in cultivation. According to Corner (1952), "the male trees have never been found in Malaya though they are said to occur rarely in Indochina". In addition, fertile anthers are not found in the female flowers. Chevalier (Bull. Agric. Instit. Sci. Saigon, I, 1919 pg. 101) in Burkill (1935) stated that the female plant produced flowers which had male organs and that one could suppress all the male plants in a garden without affecting fruit set.

Within the family Clusiaceae, the development of pollen grains has not been investigated (Davis, 1966). This present study shows that the anther of *G. mangostana* is tetrasporangiate and degeneration in female flowers has been observed at various stages of microsporogenesis. In addition, the few microspores produced were tested and found non-viable. This observation strengthens the earlier report of Corner

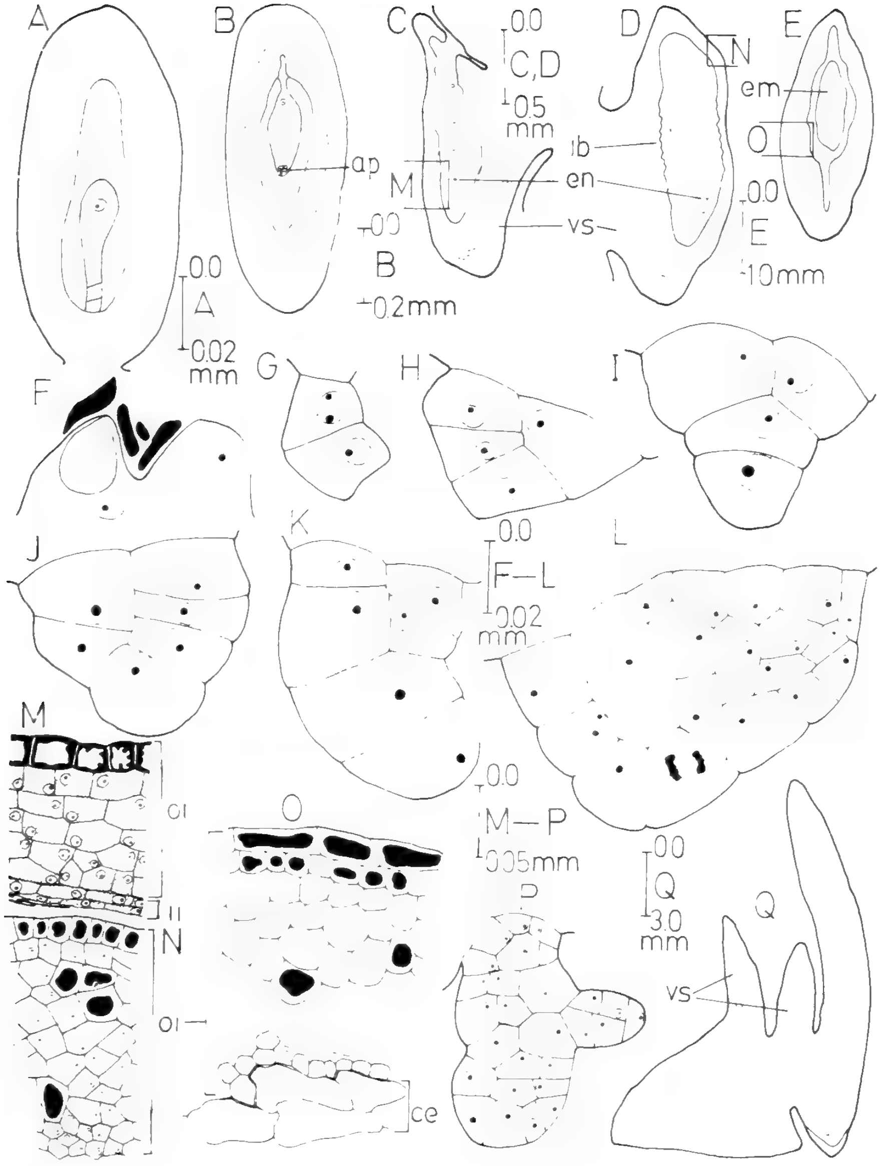

Fig. 4. Embryogeny and development of the seed coat. (*ap*, antipodal; *ce*, cellular endosperm; *em*, embryo; *en*, endosperm nucleus; *ib*, integumentary buds; *ii*, inner integument; *oi*, outer integument; *vs*, vascular system). *A*, persistent antipodal developing into embryo; *B-E*, l.s. ovule showing seed coat development; *F*, egg with endosperm nuclei, *G-L*, development of integumentary embryo; *M-O*, portions of seed coat enlarged from *C-E*; *P*, an irregularly shaped embryo; *Q*, germinated seed with multiple shoots.

(1952) and suggests apomixis as the mode of reproduction. Within the genus *Garcinia* pollen-grain degeneration has also been reported in the staminodes of the female flowers of *G. livingstonii* (Puri, 1939) whereas in *G. forbesii*, the microspore mother cells do undergo simultaneous cytokinesis to produce binucleate, mature pollen grains (Ha, 1978).

Preliminary bagging experiments confirm that the seeds are formed without fertilization. However, the fruits formed from bagged flowers with the anthers removed are slightly smaller (diameter 4.0 cm) than those with the stamens intact (diameter 4.8 cm). This is probably due to physical damage during the process of removing the anthers. Similarly, Maguire (1976) found that some *Clusia* species occurring in the semi-deciduous forests in Guayana also produced fruits from unfertilized flowers . But he did not establish the type of asexual reproduction.

The present study reaffirms the early observation of adventive embryony in *G. mangostana* by Sprecher (1919). Horn (1940) further explained that since all the seedlings were derived from essentially the same type of cells i.e., the integument, they were of exactly the same genotype. That explains that hence throughout Malaya, the fruits of *G. mangostana* taste alike and there is only one variety present. A race with a thicker rind and more acid flesh is said to occur in the Sulu Islands (Burkill, 1935).

Endosperm formation in the Clusiaceae is Nuclear in type and embryogeny conforms to the Onagrad type (Davis, 1966). In *G. mangostana*, the actual type of embryogeny could not be determined because of the irregular sequence of cell division in the integumentary buds. The various species of *Garcinia* in particular and the members within the Clusiaceae in general should be investigated extensively in order to establish the embryological pattern of development in the family.

Acknowledgements

I express my sincere thanks to the Vice-Chancellor, University of Malaya for research facilities and grant which made this study possible. I am very grateful to Dr. N. Prakash, University of New England, Australia for advice and comments.

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Multiple Branching at Nodes of *Symingtonia populnea* (Hamamelidaceae)

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Abstract

Vertically oriented sunlit shoots on *Symingtonia populnea* trees in the mountains of Malaysia produce multiple branches at nodes. The multiple axillary branches originate as branches of the vascular trace to the primary lateral bud. Plasticity in the number of branches produced per leaf axil allows *S. populnea* considerable architectural flexibility in response to environmental heterogeneity.

Introduction

Symingtonia populnea (R. Br. ex Griff.) Steen. (Syn. *Bucklandia populnea* R. Br. ex Griff. and *Exbucklandia populnea* R. W. Brown) is an early successional tree species of upper montane ericaceous forests (100–300 m) in tropical SE. Asia. On the mountains Gunong Ulu Kali and Gunong Brinchang in Peninsular Malaysia, it is prominent along roadsides but within the forest it is restricted to large treefall gaps and landslides. We were attracted to *S. populnea* by a branching pattern that is rare among dicotyledons and possibly unique among dicotyledonous trees.

Symingtonia populnea trees continuously produce leaves (Ng, 1979) and sylleptic branches, that is, branches that develop simultaneously with subtending leaves and main shoots (Tomlinson and Gill, 1973). All axes are orthotropic with distichous leaf arrangement and lateral inflorescences. Although there is no initial morphological differentiation among branch axes, some grow more slowly than others and these become displaced further from a vertical orientation than leader shoots. Using the system proposed by Hallé and Oldeman (1970) for classifying plant architectural types, this combination of characters conforms with Attim's model. However, *S. populnea* trees diverge from this familiar growth pattern when a second and sometimes a third branch emerges from a leaf axil, especially on vigorously growing leader shoots (plate 1).

The occurrence of multiple branching at nodes appears to depend on the particular shoot's vigour and position in the crown as well as on the position of the tree relative to its neighbours. Shaded trees and shaded branches on well illuminated trees rarely produce more than one branch per node. *Symingtonia populnea* trees planted in full sun in the lowlands, well below their natural altitudinal range, manage to survive but are unhealthy; the frequency of multiple branching at nodes on these trees is extremely low.

To establish the frequency with which nodes on well illuminated leader shoots and nodes on shaded subordinate branches give rise to more than one lateral branch, we counted branches at nodes on five small (3–6 m tall) trees growing in full sun on Gunong Ulu Kali. To allow branches time to develop and to avoid the potential

Plate 1. Pencil drawing of a *S. populnea* shoot showing development of multiple axillary branches along the main axis. (About 1/5 life-size).

problem of branch loss, neither the youngest nodes nor nodes on branches more than 3 cm diameter were included in the census. Branch departure from vertical orientation was used as a measure of vigour; overtopped branches became more horizontal with age.

On vertically oriented shoots (less than 10° from vertical), 177 of the 335 nodes examined had two branches, while on branches diverging from vertical by more than 10° only 51 of the 872 nodes examined had two branches. This difference is highly significant ($G = 441$, $P < 0.01$).

Buds on *S. populnea* trees are enveloped by pairs of large, tightly appressed, obovate, to oblong stipules (plate 2). When the stipules unfold, the enclosed main axis and at least one lateral branch are 1-3 cm long. The unique arrangement of twice-folded petioles (Lubbock, 1899) allows for this extended development within the stipules. In most cases in which a second branch develops, it does so slowly during which time one or two new leaves and branches are produced by the main axis. Sometimes the delay before emergence of the second branch is more prolonged but we have never observed newly expanded branches from axes more than 3 cm in diameter. The first branch produced at each node was smaller in diameter, had shorter internodes, and usually had smaller leaves than the main axis. Second branches at nodes are smaller than first branches. Where there was no branch loss, these size differences were further accentuated by differential growth.

Plate 2. *S. populnea* shoot apex with one stipule removed. (Approximately life-size).

Developmental studies of *S. populnea* shoot apices revealed that multiple axillary buds originate as branches of the vascular trace to the primary lateral bud. This branching results in a proliferation of successively higher order axillary lateral meristems (a secondary bud complex; Hallé *et al.*, 1978) forming what might be called an embryonic short shoot. In *S. populnea*, each successive axillary branch bud is oriented at approximately 90° to the previous bud, forming a spiral arrangement (fig. 1). Both left-handed and right-handed spirals were observed. Up to four orders of branching were observed within a single apex, and although such ''precocious'' branching was not limited to apices taken from vertically oriented shoots, it was more vigorously expressed there. Prophyllary buds are known to occur in a variety of species, for example, in many bamboos (McClure, 1976), *Leptocarpus simplex* (Tomlinson, 1973), *Liquidambar styraciflua* (Kormanik and Brown, 1967), and *Gossypium* spp. (Mauney and Ball, 1959; Cook, 1911). *S. populnea* shoot apices failed to reveal any prophylls, stipules, or other organs subtending the higher order branch buds. Vascular connections, however, show that each successive branch bud (both in terms of initiation and maturation) is an offshoot of the preceding bud (fig. 2).

Plasticity in branching pattern allows *S. populnea* trees to display many leaves where conditions are favourable by responding architecturally to within-crown and within-habitat environmental heterogeneity. A similar response was observed in *Acer saccharum* in which leader shoots produce a significantly greater number of

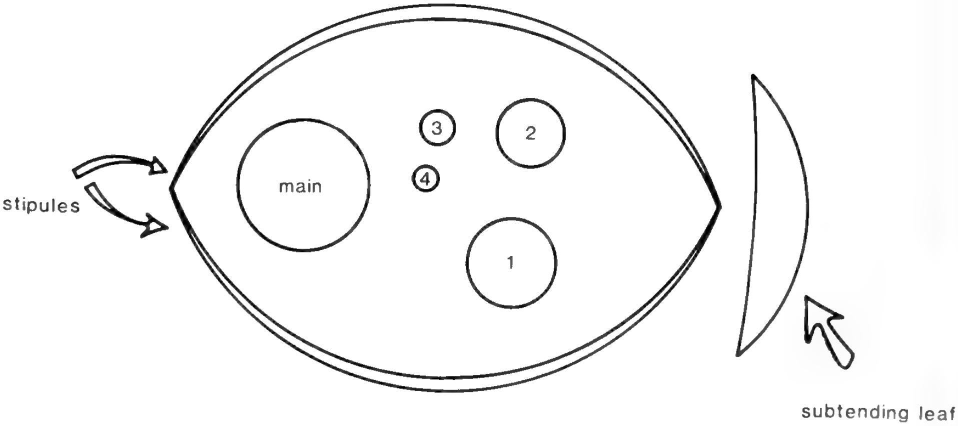

Fig. 1. Diagrammatic representation of a *S. populnea* leader shoot apex showing the terminal (main) and four axillary buds.

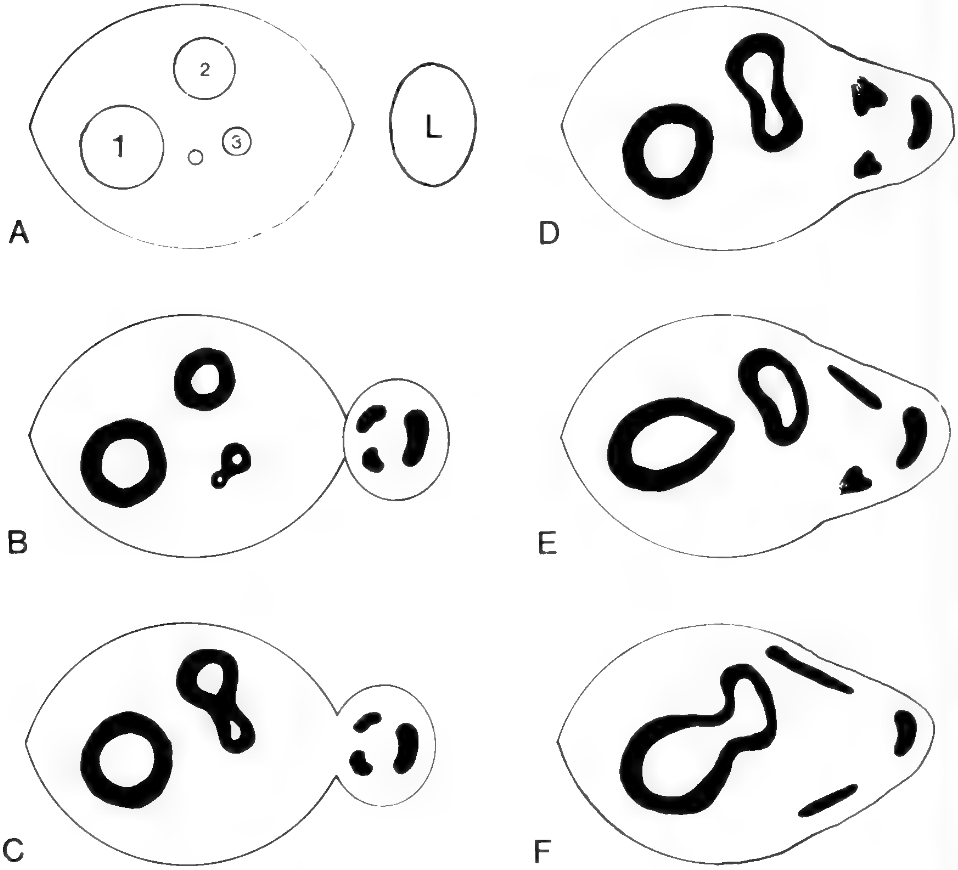

Fig. 2. Drawings of successive transverse sections of a *S. populnea* shoot apex (basipetal sequence, *A* = uppermost; solid area represents vascular tissue).

first order branches per second order branch than lower limbs (Steingraeber, 1982). However, *S. populnea* is distinctive in altering both the frequency and the pattern of branching.

Acknowledgements

We wish to thank F. S. P Ng, P. F. Stevens, B. C. Stone, P. B. Tomlinson, and J. R. Vincent for their assistance and advice.

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Trichomanes proliferum Bl.
A new record for the fern flora of Singapore

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Summary

Trichomanes proliferum Bl. is reported for Singapore for the first time. Some morphological characters are discussed.

Introduction

With the kind assistance of Dr. Chang of the Botanic Gardens I was able to collect some ferns in the Nee Soon swamp forest in July 1982. New records could hardly be expected as the fern flora of Singapore is rather well known. However, one of the plants collected was identified as *Trichomanes proliferum* Bl., which was not recorded for Singapore by either Holttum (1966) or by Johnson (1977), nor is there a specimen from Singapore in the herbarium of the Botanic Gardens (SING) (Dr. Chang, pers. comm.). It seems therefore that the following collection, deposited in the Herbarium of the State University of Ghent (GENT), is the first from the Island.

R. Viane & Noë 2369; Singapore, Nee Soon swamp-forest: on tree trunk along rivulet, just above the water level; rare; together with *Trichomanes motleyi* v.d. Bosch; 29 July 1982. Photo (plate 1) in SING.

T. proliferum is a filmy fern (Hymenophyllaceae) of the *Gonocormus* group that is characterized by its proliferous frond axes. Copeland (1938: 56) stated about *Gonocormus:* ". . . a well defined genus of exceedingly ill-defined species . . ." and distinguished six "species" of which *T. proliferum* was said to be the most characteristic. Holttum (1966: 95–97) believed *Gonocormus* to be related to the *Vandenboschia* group; he accepted two "not clearly distinct" species: *T. minutum* Bl. and *T. proliferum*, both recorded from Malaya but not from Singapore.

Distribution

T. proliferum was first described from Java by Blume (1828); according to Copeland (1933: 150) "it is probably common throughout the Malay region" (incl. Philippines). Holttum (1966) gave "Malaysia" (= area of Flora Malesiana) as the overall range and stated that the plant is "found in both lowlands and mountains". The single population seen by the present author was growing among mosses on a very sheltered wet tree trunk in the Nee Soon swamp-forest. More populations of this small and easily overlooked fern probably exist in the area. Nee Soon is one of the few remaining lowland swamp-forests that once covered large areas of Singapore and Johore (Corner, 1978).

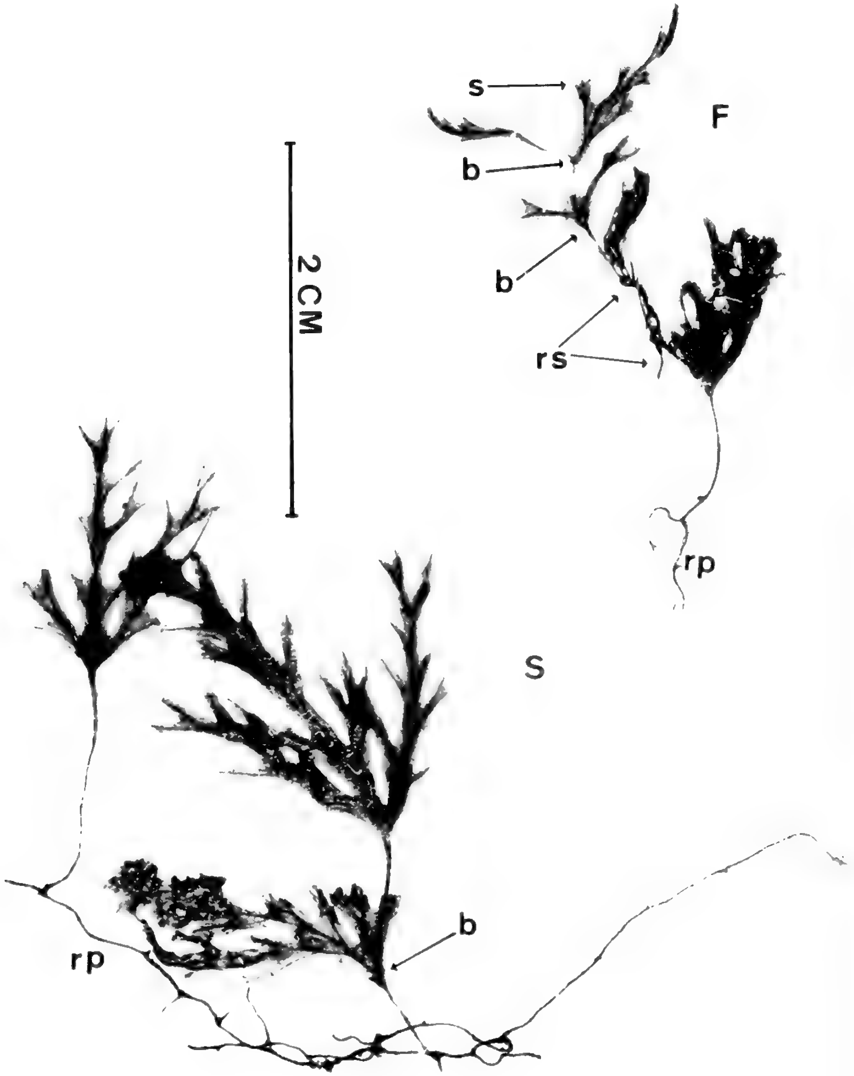

Plate 1. *Trichomanes proliferum* Bl. (*R. Viane & Noë 2369*). *F*, fertile plant; *S*, sterile plant. *b*, proliferous bud with its frond; *rp*, primary rhizome; *rs*, secondary rhizome from a bud; *s*, sorus.

Morphological Notes

A brief description and figure are given by Holttum (1966). Bierhorst (1973, 1974) studied the branching pattern in *Gonocormus* in relation to: (a) the concept of non-appendicular fronds, and (b) the rhizome morphology of other Hymenophyllaceous "genera". Yoroi and Iwatsuki (1977) discussed the variability of the frond form and the proliferation of the *Trichomanes minutum*-group along with cytological and anatomical data.

The plants from Nee Soon (plate 1) have fronds up to 4 cm long (including the stipe), well spaced on a delicate, wiry "rhizome". This "rhizome" has no roots but is covered by many multicellular uniseriate brown hairs. Few fronds were fertile (plate 1F). The stipes of (almost) all mature fronds have one to three dormant buds, visible as slight swellings of the stipe tissue covered with a tuft of brown hairs. Above these dormant stipe buds there often is a proliferating (= functional) bud (plate 1: *b*, arrows) c. 1 mm above the cuneately narrowed lamina base; it forms the "secondary" frond. This "secondary" frond is similar to the "primary" frond; it has dormant stipe buds too and the functional bud at its lamina base may produce another frond, and so on. An additional dormant bud is sometimes present on the vascular tissue of the lamina (c. 4 mm above its base). The functional buds occasionally produce "secondary rhizomes" in the abaxial axil of the secondary or higher order leaves (plate 1F, *rs*, arrow). The secondary "rhizomes" are morphologically similar to the primary and develop from the bud only after it has produced a frond. Another fern with buds forming small but conspicuous (elongate) rhizomes is the West African "*Ctenitis*" *jenseniae* (C. Chr.) Tard.

Nomenclature

If *T. proliferum* and *T. minutum* cannot be recognized as two separate species, as suggested by Copeland (1958) as well as by Yoroi and Iwatsuki (1977), then the name *T. minutum* Bl. *sensu lato* (Copeland, 1958) should be applied to the Singapore plants.

Acknowledgements

I thank Dr. Chang for her help in organizing the visit to Nee Soon and for checking the herbarium material in SING. Prof. K. U. Kramer kindly corrected the manuscript.

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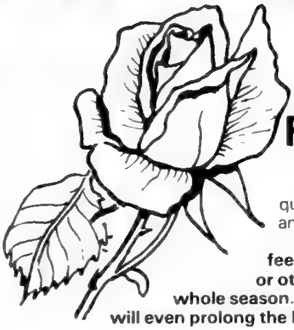

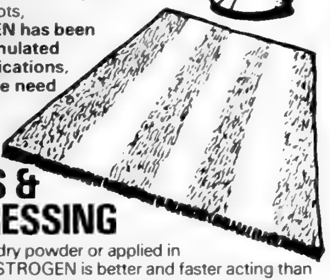

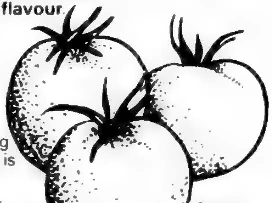

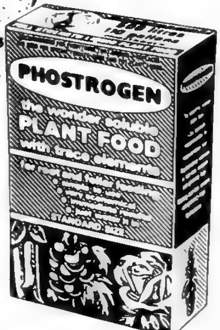
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ISSN 0374-7859

THE GARDENS' BULLETIN
SINGAPORE

VOL. 37 (Part 2) 1st December 1984

CONTENTS

Published by the Botanic Gardens
Parks and Recreation Department
Ministry of National Development
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A New Account of the Genus *Horsfieldia* (Myristicaceae), *Pt 1*

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Rijksherbarium, Leiden, The Netherlands

EFFECTIVE-PUBLICATION DATE: 7 MAR 1985

Contents

Abstract

The genus *Horsfieldia,* extending from Ceylon to the Solomon Isls. is redefined to exclude the species formerly assigned to *H. macrocoma.* The remaining 100 species are subdivided into 3 sections, *viz.* (1) the monotypic section *Horsfieldia* with *H. iryaghedhi* from Ceylon, (2) section *Irya* (40 species) and (3) section *Pyrrhosa* (59 species). Section *Irya* contains chiefly species with a 2-valved perianth and is mainly distributed in East Malesia; the species of section *Pyrrhosa* have mainly a 3- or 4- valved perianth and occur in SE. continental Asia and W. Malesia, west of Wallace's Line. A further subdivision of the sections into groups of species of closer affinity is proposed and discussed in the introduction. Warburg (1897) recognized 52 species, Sinclair (1974, 1975) accepted 38 and a number of varieties. The most important characters for the distinction of species are in the male flowers, especially the androecium. Of the presently accepted 100 species, 41 are newly described, and in addition, 14 are new subspecies and varieties. There are 6 new combinations. Most species have rather restricted but well-defined areas of distribution; *H. irya* has a very large range, covering almost that of the genus. The centres of species development are New Guinea and Borneo, and to a lesser extent Malaya-Sumatra.

A survey and discussion of all characters regarded as important in *Horsfieldia* is given. Two kinds of keys are presented: a general key to all species, mainly based on male flowering specimens, and 6 regional keys covering the whole area of the genus, concentrating on vegetative characters, for the identification of female-flowering and fruiting specimens. All 100 species are fully treated and full synonymy, typification, description, notes, and a brief enumeration of distribution and examined specimens are provided. An index of all scientific names pertaining to *Horsfieldia* will be given in Part 3.

Introduction

With the demise of James Sinclair in 1968*, only the general treatment of *Horsfieldia* — the Flora Malesiana precursor of the fourth genus of Malesian Myristicaceae — remained unpublished, but an alphabetical account of the species, which were already all worked out by him, was posthumously printed in *Gard. Bull. Sing.* 27, 1 (1974) 133-141 and 28, 1 (1975) 1-181. Unfortunately a classification system and most keys are lacking in these publications and before the treatment of the family for *Flora Malesiana* could be started, these had to be provided for. Moreover, much recently collected material needed first to be identified and described.

In Sinclair's earlier revision of the family Myristicaceae for Malaya and Singapore (*Gard. Bull. Sing.* 16, 1958) the genus *Horsfieldia* was thoroughly dealt with and keys were supplied. However, in order to grasp the whole genus, which extends over a large area from Ceylon and S. China east to the Solomon Islands and North Australia, I had to scrutinize all the species myself, and this experience led to different ideas about the circumscription of the species as a matter of course.

Because Sinclair had examined an enormous amount of specimens from all major herbaria, I needed only to restrict my study to the Leiden collection complemented by additional, personal visits to BM, K, and P, from where also rather extensive selected material including type-specimens has been put at my disposal as loans to Leiden.

Following a somewhat extended list of criteria, important for species delimitation — among which are the highly diagnostic value provided by the presence of small non-traumatic cork warts on the lower leaf surface, and a more detailed evaluation of the androecium — I was forced to recognize considerably more species than did Sinclair. Apart from new ones, most of the species accepted by Sinclair have been retained in the present study, while others have been redefined, or renamed, or taken out of synonymy, and some taxa accepted by Sinclair subspecifically have been raised in rank. An example of the few abrogated taxa is *H.* polyantha Warb., also accepted by Sinclair but presently reduced to *H. laevigata,* a name which was reduced by Sinclair to *H. parviflora.*

In Sinclair's enumeration of all species in his 1974/1975 publications, species descriptions of the wide-spread *H. irya* as well as that of the variable and deviating *H. macrocoma* are lacking. The latter possibly has some indicative value as, during the present study, it has appeared that some species to be recognized within the *H. macrocoma*-complex could be better segregated into a new genus, *Endocomia.*

Where my circumcriptions of species differ from Sinclair's, brief reasons are given in the notes.

The Characters in *Horsfieldia*

When Sinclair (1958) dealt with *Horsfieldia* for Malaya, he provided a rather limited discussion of useful species characters, and in his posthumous publication on the genus as a whole (1974, 1975), an explanation of the underlying considerations

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* Obituary in *Gard. Bull. Sing.* 23 (1968), pp. i-xxiv.

for the delimitation of the species is only given in the notes to the alphabetically arranged descriptions of the species. In those treatments of the Malayan species, two keys to all species were presented, one for fertile (male flowering) specimens, and one for sterile material and fruit. From these keys it can be learned that he regarded the following characters as important for the distinction of the species: (1) perianth either 2- or 3-valved and (2) shape of the androecium (longer than broad or the reverse, with or without a depression at the top); apparently of lesser importance to him were (3) lenticels on twigs, distinct or not, (4) size of the male perianth and length of the pedicel, (5) some properties of the leaves such as size and texture of the blade, whether glabrous or pubescent beneath, and above, nerves either raised or sunk; and, a further number of specific characters used for the distinction of some individual species.

Although Warburg (1897), Sinclair and I use essentially the same characters for the generic division, I agree with Sinclair (1958, p. 370) in discarding Warburg's subdivision into three sections; Sinclair had advocated a more natural division into two sections i.e., on the basis of how most of the perianths in a specimen split at anthesis, in 2 or 3 valves. I also have the feeling that this criterion is one of the most important characters for a generic division, one that has phylogenetic significance. However, in the case of *H. iryaghedhi* from Ceylon, I have set that apart because it deviates from all the other Horsfieldias in various ways.

Characters, which in my opinion, are important for distinguishing groups of species are given further on. They are also used in the list of species with a provisional indication of grouping closer allied species, as presented and discussed in the next chapter on the subdivision of the genus. Special attention is given to the vegetative characters because the genus is dioecious and hence in much of the material the most important taxonomical characters of the male flowers are lacking.

Measurements given in the descriptions of the species and used in the keys based on vegetative characters and fruits are all taken from dried material; those of flowers have all been measured after softening by boiling.

Vegetative characters

(1) *Habit*

The size of the tree sometimes seems specific, but most species are of medium size. *H. sylvestris* with a recorded stature of up to 60 m high ranges among the tallest whereas *H. crux-melitensis* is a shrub or shrubby treelet of 2-4 m. The growth of the main stem is essentially orthotropic with the phyllotaxis dispersed, while the plagiotropic side-branches are generally ± horizontal or drooping, with the phyllotaxis distichous. Characters of bark, buttresses, stilt roots etc., are mainly observations of Sinclair, as he was acquainted with the species in the field.

(2) *Indumentum*

As in *Knema,* the indumentum of the leaf bud, leaves and twigs, and of the inflorescences and flowers has proved to be important for the delimitation of the species (de Wilde, 1979, p. 324). Except for the flowers of some species, all the above-mentioned parts of the plant are initially covered by a tomentum, but this may be shed at a very early stage. Although there may be minor differences, generally within the same specimen, the nature and size of the tomentum-hairs on the various parts are largely similar, and to a large degree characteristic of the taxa. For practical reasons, the tomentum is described only in a general way, the lengths of the hairs (which themselves may be very complex) appearing to be of considerable importance for the recognition of the species. Much on the tomentum can be found in the study on the comparative leaf anatomy of the Asiatic Myristicaceae by Koster and Baas (1981).

(3) *Twigs*

The indumentum of the twigs is generally shed very early but sometimes may remain on the young innovations; it is generally similar to that of the leaf bud and can be simultaneously judged if required for the determination with the keys. The internodes in the leaf-bearing portion may be terete or faintly lined. Sometimes these lines, which run from both sides of the insertion of one petiole to the next, are very pronounced and may render the twig angular or faintly winged, which is characteristic for several species e.g., *H. brachiata.* The bark of older twigs i.e., behind the leaves and often where the infructescences are inserted, may be striate to various degrees; only in rare cases does older bark flake more or less characteristically or crack longitudinally, as in *H. sabulosa, H. xanthina* or *H. disticha.* The bark of young twigs usually dries brown or dark brown, contrasting little with the dark colour of the dried petioles, but in some species (e.g., H. spicata, *H. oligocarpa, H. pallidicaula*), the twigs dry to a conspicuously pale, greyish or straw-colour, contrasting well with the petioles, and the discrepancy is then used in the keys. Slightly older bark nearly always bears lenticels, rather characteristically small or large, often paler and contrasting well with the twig but at other times merging in colour and then inconspicuous. In passing, it should be noted that the presence of lenticels in Malesian taxa of the family seems to be largely or wholly restricted to the genus *Horsfieldia.*

In the descriptions, the diameter of twigs was measured not far below the apex in the leaf-bearing portion while the size cited in parentheses was taken lower down where old inflorescences or infructescences may be attached. Excepting *H. sabulosa,* Horsfieldias never flower on the older wood.

According to Armstrong and Wilson (1980) the wood of *Horsfieldia* is very homogeneous and of little taxonomic value at a specific level. At the generic level, it can be distinguished from the other three Asiatic genera of Myristicaceae. The wood of one specimen of *H. macrocoma* (placed in a new genus *Endocomia* de Wilde, 1984) is apparently not significantly distinct from wood of other Horsfieldias.

(4) *Phyllotaxis*

In the majority of the species, leaves of the plagiotropic twigs i.e., generally the fertile ones, are distichous. In some species, phyllotaxis is characteristically dispersed, mostly with leaves in 3-5 rows (e.g., *H. kingii, H. thorelii, H. sucosa, H. sabulosa*); only in a few species are the leaves either distichous or dispersed and sometimes phyllotaxis is mixed as in one collection. The phyllotaxis is usually very obvious and easy to see in older twig-portions, hence it is used in the keys. Those species which have a variable phyllotaxis have been entered in the keys twice.

(5) *Leaves*

As a matter of course, many features of the leaves, as shape, size, texture, drying colour, number of lateral nerves and length of the petiole are of importance for the recognition of the species, but only some characters of special interest will be briefly discussed here (a-e).

(a) *Pale markings on the upper surface*

Often present in many species are very small markings, regularly spaced and usually slightly raised. Their origin is unknown to me. In a few species, much larger, pale-coloured, often nearly white blotches of irregular shape and unpredictable location may prevail, sometimes only in a part of the leaves or only locally present on some of the leaves. They are likely to be an artifact of drying, of unknown origin and may be found in e.g., *H. smithii,* yet they are very characteristic of almost all *H. irya* collections.

(b) *Blackish or brown markings on the lower leaf-surface*

A fine, pale, or more often a dark punctation in the form of small blackish dots, possibly tannic conglomerations, is often present in many species, also in the fleshy tissue of perianths, androphores, or pericarps. Furthermore, there is in certain species a very specific coarser punctation, regularly spaced dots of c. 0.1 mm diam., being a sort of non-traumatic cork warts of unknown origin, most likely originating from hair-bases or hair scars. The presence or absence of these dots should always be checked when determining a specimen, their presence being very distinctive for several species e.g, *H. punctatifolia, H. glabra.*

(c) *Nerves*

In most species, whether midrib and nerves above are flattish, sunken, or distinctly raised, is of diagnostic significance. For the identification of a few "difficult" species as e.g., the distinction between *H. whitmorei* and *H. laevigata,* it is important to check on the submarginal nerve i.e., whether its arches are particularly marked and regularly shaped as is the case with the former species against the less distinctive and less regular in the latter.

(d) *The terminal leaf bud*

The terminal leaf bud is usually present in every collection. It shows up as a long subterete or ± flattened cone, usually at least five times longer than broad; in some species however, mainly in those with the leaves dispersed, it is shorter and broader. The tomentum of the leaf bud, especially the length of the hairs, has proved to be a good diagnostic character, as also indicated under item 2.

(e) *Petiole*

The petiole is usually well-developed. *H. sessilifolia* and much material of *H. sylvestris* have almost sessile leaves; the petioles of *H. sabulosa* are the longest in the genus, up to 5 cm long.

Generative characters

(6) *Inflorescences*

The inflorescences are generally situated on the younger twigs, in-between the older leaves or not far behind. Only in *H. sabulosa* does flowering occur on older wood. They are almost always panicle-like (spike-like in most of *H. spicata*), (2 or) 3 or 4 times ramified, the mode of branching being essentially racemose. Flowers are borne on the ultimate branches, either solitary or grouped in loose clusters of up to 10 each in the male inflorescence; those of *H. sylvestris,* especially in young inflorescences, may be clustered in rather dense heads, but in the rather deviating species *H. iryaghedhi,* the male flowers are grouped in true dense heads each with up to nearly one hundred flowers.

In general, all flowers of an inflorescence of both sexes are of about the same age or stage of development, only in *H. amygdalina* is there a tendency of some to develop ahead of the others. This latter situation is prevalent in the segregated genus *Endocomia* which contains the species *E. macrocoma* formerly placed in *Horsfieldia.*

Branching is subtended by bracts except the one bearing the ultimate flowers, the bracts falling off early in all cases. Bracteoles are absent in *Horsfieldia,* the segregated genus *Endocomia,* and *Gymnacranthera* but present in *Knema* and *Myristica.*

At the base of the inflorescence there are always a few cataphylls, short and triangular in outline and clothed with a tomentum similar to that on the inflorescences, leaf buds and twig-apices.

The largest inflorescences, to c. 30 cm long, are found in *H. ampla* and *H. ampliformis* from New Guinea. In almost all species the male inflorescences are larger and more elaborate as compared with the female ones; only in *H. parviflora* are male and female inflorescences often equal in these respects.

Following flowering, at fruiting stage, whole inflorescences are discarded as in *Endocomia, Gymnacranthera* and in some *Myristica,* hence unlike the situation in *Knema* and the rest of *Myristica* where flowering occurs on woody brachyoblasts, or short shoots which are essentially of unlimited growth.

(7) *Flowers*

The flowers are unisexual, dioecious. The perianth of the male is usually smaller than that of female flowers (considerably so in e.g., *H. thorelii*), or they are equal, or even considerably larger in size. Their size is fairly constant for each species. For instance, in *H. parviflora* which was described from a female specimen, the perianth of the female flower is considerably smaller than the male perianth which is one of the largest found in *Horsfieldia,* up to 4 mm wide.

According to the species, the perianth may be cleft into predominantly 2 or 3 (or 4) valves, and it is on this character that the division of the genus into sections is based. It is of interest to mention here that this manner of sectional division coincides well with the various distributional areas as is pointed out in the next chapter, on distribution.

The extent of the split of the perianth at anthesis varies with the species and cleaving outright or almost to the base (in male flowers) is limited to only a few species. At anthesis, the perianth opens only a little, the lobes neither horizontally spread nor curved nor reflexed as is often the case in *Knema, Myristica, Gymnacranthera* and always in *Endocomia.*

The flower colour ranges from yellowish green to a bright yellow or orange-yellow.

The consistency of the perianths may be diagnostic for the species, especially of male specimens, and sometimes it is useful to note whether the perianth collapses on drying or not. Flowers may be glabrous, or very early glabrescent; or they are pubescent, sometimes only so toward the perianth base or the pedicel. The inner surface of the perianth is always glabrous, in contrast with species of *Endocomia,* formerly included in *Horsfieldia* as *H. macrocoma* s.l.; it is only in *H. subtilis* var. *rostrata* (formerly *H. rostrata*) that the inner side of the female perianth was originally described as pilose, but I have not seen that specimen.

(8) *Staminate flowers*

Staminate flowers provide for the taxonomically most important characters, at various levels.

(a) The shape of the *male perianth* shows much variation. In the 2-valved species, the perianth is generally laterally compressed, in outline either circular, or pear-shaped, or reniform, but in *H. irya* which is the type of the 2-valved section *Irya,* it is subglobose and not or but little compressed. The perianth of the 3- or 4-valved species, prevalent in sect. *Pyrrhosa,* is usually globose or pear-shaped and not laterally compressed but sometimes apically depressed, and of various sizes. *H. crassifolia* has a 2-valved but globose perianth, and also because of its non-compressed androecium, joins taxonomically the 3-valved species in sect. *Pyrrhosa.*

Peculiarly long-conical 2-valved male flowers prevail in *H. crux-melitensis, H. clavata,* and *H. squamulosa;* they have club-shaped androecia, aberrant for the genus, as discussed below.

(b) The *depth to which the perianth is cleft* at anthesis is a diagnostic character for several species. Sometimes the perianth opens only at the very top e.g., in *H. triandra, H. crux-melitensis, H. sterilis* and *H. pulverulenta;* in others it is split to the base or nearly so e.g., in *H. basifissa, H. angularis, H. obscura* and several others, but in most species it is split to about halfway.

(c) The *pedicels* are usually cylindrical or subterete, sometimes subtriangular (in species of the group of *H. polyspherula*), slender or thickish, and it may be of taxonomical importance whether they are longer or shorter than the perianth. In some species with pear-shaped or club-shaped flowers e.g., *H. tuberculata* (partly so), or *H. crux-melitensis, H. lancifolia, H. decalvata* and some others, the base of the perianth gradually narrows into a tapering pedicel.

In many species the pedicel is typically articulated at the base, at least in dried specimens; however, in a few species including *H. glabra* this character does not seem to be very constant. One should be aware that the bracteal scars of the uppermost inflorescence may be mistaken for the articulation in the pedicel and therefore several pedicels should be checked. Bracteoles are lacking in *Horsfieldia,* as already noted.

(d) The *androecium* of the male flowers shows much diversity in shape and construction and provides the most important characters in the delimitation of species. Again, at the generic level, the androecium also provides major characters.

In *Horsfieldia,* as in the other Asiatic Myristicaceae, the stamens are always connate through presumably the fusion of filaments into an androphore, which usually bears a so-called central column. The androphore is generally rather short and may be absent. The degree of coalescence of the anther-bearing part or synandrium varies according to the species; in many, the anthers are completely connate or almost so, at their back, forming a broad central column usually of a rather spongy texture and showing much specific variation in shape. In many other species the coalescence of the anthers is only partial and the anthers may then have free apices of various lengths, depending on the species. Opening of the thecae is extrorse to *latrorsus* (directed sideways).

A well-developed central column, if present, may be solid, but in the majority of the species it is hollowed out in the apical portion in very diverse ways and to various depths, according to the species. The anthers may be erect or suberect, or curved and following the straight or rounded shape of the central column. The free portions of the anthers, if prevalent, may stand erect or curve inwards into the central-apical cavity of the central column to various depths according to the species. The androecium may be elliptic in transverse section, as in most species with a laterally compressed 2-valved perianth (sect. *Irya*); or circular or subcircular as in most species with 3 or 4-valved perianths (sections *Iryaghedhi* and *Pyrrhosa*). In the group of *H. polyspherula* (sect. *Pyrrhosa*) the anthers are typically erect or suberect, mutually free for the upper half while the androecium is typically triangular in transverse section.

Each anther consists essentially of a pair of bisporangiate lobes or thecae, comparable to those of the presumably more primitive condition found in *Compsoneura* and *Dialyanthera* (S. America), or *Brochoneura* (Africa) where the anthers are monadelphous with their filaments fused only towards the base. Armstrong and Wilson (1978, fig. 16) postulate that there is within *Horsfieldia* an evolutionary trend in the androecia from a condition of a relatively poorly developed central column, or a small degree of fusion of the connective columns and hence with more protrusion of the anthers, towards one with a greater fusion in the connective column (i.e., a broad and well-developed central column) and a reduction in the protrusion and pairing of the anthers. The least specialized conditions i.e., with relatively free anthers, would be those as found in species like *H. irya, H. parviflora,* or *H. ardisiifolia,* all with a predominantly 2-valved perianth i.e., in sect. *Irya.*

Schematic longitudinal and transverse sections of the typical androecium forms of almost all species are represented in figure 1A-D. I have refrained from hypothesising as regards which forms may be more primitive or more advanced, though in general, I agree with Armstrong and Wilson.

The number of anthers is generally a good species character, although in some cases, it may vary considerably. When the anthers are tightly set, they may be difficult to count, especially because they are much elongated and consist of two equal thecae.

The size of the androecium in relation to the perianth is sometimes significant; usually it almost completely fills the perianth, but in e.g., *H. ampliformis,* the perianth is largely hollow because the androecium occupies only a fraction of the space.

It is peculiar that in juvenile stages the thecae of the anthers may be typically septate, the septa being of non-tapetal origin; this phenomenon has been studied by Armstrong and Wilson (1978). I am not sure whether it occurs in all species of *Horsfieldia.* Such a septation is unknown in *Myristica* and *Knema.*

(9) *Pistillate flowers*

The female perianth is usually subglobose, ellipsoid or ovoid, and the shape varies somewhat with the species. In most species the female flowers are larger than the male for example, distinctly so in *H. thorelii,* but many exceptions exist. Within the same species the number of perianth-valves is always similar in male and female flowers, but the extent of the split in female flowers is usually considerably less.

The globose, ellipsoid or ovoid ovary may be glabrous or hairy, according to the species. There is some variation in the size and shape of the stigma, which is essentially 2-lipped and the style is usually absent or very short. In general, the small differences in the stigma are difficult to describe and this has not been exhaustively studied by me. *H. squamulosa,* for instance, has a relatively long, erect, slender style and stigma, which show up as a minute appendage on the young fruit; in *H. sepikensis* the stigma is sessile and conspicuously broad-lipped; in *H. iryaghedhi* the sessile stigma tends to be few-lobulate and not 2-lobed.

(10) *Fruits*

The fruit agrees in general appearance with other myristicaceous fruit, but is in *Horsfieldia* (and in the genus *Knema*) characterized by the aril being either complete or split into short laciniae in the apical portion only. The pericarp is glabrous or pubescent; in the latter case the hairs may remain only at the very base of the fruit, near the insertion of its stalk. Fruit size is largely diagnostic for the species. The fruit of *H. grandis,* c. 1 cm long, is among the smallest, that of *H. punctatifolia,* up to 8 cm long, is among the largest in the genus. In variable species like *H. polyspherula* and *H. pallidicaula,* I have accepted several varieties mainly on the basis of fruit size. The shape of the fruits is usually short-ellipsoid, and of the seed, ellipsoid; only in a few species is the fruit globose or nearly so e.g., in *H. subtilis* var. *subtilis* and *H. sinclairii,* but their seeds are short-ellipsoid; in *H. irya* fruit and seed are globose.

The pericarp varies in thickness according to the species; it is hard-succulent in the fresh state, shrinking considerably on drying. For example, the pericarp of large fruits of *H. punctatifolia* would usually shrink from a 4-cm thickness when fresh to 1 cm. The surface of the dry pericarp is in many species provided with conspicuous pale warts or dots, apparently becoming more pronounced with drying, showing up as lenticel-like tubercles. A striking example is the fruit of *H. laevigata.*

Finally, it may be remarked here that in several species the female perianth remains persistent under the fruit. This phenomenon occurs in species which are, if considered on other grounds, not regarded as closely related. However, it provides an easily observed character for species like *H. kingii, H. wallichii, H. splendida, H. pallidicaula* and others.

Description and Redefinition of the Genus *Horsfieldia*

Horsfieldia Willd.

Horsfieldia Willd., Sp. Pl. 4 (1806) 872 [*non* Bl. = *Harmsiopanax* Warb. (Aral.)]; Pers., Symb. 2 (1807) 635; Warb., Mon. Myrist. (1897) 130, 262; Sinclair, Gard. Bull. Sing. 16 (1958) 368; 27 (1974) 133-141; 28 (1975) 1-181. — *Pyrrhosa* Endl., Gen. Pl. (1839) 830 (see note). — Type: *Horsfieldia odorata* Willd. = *H. iryaghedhi* (Gaertn.) Warb.

Myristica sect. *Pyrrhosa Bl.*, Rumphia 1 (1837) 190-192, Tab. 62-64. — With subsequent authors the genus *Horsfieldia* as presently defined was treated partly under *Myristica* sect. *Pyrrhosa* as well as under several other sections of *Myristica viz.*, sects. *Caloneura* p.p., *Eumyristica* p.p., *Horsfieldia*, Irya); see Sinclair (1958), p. 368 and under the presently accepted sections. — Lectotype of *Myristica* sect. *Pyrrhosa: Myristica glabra* Bl. = *Horsfieldia glabra* (Bl.) Warb.

Shrubs or usually trees, 2-40 (-60) m, dioecious. Twigs usually early glabrescent, terete or sometimes angular or with two raised lines or ridges from petiole to petiole, bark usually striate, always lenticellate but sometimes inconspicuously so. Leaves distichous or in some species dispersed, usually petioled, blades up to 45 cm long, membranous to coriaceous, often brittle when dry, pubescent or glabrescent, nerves prominent or not above, reticulations above usually lax, never forming a dense, close network as in *Knema,* lower surface not glaucous, papillose (alveolar tissue) only in *H. iryaghedhi;* in some species non-traumatic cork warts present. Inflorescences axillary, situated in between and behind the leaves, rarely on the older wood (*H. sabulosa*), paniculate, usually branched several times, pubescent or glabrescent, at base of common peduncle with a few minute cataphylls; female inflorescences usually smaller than the male. Flowers usually pedicelled, glabrous or pubescent, solitary or in loose, sometimes sub-umbellate clusters or fascicles, generally all of about the same age in the same inflorescence, in *H. iryaghedhi* the male with flowers sessile in dense flower-heads; bracts broad-triangular to elliptic or boat-shaped, caducous. Perianth thin-leathery to succulent, either 2 (or 3) or (2 or) 3- or 4-lobed, inside glabrous, greenish to yellowish, never red, the lobes splitting the perianth to various depths, never spreading; bracteoles absent. Male perianth usually small, either globose, depressed-globose, transversely ellipsoid, ellipsoid, reniform, pear-shaped, or clavate, laterally compressed or not. Androecium very diverse in shape, either cupshaped, or globose to ellipsoid, cylindrical, or trigonous, laterally compressed or not, sessile or with short androphore; the anthers usually entirely or largely mutually connate and adnate at their back into a narrow or broad central column various in shape, the latter usually with a depression or excavation to various depths at apex. Anthers 2-c. 25, either straight and ± erect, or curved or the apical parts incurved or inflexed into the cavity of the column to various depths; thecae often septate in the juvenile stage, opening extrorsely. Female perianth usually larger than the male, subglobose to ovoid-ellipsoid; ovary globose or ovoid, glabrous or pubescent, style absent, stigma 2-lobed or 2-lipped, usually small, more-lobed only in *H. iryaghedhi*. Infructescences of moderate size, smaller than male inflorescences. Fruits globose or usually ellipsoid, pericarp usually somewhat fleshy, drying brown or blackish, often with lenticel-like tubercles, glabrous or pubescent, or subglabrescent, perianth sometimes persistent under the fruit; seed ellipsoid, rarely globose, testa not variegated; aril completely covering the seed, entire or at apex shallowly lobed or convoluted; albumen ruminate, with fatty oil but no starch; cotyledons connate at base.

NOTES

Fieldnotes. Trees of primary rain forest, often persisting in secondary growth; also in marshy forest, and stilt roots present in some species.

According to Sinclair (1958) the bark of Malayan species is usually reddish-brown, smooth or more often striate or rough with circular or irregular dents, sometimes flaking but mostly not. The flowers are mostly waxy yellow, and often sweet scented; those of *H. iryaghedhi* have a particularly strong smell.

Anatomy. Koster and Baas (1981) published a paper on the comparative leaf anatomy of the Asiatic Myristicaceae and found the genera anatomically quite distinct, especially in the hairs and the vascular pattern of the midrib and petiole; most species examined can be distinguished by their epidermal features.

Taxonomy. After having examined all species of *Horsfieldia,* including *H. macrocoma,* I came to the conclusion that within *H. macrocoma* s.l. four species could be distinguished. These rather deviate from all other Horsfieldias and I have segregated them into a new genus *Endocomia* (1984), which differs from *Horsfieldia* by the following characters: flowers monoecious; flowers at the ultimate ramifications of the inflorescences developing in rather different stages; perianth inside hairy or with appendages, at anthesis cleft to the base into (3 or) 4 (or 5) valves and these spreading or recurved and not erect; androecium long-stalked, of different construction; aril generally laciniated to about halfway the seed or more; testa of the seed variegated.

Synonymy. Pyrrhosa Endl. is illegitimate because *Horsfieldia* Willd., as genus, is cited in its synonymy; according to art. 7, 11 of the Code, *Pyrrhosa* Endl. should be typified by *Horsfieldia odorata* Willd., being the type of the name which should have been adopted. *Pyrrhosa* Bl. as section is presently lectotypified by *Myristica glabra,* a practice initiated by Hook. f. and Thomson (1855) with the division of *Myristica* sect. *Pyrrhosa* Bl. into three sections of smaller circumscription *viz.,* sect. *Eumyristica,* sect. *Irya,* and sect. *Pyrrhosa;* these three coincide largely with the three presently accepted sections in *Horsfieldia.*

Table I

Table I enumerates all species in *Horsfieldia* and indicates by horizontal lines demarcations between accepted sections and informal groups of species; broken lines indicate marked discrepancies within a group as is discussed in the text.

The distribution of three marked characters which are used at species level, but not primarily used to distinguish sections or groups, is indicated with symbols before the species names. A deviating perianth valve-number within a section is indicated between the brackets; ☐ = pedicel articulated at base, + = perianth persistent under the fruit, • = lower leaf surface with coarse dark-coloured dots from cork warts.

+			1. *H. iryaghedhi*
			2. *H. kingii* (valves 4)
			3. *H. longiflora* (valves 2)
			4. *H. thorelii* (valves 2 or 3)
			5. *H. amygdalina* (valves 2 or 3)
			6. *H. irya*
			7. *H. spicata*
		•	8. *H. inflexa*
			9. *H. moluccana*
			10. *H. parviflora*
			11. *H. obscurinervia*
			12. *H. ardisiifolia*
			13. *H. talaudensis*
			14. *H. samarensis*
			15. *H. smithii*
			16. *H. palauensis*
			17. *H. olens* (valves 3)
			18. *H. sepikensis* (valves 3)
			19. *H. sylvestris*
			20. *H. australiana*
			21. *H. crux-melitensis*
			22. *H. clavata*
			23. *H. squamulosa*
			24. *H. ampla*
			25. *H. ampliformis*
			26. *H. angularis* (valves 2-4)
			27. *H. iriana*
			28. *H. aruana*
			29. *H. subtilis*
			30. *H. schlechteri*
			31. *H. basifissa*

			32. *H. sinclairii*
			33. *H. psilantha*
			34. *H. whitmorei*
			35. *H. laevigata*
			36. *H. pilifera*
			37. *H. lancifolia*
			38. *H. decalvata*
			39. *H. tuberculata*
			40. *H. corrugata*
			41. *H. pachycarpa*
			42. *H. pulverulenta*
			43. *H. leptantha*
			44. *H. hellwigii*
			45. *H. ralunensis*
	□	•	46. *H. sabulosa*
		•	47. *H. atjehensis*
(+)	□		48. *H. sucosa*
(+)			49. *H. pallidicaula*
			50. *H. sparsa*
			51. *H. triandra*
			52. *H. tristis*
+	(□)		53. *H. fulva*
+			54. *H. superba*
			55. *H. sessilifolia*
			56. *H. grandis*
+		•	57. *H. wallichii*
		•	58. *H. pulcherrima*
+			59. *H. flocculosa*
			60. *H. motleyi*
			61. *H. tomentosa*
+			62. *H. gracilis*
			63. *H. paucinervis*
+			64. *H. splendida*
	(□)		65. *H. rufo-lanata*
+	□		66. *H. affinis*
	□		67. *H. reticulata*
+		•	68. *H. crassifolia* (valves 2)
			69. *H. carnosa*
+			70. *H. sterilis* (valves 2)
	□		71. *H. hirtiflora*
	□		72. *H. brachiata*
	□		73. *H. pachyrachis*
	□		74. *H. ridleyana*
	□		75. *H. obtusa*
	(□)		76. *H. disticha*
	(□)		77. *H. tenuifolia*
	□		78. *H. macilenta*
	□		79. *H. laticostata*
	□		80. *H. nervosa*
	□		81. *H. polyspherula*
	□		82. *H. oligocarpa*
			83. *H. endertii*
(+)			84. *H. valida*
	□	•	85. *H. borneensis*
+			86. *H. fragillima*
			87. *H. androphora*
+			88. *H. amplomontana*
	(□)		89. *H. montana*
		•	90. *H. punctata*
			91. *H. costulata*
			92. *H. subalpina*
			93. *H. obscura*
			94. *H. xanthina*
	□		95. *H. majuscula*
			96. *H. coriacea*
		•	97. *H. penangiana*
		•	98. *H. punctatifolia*
		•	99. *H. macrothyrsa*
	(□)	•	100. *H. glabra*

Subdivision of *Horsfieldia* into Three Sections

As can be seen in the preceding survey of characters to be used in the taxonomy of *Horsfieldia* as well as from the species descriptions, there is a large diversity in the genus. This led Warburg (1897) to subdivide the genus into 3 sections, with 5 subsections and 2 series, with 11 additional accepted species not placed in any section because their male flowers were unknown. Warburg's subdivision appears to me very artificial, at least for the greater part. For the Malayan species only, Sinclair (1958) advocated a more simple subdivision into "Bivalves" and "Trivalves", and some unnamed subsections, but a definite decision, pending on the study of the whole genus, was frustrated by his early death.

I have chosen to subdivide the 100 presently accepted species into three sections although I realize that these are of considerably unequal taxonomic weight. The three are: (1) sect. *Horsfieldia,* containing one single species, being the type species of the genus, but rather deviating from all others, (2) sect. *Irya,* containing most species with a predominantly 2-valved perianth, and (3) sect. *Pyrrhosa* with most species having predominantly a 3- or 4-valved perianth. Although the two last-named sections, which are by no means sharply segregated but which have their own range of distribution, coincide with Sinclair's subdivision, they should be named differently on nomenclatural grounds. Each contains a few species with the perianth predominantly of a deviating valve-number, but it will be argued in the discussion on the groups that these species are tentatively best regarded as casual deviations still to be placed in that section.

As regards a further formal subdivision, I have refrained from making any. Instead, I have listed in Table I all the species and indicated with horizontal lines (either continuous, or broken, according to the supposed strength of the demarcations) which groups or clusters can be distinguished. These groups, without formal status, contain species which are presumably closer to each other on grounds to be discussed in the next chapter. At first sight several of these groups of more or less coherent species seem to represent formal entities e.g., subsections or series, but in view of the diversity in the variation of all species concerned, this certainly would lead to a complicated system of entities differing much in taxonomic weight and with blurred circumscriptions.

It is obvious that the species in general have reticulate relationships, and the groups are only consistent on the basis of a single or a few putatively important characters. Other characters, which could be regarded as important as well will often be found distributed in various other groups, without necessarily expressing that such characters, respective to their groups, are less valuable or the groups unnatural. The erratic distribution of such characters not used to assemble species into groups, as the presence of non-traumatic cork warts on the lower leaf surface, the presence of an articulation at the base of the pedicel, or the calyx being persistent under the fruit, is indicated in the list of species in Table I, according to the symbols explained in the legend. I have refrained from arguing about any phylogenetic value of these groups as I feel that it is arbitrary and difficult to judge what characters should rank phylogenetically behind others, and often, one can only guess which character-states should be ranked as more primitive or more advanced.

The sections and groups will be discussed briefly below, with references to links with other groups or individual species. The majority of the characters binding a group can be extracted from those used subsequently in the general key to the species.

The Sections and a Survey of the Groups

1. Sect. *Horsfieldia*

Myristica sect. *Horsfieldia* A. DC., Prod. 14 (1856) 200; Miq., Fl. Ned. Ind. 1, 2 (1859) 63. — *Myristica* sect. *Irya auct. non* Hook. f. & Th.: Benth. & Hook.f., Gen. Pl. 3 (1880) 137, for *Horsfieldia* Willd. only. — *Myristica* sect. *Eumyristica* subsect. *Horsfieldia* (A. DC.) King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 282. — Type: *Horsfieldia odorata* Willd.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1835) 190, p.p., for *M. horsfieldii* only, not the lectotype. — *Myristica* sect. *Eumyristica* Hook.f. & Thomson, Fl. Ind. (1855) 162, p.p., for *M. horsfieldii* only.

Horsfieldia sect. *Orthanthera* Warb., Mon. Myrist. (1897) 268, p.p., for the lectotype only. — *Horsfieldia* sect. *Triavalves* subsect. *Orthanthera* (Warb.) Sincl., Gard. Bull. Sing. 16 (1958) 371, p.p., *nom. inval.*, provisional name only. — lectotype: *Horsfieldia iryaghedhi* (Gaertn.) Warb.

Phyllotaxis of plagiotropic shoots distichous. Lower leaf-surface with alveolar tissue, epidermis papillose, stomatal complex sunken; without larger dark coloured dots (cork warts). Flowers in male sessile, at base not articulate, arranged in many-flowered subglobose dense heads; perianths elongate-obconical, before anthesis ± angled, 3- or 4-(in ♀ :2- or 4-) valved, splitting the bud to c. 1/2-3/4. Androecium elongate, sub-cylindrical, androphore distinct; central column narrow, narrowly hollowed out for over 1/2-way; anthers 3-5, erect. Stigma sessile, many-lobulate. Ceylon. — Figure 1, I; 2I; species 1.

This section is monotypic with *H. iryaghedhi*[1], a species deviating from all other Horsfieldias by the following characters: — some anatomical characters of the leaf, the male flowers being sessile and arranged in dense heads which have a thick receptacle, the anthers being mostly connate but in most instances not back to back so that a narrowly hollowed central column is thereby formed, the angular perianths, and the many-lobed (not 2-lobed) stigma in the female flowers.

2. **Sect.** ***Irya*** (Hook.f. & Th.) Warb.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1837) 190, p.p., for *M. javanica* and a few other species only, excl. lectotype *M. glabra* (sect. *Pyrrhosa*) and *M. horsfieldii* (= *H. iryaghedhi*, sect. *Horsfieldia*); A.DC., Prod. 14 (1856) 202, p.p.; Miq., Fl. Ned. Ind. 1, 2 (1859) 64, p.p., excl. *M. glabra* (= sect. *Pyrrhosa*).

Myristica sect. *Irya* Hook.f. & Thomson, Fl. Ind. (1855) 159; A.DC., Prod. 14 (1856) 202; Miq., Fl. Ned. Ind. 1, 2 (1859) 64; Benth. & Hook.f., Gen. Pl. 3 (1880) 137, p.p., excl. sect. *Horsfieldia;* King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 284, p.p., for the smaller part only. — *Horsfieldia* sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Euirya* Warb., Mon. Myrist. (1897) 123, 267, p.p., for the type only. — Type: *Myristica irya* Gaertn. = *Horsfieldia irya* (Gaertn.) Warb.

Horsfieldia sect. *Pyrrhosa* subsect. Bivalves Warb., Mon. Myrist. (1897) 262 (incl. series *Smithii* and series *Globularia*). — Horsfieldia sect. *Bivalves* Sinclair, Gard. Bull. Sing. 16 (1958) 370, 371, *comb. inval.*, provisional name only. — Type not indicated, several species listed.

Phyllotaxis in plagiotropic shoots distichous. Lower leaf surface without alveolar tissue, epidermis not papillose, stomatal complex not sunken; rarely (*H. inflexa*) with larger dark coloured dots. Flowers pedicelled, base not articulate, solitary or in loose clusters; perianth rarely globose or obovoid, usually laterally compressed, in outline either circular or elliptic or pear-shaped, before anthesis not angular or in young stages of *H. sylvestris* faintly so, usually all or predominantly 2-valved, rarely 3-valved, cleft at anthesis to various depths even nearly to the base. Androecium various, nearly always more or less zygomorphic, either usually laterally compressed or in some species with 3- (or 4-) valved flowers, the androecium broad-ellipsoid with the anthers at apex bi-laterally incurved, rarely obconical and actinomorphic; androphore distinct or not, central column broad or narrow, little to much hollowed; anthers few to many, erect or sub-erect, or some or all incurved over or to various depths into the cavity of the central column. Stigma minutely 2-lobed. Mainly E. Malesia (incl. Philippines), only *H. irya* distributed over almost the whole area of the genus. — Figure 1, 6-45; 2 II; species 6-45.

Almost all of the 40 species of this section have exclusively or predominantly 2-valved perianths in the same inflorescence, and usually have a more or less zygomorphic androecium, either because it is laterally compressed or because the anthers curve in apically from two opposite sides only.

Aberrant are *H. olens*[17], *H. sepikensis*[18] with 3- or 4-valved perianths, but with the androecium distinctly tending to be zygomorphic, the anthers from two opposite sides incurved in a manner reminiscent of the condition as found in species like *H. parviflora, H. moluccana; H. angularis*[26] has a 2-4 valved perianth.

Also aberrant are the species of the group of *H. clavata* [22], with a 2-lobed perianth but a club-shaped non-zygomorphic androecium.

A few mutually related species from continental SE. Asia, presently placed in the next section, (3) *Pyrrhosa, viz. H. longiflora, H. thorelii* and *H. amygdalina* have all or partly predominantly a 2-valved perianth, and partly a zygomorphic androecium, especially *H. longiflora.* This latter species blurs the distinction between sect. *Irya* and sect. *Pyrrhosa,* because, if judged from its morphology of the perianth and androecium, it seems to agree with sect. *Irya.* However, it clearly belongs to the group of the other above-named species, which obviously link up with sect. *Pyrrhosa.* Moreover, since sect. *Irya* is mainly of East Malesian distribution, *H. longiflora* would be occupying an aberrant locality as it is restricted to Indo-China. Compared with other species in sect. *Irya, H. irya* extends far beyond their range of distribution; besides, its relationship with *H. longiflora* is rather remote. The phylogenetic backgrounds of this strayed species within sect. *Pyrrhosa,* known only from a few Vietnam collections, pose a problem. Within sect. *Irya,* 8 groups (1—8) can be distinguished.

SURVEY OF GROUPS WITHIN SECT. IRYA

(1) *H. irya-group*

H. irya-group consists of a single species, *H. irya*[6], which occupies a rather isolated position. It is distinct in habit, with thin leaves often provided with irregular pale blotches, and unique by having globose fruits and seeds, the globose 2-valved male perianth and a typical androecium which is only slightly laterally compressed, and with the anthers almost free, and attached to the rim of the cup-shaped androecium. It is linked with the next group by *H. palauensis*[16] which occupies a rather intermediate position between *H. irya* and *H. smithii*[15].

(2) *H. parviflora-group, species 7-16*

Group 2 is chiefly characterized by the distinctly laterally compressed, male perianth, which is either ± pear-shaped or circular or more or less transversely elliptic or reniform in lateral view. The laterally compressed androecium follows the shape of the male perianth and consists of anthers connate to various degrees and deeply curved inward into the central cavity at one or both sides of the androecium. This is partly Warburg's sect. *Pyrrhosa:* subsect. *Bivalvis:* series *Globularia* and series *Smithii.*

(3) *H. olens — H. sepikensis-group*

The two species of group 3, 17 and 18, are aberrant in the section because of their 3-valved perianths. The androecium is rather broadly obovoid and only slightly zygomorphic, but the apical parts of the anthers curve inwards ± bilaterally, in a manner reminiscent of that in the foregoing group.

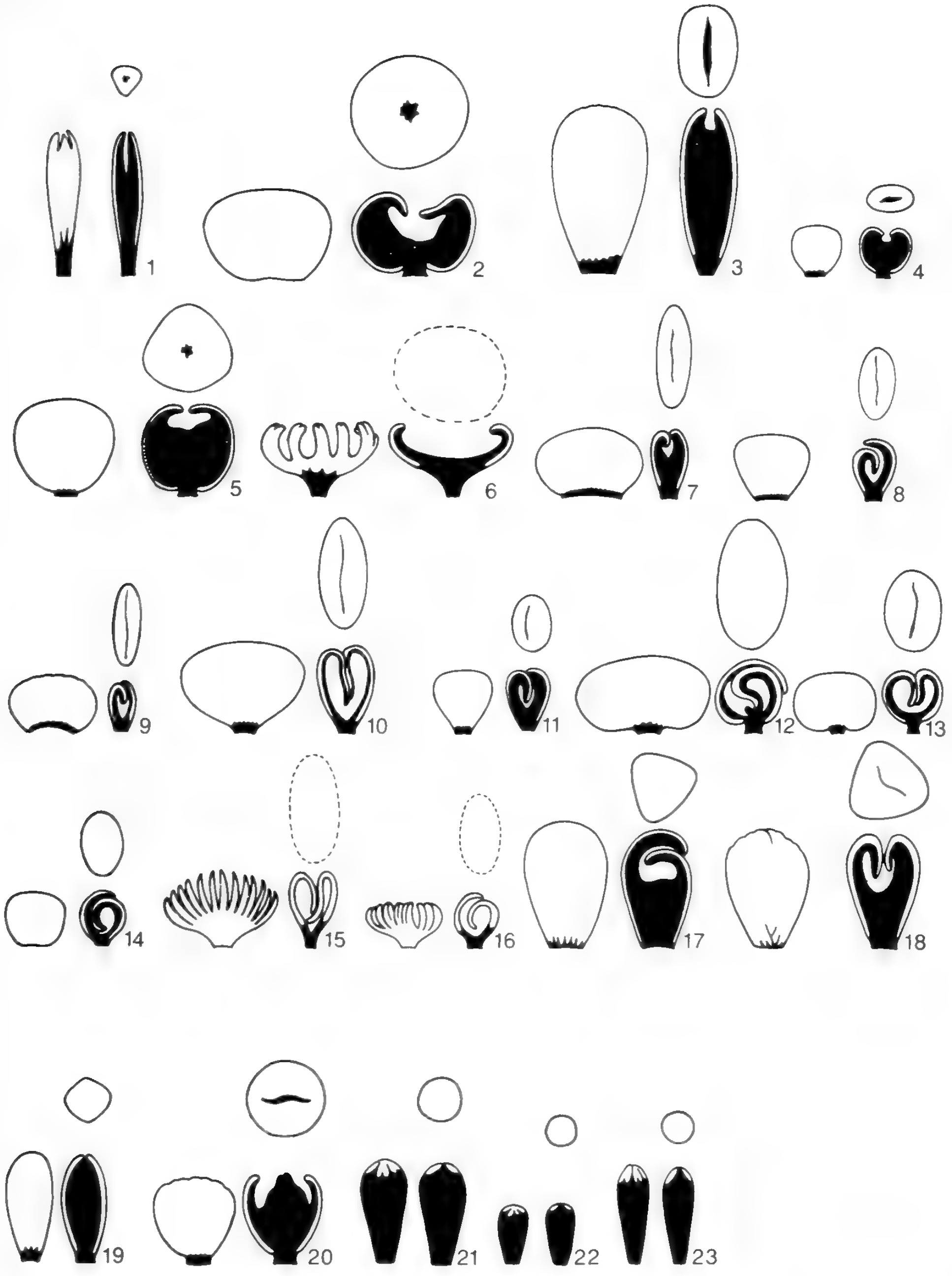
(4) *H. sylvestris-group*

H. sylvestris-group contains a sole species (16), occupying an isolated position, and is readily recognized by a number of characters. Warburg (1897) placed it with *H. iryaghedhi* and *H. ralunensis* in a separate section called *Orthanthera* because the male flowers are elongate and densely clustered in flower heads, but this latter feature only holds for *H. iryaghedhi,* because in *H. sylvestris* similar flower heads are only present in juvenile inflorescences, which later on expand into separately attached flowers. The flowers of *H. sylvestris* have an elongate perianth and androecium, not or but little compressed, and the anthers are mutually completely connate forming a narrow, completely solid, central column.

(5) *H. australiana-group*

A rather isolated species, *H. australiana*[20], is the sole member. Sinclair had assigned plants from New Guinea to this species but here I accept them as belonging to a distinct species: *H. sinclairii.* In *H. australiana* the androecium is rather broad-ovoid, overarching over a broad and ± shallow, apical hollow, into which the central column protrudes conspicuously. Based on the flower-features, *H. sinclairii* is assigned to the group of *H. laevigata*[35].

Editorial Note; superior figures following species names are numbers of the author's accepted species.



Figs. 1A-D Semi-schematic drawings of the androecium of most species of *Horsfieldia*, all depicted except species 24, 55, 62, 76; lateral view *(left)*, longitudinal section *(right)*, apical view *(top)*; *white:* anthers, *black:* sterile tissue (i.e. androphore and central column).

Fig. 1A. Species 1-23: *1, H. iryaghedhi* (x 10, *Jayasurika & Bandaranaika 1869*); *2, H. kingii* (x 10, *Haines 842*); *3, H. longiflora* (x 10, *Eberhardt 3050*); *4, thorelii* (x 10, *Poilane 19887*); *5, H. amygdalina* var. *lanata* (x 10, *Kerr 8556*); *6, H. irya* (x 10, *Muller 1020*, from Indo-China); *7, H. spicata* (x 5, *Beguin 1407*); *8, H. inflexa* (x 5, LAE *52866*); *9, H. moluccana* var. *moluccana* (x 5, *Kostermans 673a*); *10, H. parviflora* (x 5, *Ding Hou 134*); *ll, H. obscurinervia* (x 5, *For. Bur.* 26503); *12, H. ardisiifolia* (x 5, *Cuming 1702*); *13, H. talaudensis* (x 5, *Lam 2628*); *14, H.* samarensis (x 5, *PNH 117374); 15, H. smithii* (x 5, *Rutten 1776); 16, H. palauensis* (x 5, *Takahide Hosakawa 6756); 17, H. olens* (x 10, *NGF 31966); 18, H. sepikensis* (x 10, *Hoogland & Craven 10255); 19, H. sylvestris* (x 10, *Craven & Schodde 739); 20, H. australiana* (x 5, *Dunlop 3585*); *21, H. crux-melitensis* (x 5, *Schlechter 19246*); *22, H. clavata* (x 5, *Hoogland 3663*); *23, H. squamulosa* (x 5, *Pullen 8287*).

(6) *H. clavata-group, species 21-23*

The three species in the *H. clavata*-group are from New Guinea. They form a distinct group based on various characters dominated by the peculiar club-shaped, not zygomorphic androecium with small sessile anthers at the apex. A thickened sterile androecium with small, apically attached anthers is also found in *H. pulverulenta, H. sterilis* and *H. triandra* but in a somewhat different manner. The species of the *H. clavata-group* are shrubs or low trees.

(7) *H. laevigata-group, species 24-41*

The group has mainly species from New Guinea. Several sub-groups can be distinguished, but all are characterized by a laterally compressed perianth and androecium. The anthers are erect and the rather narrow central column is narrowly cleft to various depths.

The two species *H. ampla*[24] and *H. ampliformis*[25] are characterized by their large male inflorescence and the androphore in *H. ampliformis* is conspicuous.

H. angularis, H. iriana and *H. aruana,* species 26-28, are distinct by their ridged or angled twigs; *H. angularis*[26] has the male perianth variably 2- to 4-lobed.

H. subtilis[29] and *H. schlechteri*[30] are small trees; both have the androecium rather narrowly stalked with the central column somewhat thickened towards the base, and hence the androecium is often slightly sagged.

Species 31-41 are rather heterogeneous and some have special features:— *H. basifissa*[31] and *H. sinclairii*[32] both have rather small globose or subglobose fruits, but in *H. basifissa* the perianth is deeply cleft; *H psilantha*[33] comes close to *H. laevigata*[35] but its flowers are (almost) glabrous, the leaves are larger, etc., *H. lancifolia*[37] and *H. decalvata*[38] from Celebes and the Moluccas respectively, stand apart within the present group by their pear-shaped perianth with a tapering pedicel, but, the wide-spread and variable *H. tuberculata*[39] usually has somewhat pear-shaped flowers also; *H. corrugata*[40] and *H. pachycarpa*[41] are mountainous species with very large fruits as compared with the other species of the group.

(8) *H. hellwigii-group, species 42-45*

H. hellwigii-group is restricted to New Guinea and the Bismarck Archipelago, and is generally easily recognized by the rather stout habit (somewhat resembling the wide-spread *H. sylvestris*) and the coarse tomentum on the leaf bud and twig apex; *H. pulverulenta*[42] is very distinct within this group by the peculiar androecium, which is reduced to a largely sterile cone with 2 minute anthers at the top, and the hard-fleshed perianth which opens apically only by a small slit just above the anthers.

3. Sect. **Pyrrhosa** (Bl.) Warb.

Myristica sect. *Pyrrhosa* Bl., Rumphia 1 (1837) 190-192, Tab. 62-64, p.p., for the smallest part incl. the lectotype Tab. 64, fig. 1A, B; Hook.f. & Thomson, Fl. Ind. (1855) 160; A.DC., Prod. 14 (1856) 202, p.p.; Miq., Fl. Ned. Ind. 1, 2 (1859) 64, p.p.; Benth. & Hook.f., Gen. Pl. 3 (1880) 136; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 282. — *Horsfieldia* sect. *Pyrrhosa* (Bl.) Warb. subsect. *Eupyrrhosa* Warb., Mon. Myrist. (1897) 265 (excl. *H. macrocoma* = *Endocomia gen. nov.* — Lectotype: *Myristica glabra* Bl. = *H. glabra* (Bl.) Warb.

Myristica sect. *Eumyristica* Hook.f. & Thomson, Fl. Ind. (1855) 162, p.p., for *M. superba* = *Horsfieldia superba* (Hook.f. & Th.) Warb. only. — *Myristica* sect. *Caloneura* A.DC., Prod. 14 (1856) 192, p.p., for *M. superba* Hook.f. & Th. = *Horsfieldia superba* (Hook.f. & Th.) Warb. only.

Myristica sect. *Irya auct. non* Hook.f. & Th: King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 284, p.p.

Horsfieldia sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Euirya* Warb., Mon. Myrist. (1897) 267, p.p;, excl. *H. irya* (type).

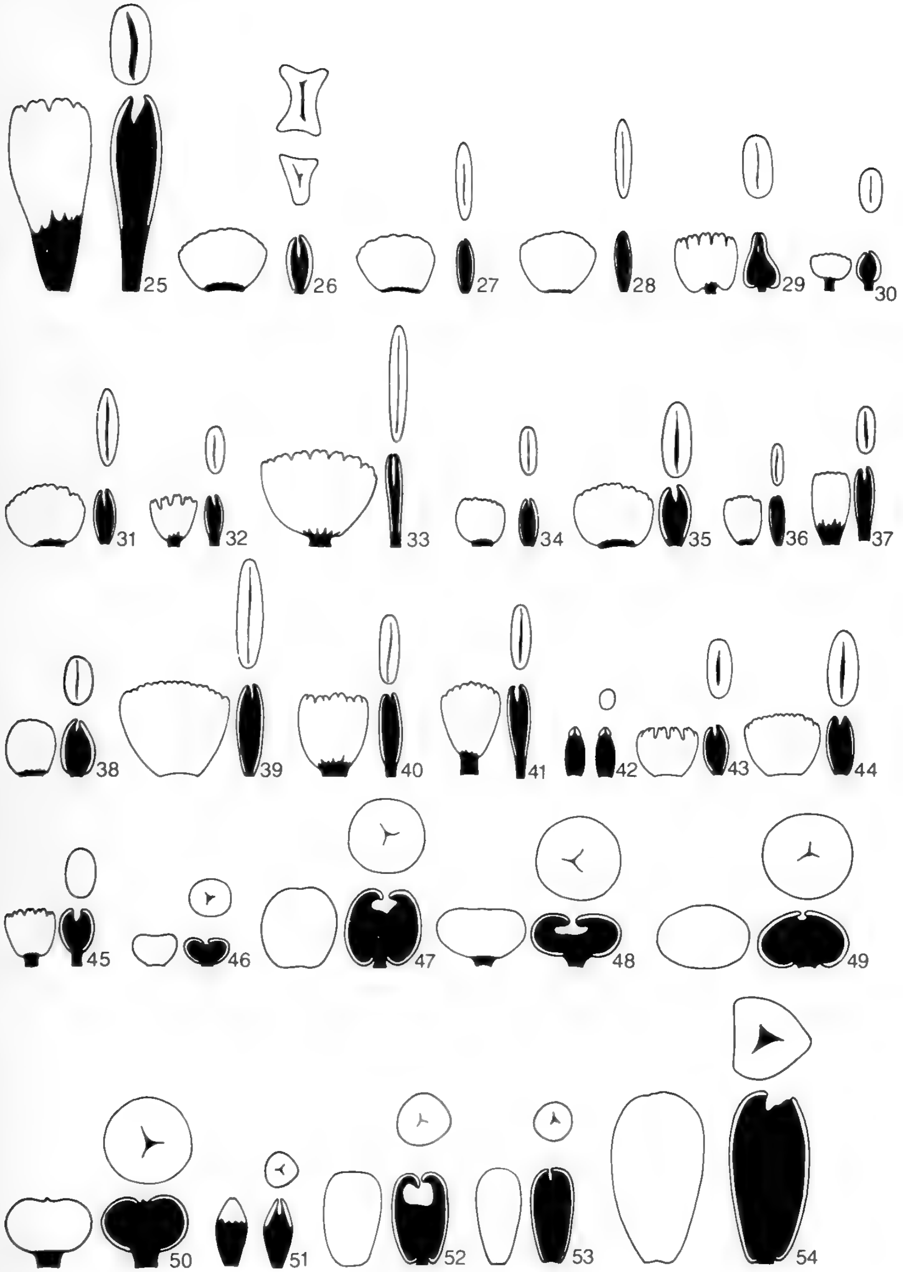


Fig. 1B. Semi-schematic drawings of *Horsfieldia* cont.
Species 24-54: (*24, H. ampla,* male flowers not extant); *25, H. ampliformis* (x 10, *Hoogland & Craven 11085); 26, H. angularis* (x 5, Iwanggin BW *5828); 27, H. iriana* (x 5, *Zipelius 139d); 28, H. aruana* (x 5, *Zipelelius s.n.); 29, H. subtilis* var. *subtills* (x 5, *Versteegh & Vink* BW *8377); 30, H. schlechteri* (x 5, NGF *13293); 31, H. basifissa* (x 5, *Womersley 3821); 32, H. sinclairii* (x 5, NGF *28886,* type); *33, H. psilantha* (x 10, *Sands et al. 2047); 34, H. whitmorei* (x 5, BSIP *7565); 35, H. laevigata* var. *laevigata* (x 5, *Craven & Schodde 874); 36, H. pilifera* (x 5, *Clemens 1710); 37, H. lancifolia* (x 5, bb. Cel./II. 464); *38, H. decalvata* (x 5, *Idjan & Mochtar 181); 39, H. tuberculata* (x 5, *Waterhouse 820B); 40, H. corrugata* (x 5, *Carr 14123); 41, H. pachycarpa* (x 5, *Manner & Street 307); 42, H. pulverulenta* (x 5, LAE *43567); 43, H. leptantha* (x 5, *Vink* BW *12194); 44, H. hellwigii* var. *hellwigii* (x 5, NGF *26253); 45, H. ralunensis)* x 5, NGF *44388); 46, H. sabulosa* (x 10, SAN 15146, immature); *47, H. atjehensis* (x 10, *Bangham 882); 48, H. sucosa* subsp. *sucosa* (x 10, SNF *40629); 49, H. pallidicaula* var. *pallidicaula* (x 10, *Hose 29); 50 H. sparsa* (x 10, FRI *7982); 51, H. triandra* (x 5, *Forbes 2465); 52 H. tristis* (x 5, S *37470); 53, H. fulva* (x 5, KEP *99334); 54, H. superba* (x 5, FRI *4511).*

Horsfieldia sect. *Irya* (Hook.f. & Th.) Warb. subsect. *Trivalves* Warb., Mon. Myrist. (1897) 267. — *Horsfieldia* sect. *Trivalves* subsect. *Trivalves* Sinclair, Gard. Bull. Sing. 16 (1958) 370, 371, *comb. inval.*, provisional name only. — Type not indicated.

Horsfieldia sect. *Orthanthera* Warb., Mon. Myrist. (1897) 268, p.p., for *H. ralunensis* and *H. sylvestris* only, excl. the lectotype *H. iryaghedhi.*

Phyllotaxis of plagiotropic shoots dispersed or distichous. Lower leaf surface without alveolar tissue, epidermis not papillose, stomatal complex not sunken; with or without larger dark coloured dots or cork warts. Flowers with a pedicel (short in *H. wallichii*), at base with or without articulation, solitary or in loose clusters; perianth (depressed) globose, or obovoid or ellipsoid, not laterally compressed, not or but faintly angular, generally perianths all or predominantly 3- (or 4-) valved, rarely 2-valved (*H. longiflora, H. sterilis*), cleft at anthesis to c. 2/3 or less. Androecium actinomorphic or more or less triquetrous in transverse section, never laterally compressed, depressed-globose or ellipsoid or obovoid, usually with a broad central column with an apical hollow of various shape and depth; androphore short or rather long, usually narrow at base; anthers various in number, ± straight or curved, either almost entirely connate or ± straight-erect and mutually free for about the upper half (*H. polyspherula*-group). Stigma minutely 2-lobed. Continental SE. Asia, West Malesia (incl. Philippines). — Figures 1, 2-5, 46-100; 2 III; species 2-5, 46-100.

This section of 59 species contains mainly those with exclusively or predominantly a 3- (or 4-) valved perianth, the rest are 3 species with a 2-valved perianth, *viz., H. longiflora* from Vietnam, *H. crassifolia* (Malaya, Sumatra, Borneo) and *H. sterilis* from Sabah. I believe that these exceptions should be placed among the species of the present section *Pyrrhosa* as is briefly discussed in the notes to the preceding section for *H. longiflora,* and argued for *H. crassifolia* and *H. sterilis* below.

Within sect. *Pyrrhosa* some 15 groups (9-23) can be distinguished, some of them are heterogeneous, others have a clear circumscription particularly the *H. polyspherula*-group or contain only a single aberrant species.

SURVEY OF GROUPS WITHIN SECT. PYRRHOSA

(9) *H. amygdalina-group, species 2-5*

Group 9 clearly links up with the *H. glabra*-group (sp. 97-100) because of the largely identical construction of the male flowers, and the phyllotaxis which is either distichous or dispersed, but differs in the absence of cork warts on the lower leaf surface. The group is keyed out at the beginning: — because it has a distinct distributional area in continental SE Asia, and because of the variable number of perianth-valves (2-4) and the variable phyllotaxis, and this situation rather interferes with the keying out of most of the West Malesian species, which are clearly distinctive. *H. kingii* is readily distinguished by its pubescent, 4-valved male perianth.

(10) *H. sabulosa-group*

Group 10 consists only of *H. sabulosa*[46], which, from the study of the rather immature male flowers, links up with the group of e.g. *H. borneensis*[85] or *H. punctata*[90]. It is however readily distinguished by its ramiflorous flowering, dispersed phyllotaxis, long-petioled leaves, dark-coloured dots or stripes on the lower leaf surface, etc. The leaves have an iso-bilateral anatomy as was discovered by Koster and Baas (1981).

(11) *H. pallidicaula-group, species 47-50*

The species in group 11 are usually easily distinguished by the pale, grey-brown or straw-colour of the dried twigs, contrasting with the blackish colour of the dried leaves. Usually the flowers, leaves and fruits also dry to a relatively black colour. The phyllotaxis is mostly dispersed. In *H. sucosa*[48] and *H. pallidicaula*[49]p.p. the calyx remains persistent under the fruit; *H. atjehensis*[47] is distinct by the presence of blackish brown dots or cork warts on the lower leaf surface. The architecture of the androecium of this group links up with that of many other species, e.g., the *H. glabra*-group. In *H. sucosa* subsp. *bifissa*[48b] the perianth is predominantly 2-valved, which is aberrant in the present section.

(12) *H. triandra-group*

Group 12 consists of a single species, *H. triandra*[51], from C. and S. Sumatra, and is distinct by flowers in that the perianth is thick-leathery and opens by 3 valves split to only c. 1/5, and in the turbinate androecium, with 3 reduced anthers at the top. Similar androecia with 'reduced' anthers occur in e.g., *H. sterilis, H. pulverulenta,* and the *H. clavata*-group of sect. *Irya,* but I doubt that these species are otherwise related.

(13) *H. fulva-group, species 52-54*

These three species occupy a separate position because of the leaves drying to a dull colour above. The male perianth and androecium are of an elongated shape. In *H. fulva* and *H. superba* the perianth remains persistent under the fruit.

(14) *H. sessilifolia-group*

Group 14 consists of a possibly isolated species (55), characterized by the almost-sessile leaves; its male flowers are not known.

(15) *H. grandis — H. motleyi-group, species 56-60*

Group 15 is named here merely for convenience, as its five constituents, *H. grandis*[56], *H. wallichii*[57], *H. pulcherrima*[58], *H. flocculosa*[59], *H. motleyi*[60] all differ considerably from each other in general habit as well as the shape of the male perianth and especially the androecium. Only *H. grandis* and *H. pulcherrima* seem more closely related according to the male flowers, but for the rest, all five species could represent separate groups as well. *H. flocculosa*[59] has a somewhat elongated male perianth and an elongate androecium, and therefore suggests connections with the *H. fulva*-group.

(16) *H. affinis-group, species 61-67*

Group 16 is characterized by a globose or depressed globose androecium with a moderate apical hollow, and a short and slender androphore; in these it seems much related to the group of *H. endertii — H. montana* (83-89). Our present group, however, is segregated by a generally persistent tomentum on the lower leaf-surface. *H. affinis*[66] and *H. reticulata*[67] have very distinctly articulated pedicels.

(17) *H. crassifolia-group*

Group 17 consists of only one species, *H. crassifolia*[68], which deviates in many respects *viz.,* a 2-valved perianth, an actinomorphic subglobose androecium with largely free anthers (fig. 1C), a persistent perianth under the fruits and a dotted lower leaf surface. The pedicels at the base are not articulated. Because of the largely free anthers and the 2-valved perianth, this species may have affinity to the widespread *H. irya*[6] from section *Irya.*

(18) *H. carnosa-group*

Group 18 possibly should not have been mentioned as a group, because its single species (69) links up with species from the group of *H. borneensis*[85] by its male flowers. Vegetatively and ecologically (heath forest, peat swamp forest) it is, however, quite distinct.

(19) *H. sterilis-group*

The position of group 19, with its single species *H. sterilis*[70] from SE. Sabah is problematic within section *Pyrrhosa*. Its perianths are 2-valved, opening at anthesis only at the very apex; the androecium is, however, actinomorphic, i.e., faintly blunt-triangular, and consists of a large sterile conical part with 6 anthers apically attached (or possibly 3 anthers each with 2 thecae). It has twigs drying rather pale and with dark leaves and is hence vegetatively reminiscent of the *H. pallidicaula*-group with which it has no affinity if judged from the androecium. The female perianth persists under the young fruit.

(20) *H. polyspherula-group, species 71-82*

Group 20 is remarkably coherent on account of the following characters: pedicels articulated at the base, androecium (generally) triquetrous in transverse section, anthers suberect and mutually free for about the upper half; furthermore, most species (except *H. ridleyana*[74]) have the lateral nerves distinctly raised above. The group can be divided in 2 subgroups based on whether the internodes are distinctly ridged (or short-winged) or angular as in species *H. hirtiflora*[71] and *H. brachiata*[72], respectively. In *H. hirtiflora*, a rather deviating species with its pubescent 4-valved perianth, and leaves partly dispersed, the androecium is rather roundish, not triquetrous in section, but the erect and largely free anthers still point to a relationship within the *H. polyspherula*-group. This group correlates with Warburg's sect. *Irya* subsect. *Trivalves*.

(21) The group of *H. endertii*[83], *H. valida*[84], *H. borneensis*[85], etc. to *H. obscura*[93] (spec. 83-93) is rather heterogeneous, but most of its species are clearly interrelated as they have in common a depressed globose narrowly-stalked androecium with a moderately deep, apical hollow. In *H. fragillima*[86] this hollow is exceedingly broad, rendering the androecium saucer-shaped; in *H. androphora*[87] the androphore is conspicuously elongated; *H. borneensis*[85] has distinctly articulated pedicels and on the lower leaf surface blackish marks, presumably cork warts. Through *H. punctata*[90], with a dotted lower leaf surface, there is a strong connection of the present group with the group of *H. glabra*[100]. Species 83-89 all have in common a coarse tomentum on the leaf bud. Through its coarse pubescence *H. endertii*[83] leads the present group though it deviates by its elongate male perianth and androecium, which it shares with the species of the next group.

(22) *H. xanthina-group, species 94-96*

Species of group 22 and *H. endertii*[83] of the foregoing group have in common an elongate male perianth and androecium. Whether these species are in reality more

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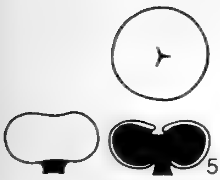
Facing Page

Fig. 1C. Semi-schematic drawings of *Horsfieldia* cont.
Species 55-89: (*55, H. sessilifolia*, male flowers not known); *56; H. grandis* (x 10, *Chew Weelek 261*); *57, H. wallichii* (x 5, FRI *12135*); *58, H. pulcherrima* (x 10, FRI *8008*); *59, H. flocculosa* (x 5, KEP *110225*); *60, H. motleyi* (x 10, *Kostermans 6859*); *61, H. tomentosa* (x 10, FRI 15957); (*62, H. gracilis*, male flowers not known); *63, H. paucinervis* (x 10, *Haviland 3075*); *64, H. splendida* (x 10, S *33723*); *65, H. rufo-lanata* (x 10, *Richards 1667*); *66, H. affinis* (x 10, S *24718*); *67, H reticulata* (x 10, *Hans Winkler 388*); *68, H. crassifolia* (x 10, SFN *40898*); *69, H. carnosa* (x 10, *van Niel 4519*); *70, H. sterilis* (x 10, SAN *30597*); *71, H. hirtiflora* (x 10, *Rahmat si Boeea 9257*); *72, H. brachiata* (x 10, *King's Coll. 4704*); *73, H. pachyrachis* (x 10, bb. 28128); *74, H. ridleyana* (x 10, *Scortechini 12*); *75, H. obtusa* (x 10, *Native Coll.* BS 821); (*76, H. disticha*, male flowers not known); *77, H. tenuifolia* (x 10, S *24945*); *78, H. macilenta* (x 10, B.N.B. *4204*); *79, H. laticostata* (x 10, S. *17252*); *80, H. nervosa* (x 10, S *16652*); *81, H. polyspherula* var. *polyspherula* (x 10, KEP *38129); 82, H. oligocarpa* (x 10, *Ashton & Whitmore BRUN 398); 83, H. endertii* (x 5, *Endert 3996); 84, H. valida* (x 5, *Lorzing 5896); 85, H. borneensis* (x 10, S *14610); 86, H. fragillima* (x 10, Bakar S *4361); 87, H. androphora* (x 10, S *35443); 88, H. amplomontana* (x 10, SAN *18843); 89, H. montana* (x 10, *Sinclair 8987).*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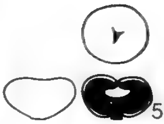
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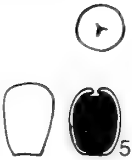
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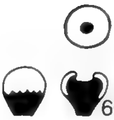
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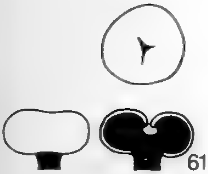
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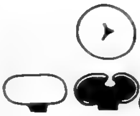
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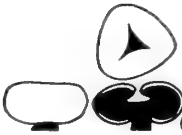
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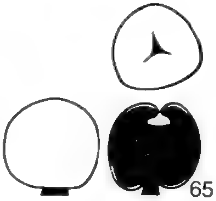
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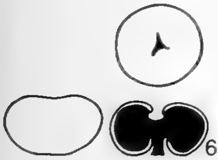
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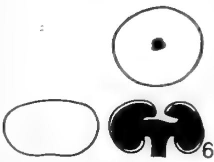
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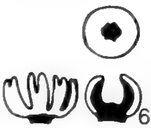
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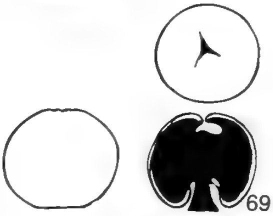
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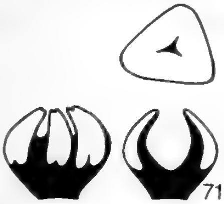
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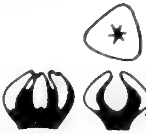
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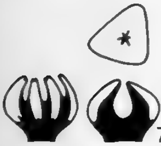
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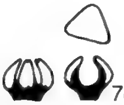
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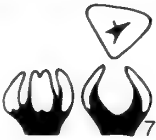
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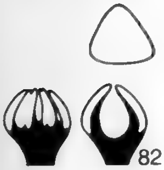
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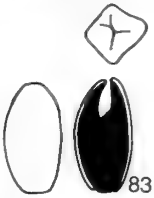
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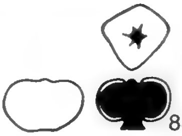
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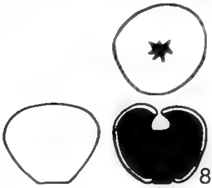
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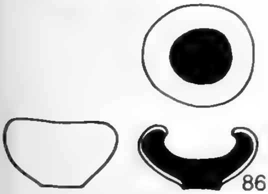
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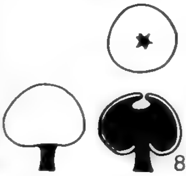
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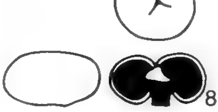
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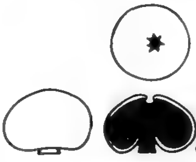
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closely inter-allied remains uncertain. The androecium of *H. majuscula*[95] is triquetrous in section and the pedicel is articulated at the base, and therefore this species might be close to the *H. polyspherula*-group (species 71-82).

(23) *H. glabra-group, species 97-100*

As already mentioned under the *H. amygdalina*-group (spec. 2-5), and e.g., also in the comments on *H. punctata*[90], *H. glabra*-group has several connections with others, especially in its largely similar, subglobose or ellipsoid androecium with a smallish apical cavity. The group is readily distinguished by the very short tomentum of the leaf bud and of the inflorescence, and by the presence of dark-coloured dots, i.e. cork warts, on the lower leaf surface.

Geographical Distribution

Horsfieldia, with 100 species, ranges from Ceylon through NE. India to S. China (Kwangsi, Hainan) and through Malesia and the Caroline Isls. east to the Solomon Isls. and N. Australia. It is absent from the Lesser Sunda Isls. Apart from a few widely distributed species, e.g., *H. irya, H. glabra, H. amygdalina, H. laevigata,* or *H. tuberculata,* most species are of limited distribution. Distinct centres of species-development are New Guinea and Borneo, and to a lesser extent Malaya-Sumatra. Here recognized are three sections, which occupy largely mutually exclusive areas. Section *Horsfieldia,* with only *H. iryaghedhi,* is confined to Ceylon. Section *Irya* (with 40 species) is, except for the wide-spread *H. irya* (see fig. 2), confined to E. Malesia and the Solomon Isls. and N. Australia, as indicated in figure 2. The section *Pyrrhosa* occurs west of Wallace's Line as also indicated in that figure by a broken line.In distribution, Sections *Irya* and *Pyrrhosa* overlap for a relatively narrow area in the Philippines and Celebes. They are segregated mainly because of a different valve-number of the perianths *viz.,* predominantly 2 in the east-occurring sect. *Irya* and predominantly 3 in the west-occurring sect. *Pyrrhosa.* Some species with the perianth-valve number deviating from that in the section but still regarded as belonging to it are for sect. *Irya: H. olens*[17], *H. sepikensis*[18], and *H. angularis*[26]. In the west-occurring section *Pyrrhosa* the deviating valve number 2 is found in: *H. longiflora*[3], *H. thorelii*[4] (and *H. amygdalina*[5], for a minor part), *H. crassifolia*[68] (see fig. 2) and *H. sterilis*[70]. Why these species are better listed in this section is briefly explained in the foregoing chapter in the discussion on sections and groups. Apart from these few species with a deviating valve-number, the division into the sections *Pyrrhosa* and *Irya* based on the character of the perianth being 3- and 2-valved respectively, correlated with their respective different geographical distribution is peculiar because in most individual specimens the number of perianth-valves is not at all constant: perianths with a deviating valve-number are usually found in low percentages. In general, however, though not strictly constant, even in the specimens, the character of the predominant valve-number has apparently some phylogenetic significance connected with Wallace's Line.

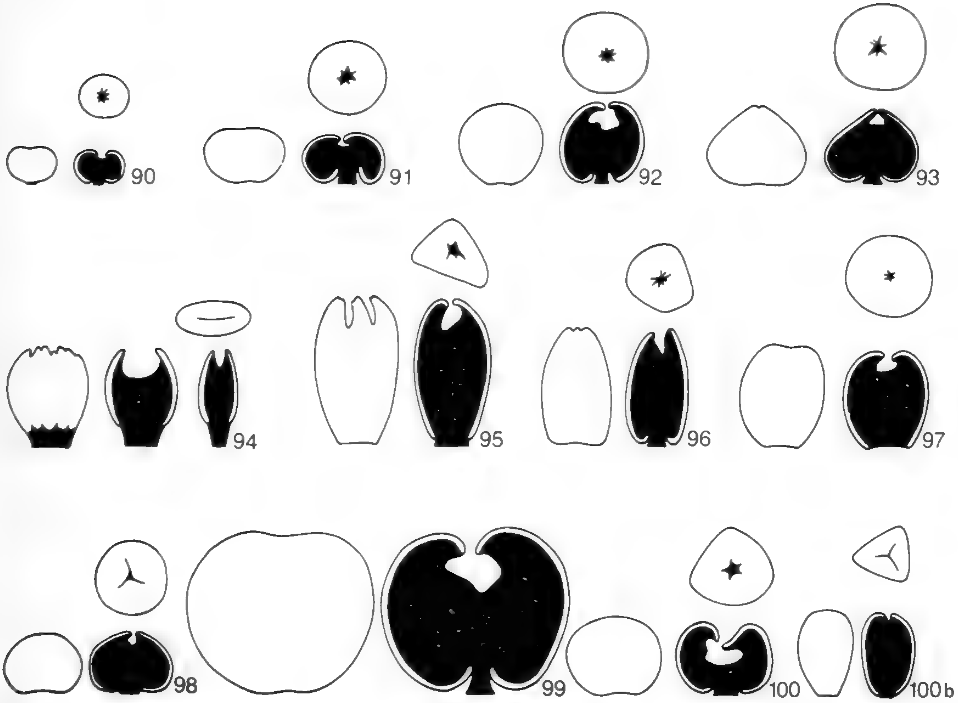

Fig. 1D. Semi-schematic drawings of *Horsfieldia* cont.
Species 90-100b: *90, H. punctata* (x 10, FRI *9014*, slightly immature); *91, H. costulata* (x 10, PNH *2685*); *92, H. subalpina* subsp. *subalpina* (x 10, *Whitmore* FRI *3884*); *93, H. obscura* (x 10, *Kostermans 13773*); *94, H. xanthina* subsp. *xanthina* (x 10, *Richards 1927*); *95. H. majuscula* (x 10, *Ramat si Boeea 8772*); *96, H. coriacea* (x 10, bb. Cel. III/-27); *97, H. penangiana* (x 10, Curtis 2406 in BM); *98, H. punctatifolia* (x 10, S 36580); *99, H. macrothyrsa* (x 10, *Lorzing 17195); 100, H. glabra* var. *glabra* (x 10, *Nengah Wirawan 95); 100 b, H. glabra* var. *javanica* (x 10, *Koorders 21635 β*).

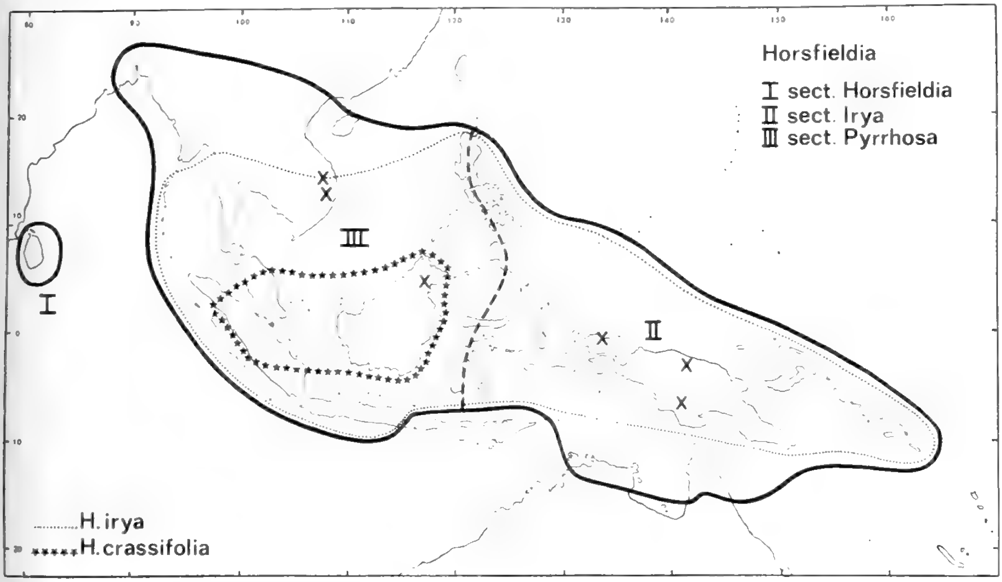

Fig. 2. Distribution of *Horsfieldia*
I. sect. *Horsfieldia* (1 species). — II. sect. *Irya,* 40 species, distributed east of Wallace's Line as drawn by broken line; distribution of *H. irya* as stippled line — III. sect. *Pyrrhosa,* 59 species, distributed west of Wallace's Line. Crosses indicate the approximate locatlities or areas of species with valve-number of perianth straying from the sectons. For further explanation see the text.

Keys to the Species

Seven keys are presented, a general key (1) to all species of *Horsfieldia,* based on male flowering specimens, and six regional keys (2-7) for female flowering and fruiting specimens, based partly on vegetative characters and partly on distribution.

(1) GENERAL KEY TO THE SPECIES

based on male flowering specimens

1a. *Male flowers sessile,* packed into dense subglobose capitula; perianths ± obconical, in bud mutually appressed and angular. Male perianth 3-valved, at anthesis cleft to c. 1/5-2/3. Androecium stalked, anthers 3-5. Leaves papillose beneath. *Ceylon, elsewhere cultivated* .... **H. iryaghedhi**[1]

b. Male flowers subsessile or usually pedicelled; perianths various, in bud not or only somewhat angular, mutually free or at least not densely clustered (perianth densely clustered before anthesis in *H. sylvestris* from *E. Malesia*). Leaves not papillose beneath 2

2a. Phyllotaxis of plagiotropic (fertile) twigs distichous. Leaves membranous, usually with largish whitish marks of irregular shape and size. Male perianth 2-valved, globose, c. 1-1.5 (-2.0) mm diam. Androecium not or hardly laterally compressed; androphore distinct, tapering, broad above and hollowed to a saucer-shape, shallowly to deeply; anthers 6-10, their apices free for only c. 0.3 mm and ± in-curved. *Ceylon to Solomon Isls., generally not too far from the coast* .... **H. irya**[6]

b. Phyllotaxis of plagiotropic twigs either distichous (alternate), or dispersed (spirally), or mixed in the same specimen. Leaf consistency various, usually, without whitish marks. Male perianth 2-4 valved, various in shape and size. Androecium various, but if the hollow deeply cup- or saucer-shaped then the anther-apices either mutually free for at least 1/2-way, or the anthers strongly inflexed into the cup (anthers connate or mutually free, number of anthers few to many) 3

3a. Perianths in any one inflorescence either 2- and 3-valved evenly mixed, or all the flowers with perianths either 2-, or 3-, or 4-valved. Phyllotaxis of plagiotropic (fertile) twigs at least partly dispersed (1/3-2/5 spiral), except in *H. longiflora (Annam)* with leaves distichous (always?). Leaves without brown or blackish dots of non-traumatic origin (lens!) beneath. Dried twigs dark brown, not pale and not much contrasting with the colour of the petioles. *Continental SE. Asia, Andaman Isls., not S. of the Isthmus of Kra* 4

b. Perianths either 2-, or 3-, or 4-valved, the valve number in flowers of any one specimen constant or almost so; sometimes a few flowers excepted. Phyllotaxis distichous or dispersed. Leaves with or without dark dots beneath. Dried twigs straw or grey (pale) to dark brown, much contrasting with the dark colour of the dried petioles or not. *Peninsular Thailand through Malesia to Solomon Isls. and N. Australia* 7

4a. Perianths (2- or) 3- or 4-valved, pubescent, in male c. 3.0-4.0 mm diam. .... **H. kingii**[2]

b. Perianths either 2-, or 3-valved, or 2 and 3 valves mixed, outside glabrous, in male c. 1.0-3.0 mm long 5

5a. Phyllotaxis of plagiotropic shoots (fertile) distichous (always?). Male perianth ± elongate-ellipsoid, 2.2-3.0 mm long. Androecium ellipsoid, c. 2.0 mm long. *Annam* .... **H. longiflora**[3]

b. Phyllotaxis, usually at least partly, dispersed. Male perianth shorter, c. 1.0-2.3 mm long. Androecium depressed-globose to obovoid, rarely ellipsoid, c. 0.6-2.0 mm long 6

6a. Male perianth subglobose or depressed-globose, 1.0-1.5 (-1.7) mm long. Anthers 7-10. *Thailand, Laos, Cambodia, Vietnam: Annam, Cochin-China* .... **H. thorelii**[4]

b. Male perianth short-ellipsoid, or subglobose, or obovoid, c. 1.5-2.3 mm long. Anthers 8-15. *S. China, Indo-China (excl. Annam, Cochin-China) NW. to Assam, Andaman Isls. (2 vars.)* .... **H. amygdalina**[5]

7a. Perianths predominantly 2-valved, or sometimes a few flowers in an inflorescence 3- or 4-valved. *Species mainly from E. of Wallace's line, or the following from W. Malesia: H. crassifolia (Malaya, Singapore, Sumatra, Borneo), H. penangiana, p.p. (Sumatra), H. sterilis (Borneo), H. sucosa subsp. bifissa (Borneo)* 8

b. Perianths predominantly 3-valved, or predominantly 4-valved, or both 3 and 4 valves present; sometimes the odd flower in an inflorescence has a 2-valved perianth. *Species from W. Malesia and penins. Thailand, and the following from New Guinea: H. angularis, H. olens, H. sepikensis* 48

8a. Androecium not laterally compressed, in transverse section ± circular; never distinctly longer than wide. *W. Malesia* 9

b. Androecium laterally compressed or not; if not or only slightly then the androecium including androphore longer than wide; androecium not or little laterally compressed in occasional 3- or 4-valved flowers. *E. Malesia: Moluccas to Solomon Isls., N. Australia* 12

9a. Leaves coriaceous, with inconspicuous, subpersistent, dense tomentum of stellate-scaly hairs with scattered emergents beneath (in specimens of *Borneo* the hairs often deciduous, leaving distinct scars); leaves with scattered brown or blackish dots or streaks (lens!) beneath. Colour of dried twigs and of petioles not much contrasting. *Peat swamp forest, swampy forest on sandy soil* .... **H. crassifolia**[68]

b. Leaves ± membranous, glabrous or early glabrescent beneath. *Not from peat swamp forest* 10

10a. Twigs slender, towards apex c. 2 mm diam.; bark not drying to a pale colour. Leaves small, c. 7-12 cm long, with regularly scattered dark dots beneath; lateral nerves flat and inconspicuous above .... **H. penangiana**[97]

b. Twigs towards apex c. 2-5 (-10) mm diam.; bark usually drying to a pale colour and contrasting with the blackish dried petioles or not. Leaves 14 cm long or more, not dotted beneath 11

11a. Androecium depressed-globose, largely consisting of anthers; central-apical cavity flat and shallow .... **H. sucosa** subsp. **bifissa**[48]

b. Androecium broadly obovoid, consisting of a large sterile base, and an upper half bearing 3 (or 6?) inconspicuous anthers .... **H. sterilis**[70]

12a. Male inflorescence spike-like, i.e., either not so or but slightly so and short-ramified, lateral branches up to 5 mm long. Inflorescences, flowers and petioles drying blackish, usually contrasting with the paler grey-brown dried twigs. Anthers inflexed inwards. *Moluccas* .... **H. spicata**[7]

b. Male inflorescence usually ramified, the side branches at least 5 mm long. Inflorescences, flowers, and petioles drying brownish or blackish, usually not contrasting with the colour of the dried twigs 13

13a. Androecium ± cup-, or bowl-, or saucer-shaped, moderately laterally compressed; the anthers at one or both sides of the androecium distally distinctly incurved or inflexed into the cup-shaped central cavity. *E. Malesia: Philippines, Celebes, Moluccas, NW. New Guinea, Palau Isls*............... 14

b. Androecium laterally flattened or not, the central column either (1) solid, or at apex, (2) broadly but shallowly hollowed only up to c. 1/3, or (3) narrowly channelled like a slit to various depths; the anthers straight or only slightly in curved, never inflexed into the cup-shaped central cavity. *E. Malesia: Moluccas to Solomon Isls., N. Australia* 22

14a. Leaves below with regularly spaced reddish-brown to brown-black dots presumed to be non-traumatic cork warts originating from hair-scars (lens!), not to be confused with a much finer punctation if also present. Twigs angular or ridged especially in the upper portion .... **H. inflexa**[8]

b. Leaves without dots. Twigs either terete, or angular, or winged 15

15a. Male perianth together with the pedicel ± pear-shaped, the pedicel tapering. Petiole relatively long, c. 1.0-2.6 cm, leaf blade (6-) 8-22 (-25) cm. Twigs at apex generally terete, not angular .... **H. moluccana**[9]

b. Perianth (in laterally view, on the broad side) either short-cuneate, or rounded, or subtruncate at base; the pedicel not tapered, ± abruptly passing into the perianth. Petioles generally shorter. Twigs terete or angular 16

16a. Anthers entirely connate; androphore short or absent. Male perianth at anthesis cleft to c. 1/2-way 17

b. Anthers or thecae mutually free at least in the incurved or inflexed portion. Male perianth at anthesis cleft to c. 2/3 or over 18

17a. Anthers 18-25, usually inflexed at both sides of the laterally compressed androecium into the thin-walled androecium-cup. Male perianth 2.5-4 mm wide. Leaves membranous, drying matt. *Moluccas* .... **H. parviflora**[10]

b. Anthers 11-12, usually inflexed at only one side of the androecium-cup; the cup thick- and firm-walled. Male perianth c. 2-2.2 mm wide. Leaves chartaceous, ± glossy above. *Philippines: Luzon* .... **H. obscurinervia**[11]

18a. Anthers mutually free only in the inflexed distal portions, the basal non-inflexed portions connate into a cup-shaped androecium. Androphore minute, only c. 1/10 of the androecium-length.................................. 19

b. Anthers free for at least 2/3. Androphore relatively large, its length c. 1/3 of the androecium-length 21

19a. Twigs angular or winged. Male perianth c. 4 mm wide, glabrous. *Philippines* .... **H. ardisiifolia**[12]

b. Twigs terete, neither ridged nor winged. Male perianth 2.5-3 mm wide ... 20

20a. Pedicel of male flowers pubescent, shorter than the perianth. Inflorescences rather densely finely pubescent. Anthers inflexed at both sides of the laterally compressed androecium. *Talaud Isls* .... **H. talaudensis**[13]

b. Pedicels of male flowers glabrous, longer than the perianth. Inflorescences sparingly pubescent with hairs less than 0.1 mm long. Anthers inflexed only at one side into the androecium-cup. *Philippines: Samar Isls*. .... **H. samarensis**[14]

21a. Twigs generally angular or ridged. Male perianth c. 3-4 mm wide; pedicel glabrous. Anthers all inflexed into the centre of the androecium. *Moluccas* .... **H. smithii**[15]

b. Twigs terete, usually lined. Male perianth c. 2-2.5(-3) mm wide; pedicel pubescent or glabrescent. Anthers deeply inflexed at one side of the androecium, always partly covered over by those of the other side. *Palau Isls*. .... **H. palauensis**[16]

22a. Male perianths angular before anthesis, arranged into dense semi-globose clusters. Androecium much longer than wide, not or but slightly laterally compressed. Leaves lanceolate to lanceolate-linear, usually ± parallel-sided .... **H. sylvestris**[19]

b. Flowers not densely clustered, not angular in mature buds 23

23a. Mature male perianth either ± lengthwise ellipsoid, or subglobose, c. 2-3 mm long, very thinly pubescent; at anthesis cleft to c. 1/2-way. Androecium only slightly laterally compressed, the central column broad, broadly hollow in the apical portion, but the central column protruding centrally into this cavity. *Australia* .... **H. australiana**[20]

b. Male perianth various. Central column of androecium not protruding. *E. Malesia, Pacific* 24

24a. Twigs sharply angular, or markedly ridged, or winged from petiole to petiole at the apex of the twig as well as lower down in between the older leaves and in older wood; i.e., twigs not merely more or less distinctly lined 25

b. Twigs not winged, i.e., terete or only somewhat angular at apex, lower down terete or merely provided with lines from petiole to petiole (the bark striate or not) 27

25a. Male perianth either 2-, or 3-, or 4-valved, subspherical, hardly or not laterally compressed, drying ± glossy, not collapsing on drying. *New Guinea: Vogelkop penins.* .... **H. angularis**[26]

b. Male perianth predominantly 2-valved, little or much laterally compressed, drying matt, slightly or strongly collapsing on drying 26

26a. Leaves thinly coriaceous. Pedicels of male flowers about as long as or longer than the perianth. Perianth at anthesis cleft almost to the base. Hairs of inflorescence and pedicels c. 0.2-0.3 mm. Anthers 10-14; the central column of androecium at apex hollow for c. 1/4 .... **H. iriana**[27]

b. Leaves membranous. Pedicel shorter than the perianth. Perianth at anthesis cleft to c. 2/3-3/4. Inflorescences and pedicels almost glabrous, with hairs of c. 0.1 mm or less. Anthers (12-) 14-18; the central column of androecium solid or almost so .... **H. aruana**[28]

27a. Male inflorescence large, 25-35 cm long. Male perianth ± pear-shaped. Androecium longer than broad; androphore c. 0.5 mm long or more, about half as long as the anthers or longer 28

b. Male inflorescences c. 20 cm long or less. Male perianth of various shapes. Androecium longer or shorter than broad; androphore short or long 29

28a. Male perianth glabrous (?), c. 4 × 2 mm. Anthers 10, androphore nearly as long as the anthers. Inflorescence glabrescent, to 25 cm long .... **H. ampla**[24]

b. Male perianth pubescent, c. 3 × 3 mm. Anthers 7, androphore about half as long as the anthers. Inflorescence pubescent, c. 25-35 cm long .... **H. ampliformis**[25]

29a. Male inflorescence delicate, 2-5(-8) cm long, 1 or 2 (or 3) times ramified. *New Guinea, incl. Aru Isls.* 30

b. Male inflorescences generally stouter, c. 5-20 cm long, not or 1-4 times ramified (inflorescences of *H. sinclairii* and *H. basifissa* from New Guinea sometimes small). *Whole of E. Malesia, incl. Celebes, Pacific; not in the Philippines* 34

30a. Male perianth pubescent or late glabrescent, distinctly or only somewhat longer than broad. Anther-bearing part of the androecium much shorter than the elongate club-shaped androphore 31

b. Male perianth glabrous or early glabrescent, about as long as or shorter than broad. Androphore much shorter than the anthers 33

31a. Leaves broadly obovate or elliptic to oblong, c. 12-17 × 5-11 cm. Male perianth gradually passing into the thick and tapered pedicel, both together c. 10-12 mm long. Androphore glabrous .... **H. crux-melitensis**[21]

b. Leaves elliptic to lanceolate, 4.5-20 × 0.7-6 cm. Male perianth with pedicel 4-6(-9) mm 32

32a. Leaves drying olivaceous. Male perianth with pedicel together club-shaped, c. 5-5.5 × 2-2.2 mm. Androphore glabrous .... **H. clavata**[22]

b. Leaves drying dark brown. Male perianth broadly ellipsoid, c. 2.0-2.4 × 1.8-2.2 (-2.4) mm, at base narrowed into a slender pedicel 2-3.5(-6) mm. The surface of the androphore in the upper part wrinkled-bullate, towards the base either densely, minutely scaly-hairy, or striate but glabrous .... **H. squamulosa**[23]

33a. Male perianth ± laterally compressed, generally ± obtriangular in lateral view, 1.8-3 mm wide, usually ± collapsing on drying. Androphore slender, c. 0.2.-0.5 mm long, usually much shorter than the anthers ..... **H. subtilis**[29]

b. Male perianth generally subglobose, 1-2 mm wide, not or but slightly compressed, the surface wrinkled on drying but not collapsing. Androphore 0.4.-0.5 mm long, about half the length of anthers .... **H. schlechteri**[30]

34a. Male perianths together with the pedicels generally ± pear-shaped; the upper part of the perianth broadly rounded in lateral view, the lower (1/4-) 1/3-1/2 tapered and gradually passing into the ± tapered pedicel (these characters not always clear in certain specimens of *H. tuberculata*). Perianth glabrous, pubescent or glabrescent 35

b. Male perianth in lateral view of various shapes, either circular, or ovate, or obovate, or elliptic, or transversely elliptic, or reniform; at base either short-attenuate, or rounded, or truncate; not tapered, the pedicels generally not thickened towards the perianth. Perianth either hairy, at least at the base, or in *H. psilantha, H. basifissa, H. sinclairii* glabrous, subglabrous, or glabrescent 39

35a. Perianth glabrous. *A variable species* .... **H. tuberculata**[39]

b. Perianth minutely pubescent, or early glabrescent in *H. corrugata* 36

36a. Leaves small, ± lanceolate, 5-16 cm long. Male perianth at anthesis cleft to only c. 1/6. *Celebes* .... **H. lancifolia**[37]

b. Leaves elliptic to lanceolate, generally much larger, 12-30 cm long. Male perianth at anthesis cleft to c. 1/2-way 37

37a. Pedicel c. 1.5-2 mm long; perianth c. 2.3 mm long, thinly pubescent. Anthers c. 6. *Moluccas, at low altitude* .... **H decalvata**[38]

b. Pedicel generally longer; perianth c. 2.5-3.5 mm long. *New Guinea, at c. 450-2000 m alt. Vegetatively and sometimes in fruit much resembling H. laevigata*[35] 38

38a. Male pedicel stoutish, 2-4 mm long. Male perianth ± membranous, glabrescent, with or without a few scattered blackish warts. Anthers c. 8-12 .... **H. corrugata**[40]

b. Male pedicel stout or rather slender, 2-5 mm long. Male perianth ± fleshy, pubescent, without blackish warts. Anthers 5-10 .... **H. pachycarpa**[41]

39a. Inflorescence moderately pubescent to nearly glabrous. Tomentum on leaf buds and apical portions of twigs short, rusty or greyish, the hairs 0.1-0.4(-0.5) mm long. Leaf largely or entirely (early) glabrescent, or with scattered stellate hairs beneath especially the younger ones 40

b. Inflorescence generally thick-woolly tomentose. Tomentum on leaf bud and apical portion of twig usually rust-coloured, conspicuous, its hairs coarse and long, (0.3-) 0.5-1.5 mm. Leaves with (sub) persistent tomentum, at least on and near the midrib beneath 45

40a. Male perianth largely glabrous, subglobose, 2-3 mm diam., at anthesis cleft to the base, not collapsing on drying............................ **H. basifissa**[31]

b. Male perianth glabrous or hairy, of various sizes and shapes, at anthesis cleft to c. 1/2-way to near the base; perianth collapsing on drying or not 41

41a. Male perianth wholly or almost wholly clothed with ± persistent tomentum, the hairs may be scattered and very minute. Leaves drying olivaceous to brown, without a reddish tinge; marginal nerve not conspicuously regularly looped. Hairs of leaf bud c. 0.1-0.2 mm long, usually greyish. *Moluccas, New Guinea, New Britain; not in the Solomon Isls.* 42

b. Male perianth either glabrous, or early or late glabrescent, at least the upper 4/5. *E. New Guinea to Solomon Isl.* 43

42a. Mature male perianth small, c. 1.2-1.9 mm diam. *A variable species* .... **H. pilifera**[36]

b. Mature male perianth 2.0-3.3 mm diam. *A variable species* ... **H. laevigata**[35]

43a. Perianths and pedicels glabrous; male perianth c. (20-) 2.5-3.5 (-4.0) mm diam. Leaves rather large, 20-40 cm long, drying olivaceous to brown, the marginal nerve rather indistinct and not very regularly looped. *Bagabag Isls., Long Isl., New Britain, New Ireland* .... **H. psilantha**[33]

b. Perianths and pedicels glabrous or pubescent; male perianth (1.0-) 1.5-2.0 (2.5 mm diam., see note 5 under *H. sinclairii*). Leaves drying generally with a reddish tinge, especially the midrib and nerves 44

44a. Leaves usually large, 9-30 (-40) cm long, the marginal nerve very distinct and conspicuously regularly looped. Hairs on leaf bud 0.1-0.4 mm, average c. 0.3 mm long, usually reddish brown, sometimes greyish. Pedicel and base of perianth minutely pubescent. Male perianth c. 1.5-2.0 mm diam., cleft at anthesis to c. 9/10. *Solomon Isl.* .... **H. whitmorei**[34]

b. Leaves smaller, 6-20 cm long, the marginal nerve indistinct and not very regularly looped. Hairs of leaf bud to c. 0.1 mm long, greyish brown. Pedicel and perianth glabrous (but see the notes). Male perianth c. 1.1-2.0 mm diam., at anthesis cleft to c. 1/2-way; perianth larger and pedicel pubescent in deviating specimens as discussed in note 5. *E. New Guinea* .... **H. sinclairii**[32]

45a. Perianth in the male largely pubescent, towards the base thick-walled and coriaceous, the remainder collapsing on drying; both ♂ and ♀ opening at apex by small pore-like slit less than 1 mm long. Androecium subellipsoid, mainly consisting of the column with 2 minute anthers situated at the top, just below the pore. Leaves usually coriaceous, ± bullate; clothed with harsh hairs which when shed leave rough thickened bases . **H. pulverulenta**[42]

b. Perianth glabrous or pubescent, membranous or chartaceous, not much collapsing on drying, opening by a slit to at least c. 1/3. Androecium mainly consisting of 10-16 sessile anthers. Hairs on lower leaf surface not harsh, when shed not leaving rough thickened bases 46

46a. Perianth pubescent, in male at anthesis cleft to c. 3/4-5/6. Anthers 10-14. Leaves chartaceous or membranous .... **H. leptantha**[43]

b. Perianth glabrous, except at the very base; at anthesis cleft to c. 1/2-way or less. Leaves generally membranous 47

47a. Male perianth subglobose. Anthers 12-16. Leaves generally oblong to oblong-lanceolate, at apex not-caudate (always?) .... **H. hellwigii**[44]

b. Male perianth obovoid or ellipsoid. Anthers c. 10(-12). Leaves generally oblong-lanceolate, at apex caudate .... **H. ralunensis**[45]

48a. Phyllotaxis in plagiotropic shoots (i.e. usually the fertile) dispersed, i.e., leaves in 3 or more rows along the twigs. Terminal leaf bud generally rather short and broad 49

b. Leaves in plagiotropic shoots distichous (alternate), in rare cases, a few on the same plant in 3 rows. Terminal leaf bud generally more slender 57

49a. Leaves bunched towards the end of the twigs. Leaf bud and inflorescence pubescent with hairs c. 0.5-1.0 mm long. Bark of older twigs often blackish and flaking. *Borneo* .... **H. sabulosa**[46]

b. Leaves bunched or not. Tomentum on leaf bud and inflorescence short, the hairs up to c. 0.2 mm long, or, if plant from *Continental Asia,* then hairs short or long, up to c. 1 mm. Bark of older twigs flaking slightly or not 50

50a. Lower leaf surface with scattered brown to blackish non-traumatic dots (lens!) 51

b. Lower leaf surface without dots 52

51a. Bark of twigs generally drying brown or grey-brown, not contrasting with the dark colour of the dried petioles; older bark not flaking. Leaves in 2 or 3 rows .... **H. glabra**[100]

b. Bark rather pale, grey-brown to pale yellowish-brown, rather contrasting with the petioles; older bark ± flaking. Leaves in 3-5 rows. *Aceh (N. Sumatra)* at c. 1300 m .... **H. atjehensis**[47]

52a. Bark of twigs drying brown, not contrasting with the colour of the dried petioles 53

b. Bark of twigs drying pale, greyish-white or straw, contrasting rather well with the blackish brown colour of the dried petioles 55

53a. Twigs distinctly ridged or short-winged. *Sumatra* .... **H. hirtiflora**[71]

b. Twigs terete, neither ridged nor winged 54

54a. Leaf pubescent beneath. *Sumatra, Malaya* .... **H. superba**[54]

b. Leaf glabrous beneath. *Borneo* .... **H. fragillima**[86]

55a. Male pedicles at base articulated. Androecium much depressed, with the apical cavity conspicuous, broad, either shallow or rather deep, reaching up to nearly 1/2-way the androecium and bottom flattish; androphore narrow, largely hidden by the anthers. The leaves in most specimens distichous, sometimes 3-stichous). *Malaya, Sumatra* .... **H. sucosa** subsp. **sucosa**[48]

b. Male pedicels all or mostly not articulated. Androecium not or but slightly depressed, the apical cavity usually narrow and inconspicuous. Leaves generally in 3-5 rows 56

56a. Androphore indistinct or absent. Leaves generally drying blackish-brown. *Borneo* .... **H. pallidicaula**[49]

b. Androphore relatively distinct, 0.3-0.4 mm long. Leaves generally drying bright brown. *Sumatra, Malaya, penins. Thailand* .... **H. sparsa**[50]

57a. Male perianth ± obconical-obovoid, very leathery, at anthesis opening for 1/6-1/5 only. Androecium turbinate, anthers 3. *Sumatra* .... **H. triandra**[51]

b. Male perianth of various shapes, opening for c. 1/5 or more. Androecium various, anthers 4 or more 58

58a. Mature male perianth in bud ellipsoid or obovoid, 3-8 mm long, at anthesis splitting c. 1/5-1/4 (-1/3). Leaves usually ± parchment-like, on drying matt above owing to the finely wrinkled surface (in *H. sessilifolia* male flowers not known and leaves not so distinctly matt) 59

b. Mature male perianth in bud either (1) ellipsoid or short-pear-shaped, c. 3.5 mm long or less (though sometimes rather large in *H. endertii, H. flocculosa, H. majuscula, H. wallichii)*, or (2) perianth somewhat globose or depressed globose; perianth at anthesis cleft to (1/4-) 1/3-1/2, or more. Texture of leaves various including coriaceous, but never parchment-like and leaves not typically matt above 62

59a. Plant stout: twigs towards apex 5-7 (-10) mm diam.; leaves 25-70 cm long, tomentum present and persistent beneath 61

b. Twigs towards apex 3-5 mm diam. Leaves up to 30 cm long, (largely) glabrous beneath, or with some hairs persisting on the midrib. Male perianth 3.0-5.0 mm long 60

60a. Leaves drying dark olivaceous; up to 32 cm long. Bark of twigs bright brown or yellowish-brown, coarsely striate and tending to crack longitudinally. Inflorescence (almost) glabrous. Pedicel not articulated. Anthers 12-20 .... **H. tristis**[52]

b. Leaves drying fulvous-brown; up to 24 cm long. Bark of twigs brown, finely striate, not cracking. Inflorescence pubescent. Pedicel articulated at base. Anthers 10-12 .... **H. fulva**[53]

61a. Male perianth 7-8 mm long, perianth and pedicel glabrous. Petiole 6-15 mm long. *Malaya, Sumatra* .... **H. superba**[54]

b. Male flower not known; female perianth and pedicel pubescent. Petiole almost absent. *Borneo (Sarawak)* .... **H. sessilifolia**[55]

62a. Leaves with a persistent or subpersistent tomentum below, in *H. gracilis* and *H. wallichii* the tomentum sometimes vestigial on and near midrib and nerves 63

b. Leaves either glabrous or early glabrescent beneath, or in some species often with a vestigial pubescence on the lower midrib 74

63a. Leaf venation reticulate or not, not scabrous above 64

b. Venation distinctly reticulate on both surfaces, older leaves scabrous above .... **H. grandis**[56]

64a. Leaves with scattered dark brown or blackish dots and/or streaks beneath, obscured by hairs or not 65

b. Leaves without dots or streaks beneath 66

65a. Mature male perianth in bud short-pear-shaped, c. 2-2.5 mm long; pedicel indistinct, c. 03-1.0 mm long. Leaves rather thinly pubescent, often ± glabrescent beneath .... **H. wallichii**[57]

b. Mature male perianth subglobose, c. 1-1.5 mm diam., pedicel distinct, c. 1-1.5 mm long. Leaves with persistent, conspicuous tomentum beneath .... **H. pulcherrima**[58]

66a. Mature male perianth in bud broadly ellipsoid or obovoid, 2-3 mm long; androecium longer than broad. Pedicel (1.5-) 3-4 mm long. Tomentum on twigs and lower leaf surface with hairs c. 1.5-2 mm long ..... **H. flocculosa**[59]

b. Mature male perianth subglobose or depressed globose, c. 2.5 mm diam. or less; androecium as broad as or broader than long. Pedicel 3 mm long or less. Tomentum on twigs and lower leaf surface with hairs to c. 1.5 mm long 67

67a. Male perianth to c. 1 mm diam., with persistent tomentum or late glabrescent .... **H. motleyi**[60]

b. Male perianth c. 1.0-2.5 mm diam., glabrous or early glabrescent 68

68a. Male pedicel at base not articulated (character not quite clear in *H. rufolanata;* male flower not seen in *H. gracilis*) 69

b. Male pedicel with distinct articulation at base 73

69a. Upper leaf surface drying dark brown, with the venation (reticulation) usually indistinct. *Malaya, S. penins. Thailand* .... **H. tomentosa**[6]

b. Leaves drying olivaceous to brown, with the reticulation on upper surface distinct or not. *Borneo* 70

70a. Twigs stoutish, diam. towards the apex 3.5-7 (-13) mm. Leaves 10-45 cm long. Tertiary venation usually distinct above. Lateral nerves c. 11 pairs or more. Male perianth c. 1.5-2.3 mm diam.; anthers 8 or more. *Plant growing generally on soils richer than kerangas or sand* 72

b. Twigs slender, diam. towards the apex up to c. 3 mm. Leaves small, c. 7-21 cm long. Tertiary venation usually indistinct above 71

71a. Twigs 1.5-2.5 mm diam. Leaves thinly membranous, 12-21 cm long; lateral nerves 14-17 pairs. Lower leaf surface with tomentum rather sparse, subpersistent, the hairs vestigial mainly on nerves and midrib. Male flower not seen. *Primary lowland forest* .... **H. gracilis**[62]

b. Twigs c. 2-3 mm diam. Leaves 7-15 cm long, ± chartaceous; lateral nerves 5-9 pairs. Lower leaf-surface with denser tomentum. Male perianth c. 1.0 mm diam.; anthers 4 or 5. *Kerangas forest, or forest on coastal white sand* .... **H. paucinervis**[63]

72a. Leaves generally large, 18-45 cm long; lateral nerves 18-25 pairs, sunken in upper surface. Male perianth c. 1.5-2.0 mm diam., anthers 8-10 .... **H. splendida**[64]

b. Leaves smaller, 10-23 cm long; lateral nerves 11-16 pairs, raised above. Male perianth c. 2-2.3 mm diam.; anthers c. 15. *A montane species at c. 900-1400 m alt. in Sarawak, Sabah* .... **H. rufo-lanata**[65]

73a. Leaves membranous, not bullate; veins in upper surface flat or sunken, reticulation rather faint to distinct. Male perianth 1.5-2.2 mm diam.; pedicel equal to or somewhat longer than the perianth .... **H. affinis**[66]

b. Leaves chartaceous, bullate; veins sunken, reticulation very distinct. Male perianth 2-2.5 mm diam.; pedicel as long as or shorter than the perianth .... **H. reticulata**[67]

74a. Twigs in apical portion pale, grey-whitish or pale straw coloured, contrasting with the blackish or dark brown colour of the dried petiole 75

b. Twigs in apical portion drying brown to dark grey-brown, not contrasting with the brown to blackish colour of the dried petiole 78

75a. Androecium in transverse section triangular. Anthers mutually free for the upper half of more. *Borneo: heath forest on sand or peat soil* ....**H. oligocarpa**[82]

b. Androecium in transverse section circular or subcircular. Anthers largely connate 76

76a. Leaves chartaceous, drying bright brown. Pedicel at base not articulate. Androecium with small apical cavity. *Borneo: mostly in heath forest or kerangas forest on sandy soils* .... **H. carnosa**[69]

b. Leaves membranous, drying usually ± brown or blackish brown. *Plant growing usually in forest on richer soils, incl. sand.* 77

77a. Pedicel articulated at base. Androecium strongly-depressed globose, with the apical cavity broad and the bottom flattish, cavity nearly 1/2-way deep.

Malaya, Sumatra .... **H. sucosa** subsp. **sucosa**[48]

b. Pedicel not articulated at base. Androecium ellipsoid to slightly depressed globose, the apical cavity small and narrow. *Borneo* .... **H. pallidicaula**[49]

78a. Twigs distinctly ridged or nearly winged in between the petiole insertions, also in the older wood 79

b. Twigs not ridged; sometimes twigs faintly ridged, or lined or angular in the apical portion only 82

79a. Male perianth at anthesis cleft nearly to the base. *New Guinea* 80

b. Male perianth at anthesis cleft to c. 1/2-2/3. *West Malesia* 81

80a. Male perianth slightly broader than long, short-pubescent in the lower half. Androecium slightly broader than long; anthers erect, not incurved .... **H. angularis**[26]

b. Male perianth subglobose to broadly ellipsoid, glabrous. Androecium longer than broad, ± obovoid, the anthers with apex free and incurved, those of one side of the androecium clasping the others .... **H. olens**[17]

81a. Mature male perianth in bud c. 2.5 mm diam., pubescent. *N. Sumatra* .... **H. hirtiflora**[71]

b. Mature male perianth in bud c. 1.0-1.5 mm diam., glabrous. *S. penins. Thailand, Malaya, Sumatra, Borneo* .... **H. brachiata**[72]

82a. Mature male perianth in bud short-pear-shaped, c. 2.0 (-2.5) mm long, subsessile; the pedicel much shorter than the perianth, c. 0.3-1.0 mm long, thickish. Leaves coriaceous; lateral nerves flat or usually sunken above, pubescent or glabrescent beneath and with scattered blackish dots and streaks (lens!). Twigs towards the apex usually conspicuously hollow .... **H. wallichii**[57]

b. Male perianth various in shape and size, the pedicel proportionally longer and more slender; perianth obovoid with pedicel short in *H. glabra* var. *oviflora*. Leaves various, nerves raised or sunken, dotted or not beneath. Twigs solid or generally less strikingly hollow 83

83a. Male inflorescence very stout, the rachis towards the base 5-8 mm diam. Androecium about as broad as long, triquetrous, the anthers entirely connate. *W. Borneo* .... **H. pachyrachis**[73]

b. Male inflorescence large or small, the rachis towards base c. 4.0 (-4.5) mm thick or less. Androecium of various shape, in transverse section triquetrous or circular. *Whole of W. Malesia* 84

84a. Androecium in transverse section 3- or 4-angular. Anthers ± erect, for a large part mutually free, usually for c. 1/2-way or more. Lateral nerves raised above, except in *H. ridleyana* (with leaves small, and male perianth c. 1 mm diam.). Leaves not dotted beneath. Male perianth c. 1.5 (-2.0) mm diam. or less. Pedicel articulated at base. *Most of W. Malesia, not in Celebes, rare in the Philippines* 85

b. Androecium in transverse section either circular or ± ellipsoid, or subtriangular with rounded angles, neither triquetrous nor quadrangular. Anthers ± curved, almost entirely connate; free apices c. 1/3 or less. Leaf, with the lateral nerves raised above, or level, or sunken; with or without blackish dots (lens!) beneath, the dots not to be confused with a much finer punctation present or not. Male perianth c. (1.3-) 1.5 mm diam. or more.

Pedicel at base articulated or not 92

85a. Leaves small, 5-16 cm long. Lateral nerves ± level or sunken above; midrib either little raised, or flat, or sunken 86

b. Leaves small or large, 5-28 cm long. Midrib and lateral nerves raised above 87

86a. Anthers 4-6. Nerves above usually indistinct or invisible. Leaf apex acute or acute-acuminate. Twigs at apex and inflorescence rather glabrescent. *Malaya, Borneo* .... **H. ridleyana**[74]

b. Anthers 9 or 10. Nerves flat or but little raised above, well visible. Leaf apex blunt. Twig apex rather late glabrescent, inflorescence with persistent tomentum. *Sarawak* .... **H. obtusa**[75]

87a. Flower not seen. Leaves early glabrescent, also on the midrib; leaf apex long acute-acuminate. Bark of twigs rather smooth, lower down cracking longitudinally. *Brunei* .... **H. disticha**[76]

b. Leaves early glabrescent, the midrib beneath early or later glabrescent; leaf apex acute-acuminate. Bark of twigs striate, lower down coarsely striate or finely cracking 88

88a. Twigs slender, towards apex 1-2 (-4) mm diam. Leaves rather small, 7-18 cm long, thinly membranous to subchartaceous; petiole slender, diam. 1-1.5 (-2.0) mm. Male inflorescence delicate, up to 9 cm long. Mature male perianth small, diam. c. 1.0 mm 89

b. Twigs towards apex 1-5 (-8) mm diam. Leaves of various size, chartaceous to coriaceous; petiole 1.5-4 (-8) mm diam. Male inflorescence up to 15(-20) cm long. Male perianth 1.0-2.0 mm diam 90

89a. Leaf bud with tomentum composed of hairs c. (0.1-) 0.2 mm long; twigs at apex and leaves glabrous; inflorescence with rather sparse tomentum of stellate hairs c. 0.2 mm long, glabrescent. Leaves drying to a greyish tinge. Mature male perianth in bud rather short-pear-shaped, shortly tapering into the pedicel .... **H. tenuifolia**[77]

b. Leaf bud, apical portion of twig, petiole and inflorescence with woolly tomentum of stellate-dendroid hairs c. (0.2-) 0.5 mm long; leaves with rather persisting hairs on midrib beneath, drying olivaceous. Mature male perianth in bud globose or depressed-globose .... **H. macilenta**[78]

90a. Plant robust, twigs stout, leaves coarse, the midrib broad above, at the transition to the petiole at least 3 mm wide. Male inflorescence 10-20 cm long. *Borneo: forests on poor soil, including sand and peat* .... **H. laticostata**[79]

b. Plant generally less robust; leaves various, the midrib above towards the insertion of the petiole less than 3 mm wide. Male inflorescence up to 15 cm long. *Forests, on poor or rich soil* 91

91a. Leaves 16-28 cm long; nerves 16-19 pairs, very prominent above; leaf base ± rounded or short-attenuate. *Borneo: Sarawak* .... **H. nervosa**[80]

b. Leaves 7-28 cm long, base short- to long-attenuate; nerves 6-16 pairs, raised to various degree above. On drying, colour of leaves above and below usually much contrasting, generally more so than in the related species. (A variable species, especially the fruits.) *Malaya, Sumatra, whole of Borneo, Philippines (Mindanao)* .... **H. polyspherula**[81]

92a. Leaf bud, apical portion of twig, and inflorescence with tomentum of hairs c. 0.2 mm long or more; hairs 0.1-0.4 mm long in *H. punctata* 93

b. Leaf bud, apical portion of twig, and inflorescence with tomentum of hairs less than 0.2 mm long; hairs usually c. 0.1 mm long or less 100

93a. Mature male perianth in bud ellipsoid, c. 2.5-3.5 mm long; androecium longer than broad. Leaves generally drying thick and brittle, tip bluntish. Lower leaf surface usually with conspicuous pale golden hair scars (lens!) ... . **H. endertii**[83]

b. Mature male perianth globose or subglobose; androecium not longer than broad 94

94a. Mature male perianth in bud c. 2.5-3.0 mm diam. (or c. 1.5 mm in a deviating specimen *Hallier 624* from *W. Borneo,* see the notes), at anthesis cleft to c. 4/5. *Sumatra* .... **H. valida**[84]

b. Mature male perianth in bud c. (1.0-) 1.2-2.5 mm diam., at anthesis cleft to 1/3-2/3 (-3/4). *Malaya, Borneo* 95

95a. Pedicel in male flowers not articulated at the base. Leaves without blackish dots or streaks below (lens!). Lateral nerves largely raised above. On drying, colour of upper and lower leaf surface not much contrasting 96

b. Pedicel at base articulated. Leaves with scattered blackish brown dots and stripes beneath. Lateral nerves above largely flat or sunken, rarely faintly or partially raised. Upper leaf surface drying greenish or blackish brown, usually rather contrasting in colour with the cinnamon- or chocolate-coloured lower surface .... **H. borneensis**[85]

96a. Male perianth c. 2.0-2.5 mm diam. Androecium sessile, ± saucer-shaped and broadly hollow. Leaves 20-45 cm long. *Lowland forest* .... **H. fragillima**[86]

b. Male perianth c. (1.0-) 1.4-2.2 mm diam. Androecium ± globose or depressed-globose, with the apical cavity small, concealed by the overhanging anther tips. Leaves 4-35 cm long. *Montane forest at 800-200 m* 97

97a. Androecium borne by a distinct slender androphore c. 0.3-0.8 mm long, not hidden by the anthers. Leaves membranous, 9-18 cm long, drying dark brown, leaf tip acute-acuminate .... **H. androphora**[87]

b. Androecium sessile, with the androphore absent or short, up to 0.5 mm, largely or completely hidden by the anthers 98

98a. Leaves chartaceous or membranous, to c. 35 cm long, drying olivaceous to brown above; leaf tip acute-acuminate. Male inflorescence large, to c. 20 cm long. *Borneo* .... **H. amplomontana**[88]

b. Leaves coriaceous, 4-14 cm long, drying olivaceous brown or blackish above; leaf tip obtuse to subacute. Male inflorescence 4-16 cm long 99

99a. Leaves drying dark brown to blackish, lower surface not punctate. *Borneo* .... **H. montana**[89]

b. Leaves drying olivaceous brown, lower surface densely brown-black punctate (lens!). *Malaya* .... **H. punctata**[90]

100a. Leaves dotted or coarsely punctate beneath; dots brown to blackish, or rarely pale brown, ± regularly spaced and equal-sized, of non-traumatic origin 107

b. Leaves not dotted beneath (dotting should not be confused with generally smaller, irregularly spaced, blackish mottles or points, or with dots of various sizes of traumatic origin) 101

101a. Male perianth ± ellipsoid; androecium ± obovoid, the anthers with their apical portions deeply inflexed into a deep apical cavity. *New Guinea* .... **H. sepikensis**[18]

b. Male perianth and androecium of various shapes; the anthers ± straight or curved, at apex not inflexed. *W. and E. Malesia, not in New Guinea* 102

102a. Male perianth coriaceous; valves thick, towards the base (0.3-) 0.4-1.0 mm thick. Androecium ellipsoid-obovoid, longer than broad 105

b. Male perianth thinner, valves at base c. 0.2-0.3 mm thick. Androecium subglobose or broadly ellipsoid or broadly obovoid, not or but little longer than broad. Androphore narrow, and only c. 0.2 mm long. Leaves membranous to chartaceous 103

103a. Male pedicel (1-) 1.5-2 mm long, about as long as the perianth. *Malaya, Borneo* 104

b. Male pedicel shorter than the perianth, c. 0.5 mm long. *Celebes, Philippines* .... **H. costulata**[91]

104a. Male perianth at anthesis cleft to c. 1/2-way .... **H. subalpina**[92]

b. Male perianth at anthesis cleft to c. 2/3-4/5 .... **H. obscura**[93]

105a. Bark of twigs not flaking. Leaves membranous 106

b. Bark of twigs flaking or not. Leaves coriaceous. Male pedicel at base not articulated. Anthers 5-8. Androphore rather broad, tapering, (0.1-) 0.2-0.3 mm long. *Kerangas forest, mountain forest; 800-1200 m alt.; Sarawak, Sabah* .... **H. xanthina**[94]

106a. Pedicel of male flowers articulate at base. Anthers 7-9. Androphore rather broad and tapering, 0.2-0.5 mm long. *Forest, 0-1000 m; Malaya; Sumatra* .... **H. majuscula**[95]

b. Pedicel at base not articulated. Anthers 5 or 6. Androphore narrow, 0.1-0.2 mm long, hidden by the anthers. *Forest, c. 100-450 m; C. Celebes* .... **H. coriacea**[96]

107a. Twigs moderately stout, towards the apex c. 2.5-3 (-4) mm diam. Leaves (8-) 12 cm long or more. Male perianth globose or subglobose, diam. c. 1.5-4.2 mm 108

b. Twigs slender, diam. towards the apex 1.5-2.0 mm. Leaves c. 5-12 cm long. Perianth ± ellipsoid to globose, 1.2-1.8 mm long .... **H. penangiana**[97]

108a. Male perianth at anthesis cleft to c. 3/4-4/5. Anthers 7-11 109

b. Male perianth at anthesis cleft to c. 1/3-2/3. Anthers 9-20. *Sumatra, Java* 110

109a. Anthers 7-9. Dry fruits c. 4-5 cm long, pericarp 10-20 mm thick. *N. Sumatra, Malaya, Borneo* .... **H. punctatifolia**[98]

b. Anthers c. 11. Dry fruits c. 2 cm long, pericarp c. 1.5 mm thick. *Malaya* .... **H. punctata**[90]

110a. Male perianth 3.0-4.2 mm diam.; anthers 15-20 .... **H. macrothyrsa**[99]

b. Male perianth c. 1.5-2.5 mm diam.; anthers 9-15. *A variable species with 3 varieties* .... **H. glabra**[100]

(2-7) REGIONAL KEYS TO THE SPECIES FOR FEMALE FLOWERING AND FRUITING SPECIMENS

based partly on vegetative characters and distribution

(2) CEYLON, CONTINENTAL SE. ASIA (INCL. PENINSULAR THAILAND, EXCL. MALAYSIA AND SINGAPORE), AND ANDAMAN SL.

1a. Ovary pubescent. Fruit pubescent at least at the base, or in *H. kingii* glabrescent 2

b. Ovary glabrous. Fruit glabrous 4

2a. Female perianth pubescent at least at the base. Leaves glabrous or late-glabrescent below, or with vestigial tomentum on the midrib. Fruit c. 2.5 cm long or more 3

b. Perianth glabrous. Leaves with persistent tomentum below. Fruit c. 1.5-2.0 cm long, glabrescent but with vestigial tomentum towards the base; perianth not persisting. *S. penins. Thailand* .... **H. tomentosa**[61]

3a. Perianth pubescent at base. Fruit ellipsoid, c. 2.5-4 cm long, wholly pubescent; perianth not persisting. *Ceylon* .... **H. iryaghedhi**[1]

b. Perianth wholly pubescent, or partly glabrescent. Fruit ± ellipsoid-oblong, (3-) 4-6 cm long, glabrescent, with the perianth persisting. *NE. India to S. China* .... **H. kingii**[2]

4a. Twigs towards apex either subterete, or usually ± flattened or angular, and lined or ridged from petiole to petiole. Phyllotaxis distichous 5

b. Twigs terete, not lined. Leaves distichous or in 3-5 rows along the twigs. Fruit ellipsoid 6

5a. Twigs lined. Perianth 2-valved. Leaves often with irregularly shaped whitish marks or blotches here and there. Fruit globose, c. 1.5-2.0 cm diam., pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Twigs more prominently lined or ridged, usually distinctly angular in section. Leaves without whitish marks. Fruit ellipsoid, c. 2.0-3.0 cm long, pericarp 1.5-4 mm thick; seed ellipsoid. *Not coastal penins. Thailand* .... **H. brachiata**[72]

6a. Bark of twigs drying pale, grey-brown, contrasting with the blackish colour of the dried petiole . Fruit drying blackish, c. 3.0-5.5 cm long; pericarp c. 5-15 mm thick. Perianth 3- (or 4-) valved. *Penins. Thailand* .... **H. sparsa**[50]

b. Twigs drying brown, not much contrasting with the petiole. Fruit usually (dark) brown, c. 1.5-3.5 cm long; pericarp c. 1-2.5 mm thick. Perianth 2- or 3-valved 7

7a. Fruit c. 1.5 cm long. Leaves distichous.C. *Vietnam (Annam)* **H. longiflora**[3]

b. Fruit generally larger, c. 1.8-3.4 cm long. Leaves distichous or dispersed .. 8

8a. Leaves in 3-5 rows along the twigs. Tomentum of leaf bud composed of hairs c. 0.1-0.3 mm long. Male perianth c. 1.0-1.5 mm diam. *Indo-China*

.... **H. thorelii**[4]

b. Leaves either distichous or dispersed in 3 or 5 rows. Tomentum of leaf bud composed of hairs either c. 0.1 mm long or c. 0.5-1.0 mm long. Male perianth c. 1.5-2.3 mm diam. *NE. India, S. China (Yunnan), Indo-China, Andaman Isl.* .... **H. amygdalina**[5]

(3) MALAYA, SINGAPORE

1a. Female perianth at base pubescent; ovary and fruit pubescent. Fruit ellipsoid, c. 2.5-4 cm long. Flowers in dense clusters and strongly fragrant in male specimens. *Originating from Ceylon, cultivated in Penang, Singapore* .... **H. iryaghedhi**[7]

b. Perianth glabrous 2

2a. Perianth 2-valved. Ovary glabrous 3

b. Perianth 3- (or 4-) valved. Ovary glabrous or pubescent 5

3a. Twigs usually shallowly ridged or lined from petiole to petiole. Leaves membranous, often with irregularly shaped whitish marks or blotches here and there. Fruit globose, c. 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Twigs not lined. Leaves without pale blotches. Fruit and seed ellipsoid 4

4a. Leaves membranous, glabrous beneath, not brown dotted. *Gardens' Jungle, Singapore* .... **H. parviflora**[10]

b. Leaves coriaceous, pubescent below and with regularly spaced, small, brown to blackish dots (lens!). *Kerangas forest, peat swamp forest* ....**H. crassifolia**[68]

5a. Leaves on lower surface with ± regularly spaced, dark brown or blackish dots being cork warts originating from hair scars; dots not to be confused with usually smaller dark punctation of different origin, present or not (lens!) 19

b. Leaves not dotted beneath 6

6a. Leaves with persistent tomentum beneath 7

b. Leaves glabrous or glabrescent beneath 11

7a. Ovary pubescent. Fruit pubescent or at least with vestigial tomentum near the base; perianth not persisting under the fruit .... **H. tomentosa**[61]

b. Ovary glabrous or only with some incidental minute hairs. Fruit glabrous, the perianth (at least at first) persisting 8

8a. Hairs on lower (and upper) leaf surface harsh, with hardened hair-bases, in older leaves rendering the surface scabrous. Fruit c. 1.0-1.4 cm long .... **H. grandis**[56]

b. Leaves not scabrous. Fruit c. 2 cm or more long 9

9a. Twigs of moderate habit, towards the apex c. 3-5 mm diam. Tomentum of leaf bud and the very twig apex composed of hairs c. 0.2-0.3 mm long. Leaves drying dull above, 13-21 cm long. Fruit c. 2.2-2.4 (-3.0) cm long .... **H. fulva**[53]

b. Twigs stouter, diam. towards apex c. 5-10 mm. Tomentum with hairs c. 0.5 mm long or more. Leaves c. 20-40 (-70) cm long 10

10a. Tomentum of leaf bud, twig apex and lower leaf surface with hairs c. 0.5-1.0 mm long, rather stiff, rust-coloured. Fruit c. 3.8-5.5 cm long .... **H. superba**[54]

b. Tomentum composed of woolly hairs c. 1.0-2.0 mm long, yellow-brown or pale brown. Fruit c. 3 cm long .... **H. flocculosa**[59]

11a. Bark of twigs drying rather pale, pale brown or yellowish brown, or straw, contrasting with the blackish colour of the dried petiole. Phyllotaxis either distichous, or the leaves in 3-5 rows along the twigs 12

b. Twigs drying brown, the colour not considerably contrasting with the petiole. Leaves distichous 13

12a. Leaves distichous or in 3 rows. Fruit c. 2.5-3.5 cm long, with the perianth persisting. Pedicel articulated at base (this character best seen in male flowers) .... **H. sucosa** subsp. **sucosa**[48a]

b. Leaves in 3-5 rows along the twigs. Fruit c. 3-5.5 cm long, the perianth not persisting. Pedicel at base not articulated .... **H. sparsa**[50]

13a. Leaves drying very dull above because of finely wrinkled surface; nerves flat or sunken. Fruit usually with persistent perianth .... **H. fulva**[53]

b. Leaves above not particularly dull, not finely wrinkled; nerves flat or raised. Perianth not persisting under the fruit 14

14a. Lateral nerves flat or but faintly raised above 15

b. Lateral nerves on upper leaf surface distinctly raised. Pedicel at base articulated (this character best seen in male flowers) 16

15a. Tomentum of leaf bud composed of hairs c. 0.1 mm long. Twigs towards the apex c. 2.5-5 mm diam. Leaves 15-27 cm long. Pedicel at base not articulated .... **H. subalpina** subsp. **subalpina**[92a]

b. Tomentum of leaf bud with hairs c. 0.2-0.4 mm long. Twigs slender, towards the apex c 1.5-3.5 mm diam. Leaves c. 5-15 cm long. Pedicel at base articulated .... **H. ridleyana**[74]

16a. Tomentum of leaf bud composed of hairs c. 0.1 mm long. Midrib beneath early glabrescent. Fruit c. 4.5-6.5 cm long, usually with thick pericarp .... **H. majuscula**[95]

b. Tomentum of leaf bud with hairs c. 0.1 mm long or usually much longer. Midrib beneath often rather late glabrescent. Fruit c. 2-4 cm long, pericarp c. 2-5 (-7) mm thick 17

17a. Twigs ± angular by lines or low ridges from petiole to petiole. Fruit c. 2-3 (-4.0) cm long .... **H. brachiata**[72]

b. Twigs terete, neither lined nor ridged 18

18a. Twigs towards the apex c. 2-5 mm diam. Leaves usually chartaceous. Fruit 1.9-3.5 cm long .... **H. polyspherula**[81]

b. Twigs more delicate, towards the apex c. 1-3 mm diam. Leaves membranous. Fruit c. 2.3-2.4 cm long .... **H. macilenta**[78]

19a. Leaves usually with persistent tomentum beneath 20

b. Leaves glabrous or glabrescent beneath 21

20a. Lower leaf surface with small dots and dashes; pubescent, sometimes late glabrescent. Ovary glabrous. Fruit c. 4-6 cm long, glabrous, with the perianth usually persistent .... **H. wallichii**[57]

b. Lower leaf surface always pubescent, provided with only dots, not with streaks. Ovary pubescent. Fruit c. 1.6-1.8 cm long, shaggy-hairy, the perianth not persistent .... **H. pulcherrima**[58]

21a. Twigs delicate, towards the apex c. 1.5-2 mm diam. Fruit c. 1.1-2.0 cm long .... **H. penangiana**[97]

b. Twigs somewhat stouter, diam. towards apex c. 2.5-5 mm. Fruit c. 2 cm long or more 22

22a. Leaves coriaceous, tip blunt or subacute. Fruit c. 2-2.3 cm long, pericarp thin. *A mountain species of central Malaya* .... **H. punctata**[90]

b. Leaves membranous, tip acute-acuminate. Fruit 4.5-8 cm long, pericarp 10-20 mm thick. *Forests up to c. 1100 m. alt.* .... **H. punctatifolia**[98]

(4) SUMATRA, JAVA

1a. Female perianth at base pubescent; ovary pubescent. Fruit ellipsoid, c. 2.5-4 cm long, pubescent. *Male specimens with the flowers in dense clusters, strongly fragrant. Cultivated, originating from Ceylon* .... **H. iryaghedhi**[1]

b. Perianth glabrous 2

2a. Leaves membranous, often with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit globose, c. 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Leaves of various consistency, usually not white-blotched. Fruit ellipsoid; seed ellipsoid. *Plant coastal or not* 3

3a. Perianth 2-valved. Lower leaf surface with ± regularly scattered brown to blackish dots, originating from hair scars; dots not to be confused with usually smaller punctation of different origin (lens!) 4

b. Perianth 3-(or 4-) valved. Lower leaf surface dotted or not 5

4a. Leaves coriaceous, 10-20 (-28) cm long, finely pubescent on the lower surface. Twigs towards apex 2-6 mm diam. Fruit c. 1.5-2.2 cm long, with persistent perianth. *Peat swamp forest* .... **H. crassifolia**[68]

b. Leaves membranous or thinly chartaceous, 5-12 cm long, glabrous beneath. Twigs c. 1.5-2 mm diam. Fruits 1-2 cm long; perianth not persisting. *Mixed forest* .... **H. penangiana**[97]

5a. Ovary and fruit (at least at base) pubescent. Lower leaf surface with persistent tomentum 6

b. Ovary and fruit glabrous. Lower leaf surface glabrous or pubescent 7

6a. Twigs towards the apex c. 2-5 mm diam. Leaves c. 9-27 cm long, lower surface without dots. Fruit with hairs c. 0.5 mm long or less. *Thailand,* *Malaya; specimens from Sumatra not seen* .... **H. tomentosa**[61]

b. Twigs stouter, towards apex 5-8 mm diam. Leaves c. 20-36 cm long, lower surface with regularly scattered brown to blackish dots (lens!). Fruit with hairs c. 2 mm long .... **H. pulcherrima**[58]

7a. Lower leaf surface with more or less regularly spaced brown to blackish dots (lens!). Lateral nerves in upper surface generally flat or sunken 21

b. Lower leaf surface without dots. Nerves either raised, or flat to sunken ... 8

8a. Lower leaf surface with persistent tomentum. Fruit with persistent perianth 9

b. Lower leaf surface glabrous or glabrescent. Fruit with perianth persistent or not 11

9a. Hairs harsh, the hair scars making the lower surface of older leaves scabrous. Fruit 1-1.4 cm long .... **H. grandis**[56]

b. Older leaves not scabrous beneath 10

10a. Plant stout, twigs towards apex c. 5-8 mm diam.; leaves c. 20-40 (-70) cm long. Tomentum of leaf bud with hairs c. 0.5-1.0 mm. Fruit 3.8-5.5 cm long .... **H. superba**[54]

b. Twigs towards the apex c. 3-5 mm diam.; leaves 13-21 cm long. Hairs on leaf bud c. 0.2-0.3 mm long. Fruit c. 2-3 cm long .... **H. fulva**[53]

11a. Lateral nerves in upper leaf surface flat or sunken or but faintly raised. On drying, colour of lower leaf surface generally greyish brown, not contrasting with that of the upper surface 12

b. Lateral nerves distinctly raised above. On drying, colour of the lower leaf surface bright brown or chocolate, usually much contrasting with the upper surface 16

12a. Twigs delicate, towards the apex c. 1.5-3 mm diam.; leaf bud, the very twig apex and young inflorescence woolly-pubescent with hairs c. 0.3-0.7 mm. Leaves 5-9 cm long. *Female flower and fruit not known* ...... **H. triandra**[51]

b. Twigs generally stouter, towards apex (2-) 3-10 mm diam.; hairs of leaf bud and inflorescence c. 0.1-0.3 mm long. Leaves more than 10 cm long 13

13a. Leaves distichous, drying dull because of minutely wrinkled upper surface. Bark of twigs straw-colour or brown 14

b. Leaves distichous or arranged along the twigs in 3-5 rows; not particularly dull from drying, upper surface not finely wrinkled. Bark of twigs pale, grey-brown or straw, contrasting with the blackish colour of the dried petiole 15

14a. Leaves elliptic-oblong to oblong, drying olivaceous to brown above. Stem grey-brown, not conspicuously contrasting with the colour of the dried petiole. Fruit drying brown, c. 2.2-3 cm long, perianth persistent .... **H. fulva**[53]

b. Leaves elliptic-oblong to lanceolate, drying to a rather dark olivaceous colour above. Stem pale ± yellowish-brown, rather contrasting with the petiole. Fruit drying blackish, c. 1.5 cm long, the perianth not persisting .... **H. tristis**[52]

15a. Leaves distichous or in 3 rows. Fruit c. 2.5-3.5 cm long, with the perianth persisting. Pedicel articulated at base (this character best seen in male flowers) .... **H. sucosa** subsp. **sucosa**[48a]

b. Leaves in 3-5 rows along the twigs. Fruit c. 3-5.5 cm long, the perianth not persisting. Pedicel at base not articulated .... **H. sparsa**[50]

16a. Perianth 4-valved. Pedicel at base not articulate (this character best seen in male flowers). (Female perianth known only from the remnants persisting under young fruits). Fruit c. 8-9 cm long .... **H. valida**[84]

b. Perianth generally 3-valved. Pedicel articulate at base. Fruit up to 6.5 cm long 17

17a. Twigs angular or subterete, provided with lines or ridges from petiole to petiole 18

b. Twigs terete or but faintly angular, neither lined nor ridged 19

18a. Perianth pubescent (known only from male flowers). Fruit c. 5-6 cm long. *N. Sumatra* .... **H. hirtiflora**[71]

b. Perianth glabrous. Fruit c. 2-4 cm long .... **H. brachiata**[72]

19a. Twigs delicate, towards the apex c. 1-3 mm diam. Leaves membranous, midrib beneath late-glabrescent. Fruit c. 2.3-2.4 cm long .... **H. macilenta**[78]

b. Twigs generally stouter, towards the apex c. 2-5 mm diam. Leaves usually chartaceous. Fruit 1.9-6.5 cm long 20

20a. Tomentum of leaf bud and inflorescence composed of hairs c. 0.1-0.2 mm long. Midrib beneath early glabrescent. Fruit c. 4.5-6.5 cm long .... **H. majuscula**[95]

b. Tomentum with hairs 0.1-0.6 mm long. Midrib often late-glabrescent. Fruit 1.9-3.5 cm long. *A variable species* .... **H. polyspherula**[81]

21a. Lower leaf surface usually with persistent tomentum (sometimes glabrescent), and with small scattered dots and streaks (lens!). Twigs conspicuously hollow. Fruit c. 4-6 cm long, the perianth generally persistent .... **H. wallichii**[57]

b. Leaves beneath glabrous or glabrescent; dotted, not streaked. Twigs not conspicuously hollow. Fruit various 22

22a. Bark of twigs pale, greyish to straw, much contrasting with the blackish colour of dried petiole. Phyllotaxis dispersed, with the leaves in 3-5 rows. *Female flower and fruit not known. N. Aceh, at c. 1300 m* .... **H. atjehensis**[47]

b. Bark of twigs brown, not contrasting in colour with the petiole. Leaves distichous, or in 3 rows in *H. glabra, p.p.* 23

23a. Fruit large, (4.5-) 5-8 cm long, with thick pericarp .... **H. punctatifolia**[98]

b. Fruit c. 1-2.5 cm long, pericarp much thinner 24

24a. Twigs slender, diam. towards the apex c. 1.5-2 mm. Leaves 5-12 cm long. Fruit c. 1.1-2.0 cm long .... **H. penangiana**[97]

b. Twigs generally stouter, towards apex c. 2.5-4 (-6) mm diam. Leaves (8-) 12 cm long or more. Fruit c. 1.8-2.5 cm long 25

25a. Leaves distichous. *C. & N. Sumatra* .... **H. macrothyrsa**[99]

b. Leaves distichous or dispersed in 3 rows. *Java, S. Sumatra, Mentawai Isls. north to Simeuluë Isl.* .... **H. glabra**[100]

(5) BORNEO

1a. Leaves membranous, usually with irregularly shaped, whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit globose, 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Leaves various, usually not white-blotched. Fruit subglobose or ellipsoid; seed ellipsoid. *Plant coastal or not* 2

2a. Perianth 2-valved 3

b. Perianth predominantly 3- (or 4-) valved 5

3a. Leaves coriaceous, the lower surface usually densely short-pubescent and with scattered dots and streaks (lens!). Twigs grey-brown, not much contrasting with the colour of the dried petioles .... **H. crassifolia**[68]

b. Leaves membranous, the lower surface glabrous and without dots. Twigs greyish or straw, rather contrasting with the blackish colour of the dried petiole 4

4a. Female inflorescence ± spike-like, 5-10 cm long. Perianth persistent under the fruit (always?). *SE. Sabah* .... **H. sterilis**[70]

b. Female inflorescence ramified, 1-2 cm long. Perianth not persisting under the fruit. *Sabah, E. & S. Kalimantan* .... **H. sucosa** subsp. **bifissa**[48h]

5a. Leaves in 3 or more rows along the twigs 6

b. Leaves distichous 8

6a. Leaves generally bunched towards the top of the twigs. Petiole proportionally long and slender, 25-50 mm long .... **H. sabulosa**[46]

b. Leaves not bunched. Petiole proportionally shorter 7

7a. Leaves 10-30 cm long. Twigs pale, greyish or straw, contrasting with the blackish colour of the dried petioles. Female perianth c. 2.5-3 mm long. Fruit 1.5-4 cm long .... **H. pallidicaula**[49]

b. Leaves 20-45 cm. Twigs brown, not contrasting. Female perianth c. 4-5 mm long. Fruits 6-8 cm long .... **H. fragillima**[86]

8a. Twigs in apical portion angular, i.e., distinctly lined or ridged from petiole to petiole .... **H. brachiata**[72]

b Twigs terete or but faintly angular, neither distinctly lined nor ridged 9

9a. Leaves on lower surface with persistent tomentum (sometimes largely glabrescent in *H. wallichii*) 10

b. Leaves beneath glabrous or early glabrescent (midrib sometimes late-glabrescent) 19

10a. Plant stout; leaves large, c. 50 cm long, petiole c. 3 mm long only. *Lowland Sarawak* .... **H. sessilifolia**[55]

b. Plants various in habit, petiole proportionally much longer 11

11a. Older leaves on upper and lower surface with scabrous hair scars. Fruit c. 1.0-1.4 cm long .... **H. grandis**[56]

b. Leaves not scabrous. Fruits generally larger 12

12a. Leaves on lower surface with scattered dark brown or blackish dots and/or streaks (lens!) .... **H. wallichii**[57]

b. Lower leaf surface without dots or streaks 13

13a. Perianth with persistent tomentum; perianth not persistent under mature fruit .... **H. motleyi**[60]

b. Perianth glabrous or early glabrescent, persistent under the fruit or not .. 14

14a. Leaves distinctly bullate due to deep-lying veins and with ± revolute leaf-margin. *Female flower and fruit not known* .... **H. reticulata**[67]

b. Leaves not distinctly bullate 15

15a. Ovary pubescent; fruit sometimes pubescent only towards the base 16

b. Ovary and fruit glabrous 17

16a. Twigs moderately stout, 3.5-5 mm diam. towards apex. Leaves 10-23 cm long; nerves 11-16 pairs. Fruit largely glabrescent; perianth not persisting .... **H. rufo-lanata**[65]

b. Twigs stout, 4-7 mm diam. Leaves 18-45 cm long, nerves 18-25 pairs. Fruit pubescent, with persisting perianth .... **H. splendida**[64]

17a. Twigs rather stout, towards the apex 3-6 mm diam. Leaves 18-35 cm long; nerves 17-20 pairs. Fruit 2.3-2.7 cm long .... **H. affinis**[66]

b. Twigs slender, 1.5-3 mm diam., leaves generally smaller. Fruit c. 1-1.5 cm long 18

18a. Leaves membranous; nerves 14-17 pairs .... **H. gracilis**[62]

b. Leaves thinly chartaceous; nerves 5-9 pairs .... **H. paucinervis**[63]

19a. Lower leaf surface with ± regularly spaced, brown to blackish dots or with dots and striae (lens!); dots originating from hair scars, not to be confused with usually smaller and irregularly spaced dots or punctation of different origin 20

b. Lower leaf surface without dots (sometimes with enlarged hair scars) 23

20a. Tomentum of leaf bud, the twig apex and young inflorescences composed of hairs c. 0.2 mm long or more 21

b. Tomentum very short, with hairs c. 0.1 mm long or less 22

21a. Twigs conspicuously hollow. Leaves on lower surface often with persistent tomentum. Pedicel at base not articulate. Perianth generally persistent under the fruit .... **H. wallichii**[57]

b. Twigs not conspicuously hollow. Lower leaf surface glabrescent. Pedicel at base articulate. Perianth not persisting under the fruit .... **H. borneensis**[85]

22a. Twigs rather delicate, diam. towards the apex c. 1.5-2 mm. Leaves c. 5-12 cm long; nerves 8-11 pairs. Fruit 1.1-2.0 cm long, pericarp thin .... **H. penangiana**[97]

b. Plant stouter, diam. of twigs towards apex c. 2.5-4 mm. Leaves 9-21 cm long, nerves 11-16 pairs. Fruit 4.5-8 cm long, with thick pericarp .... **H. punctatifolia**[98]

23a. Bark of twigs drying to a pale colour, grey-brown or grey-yellowish, contrasting with the dark brown or blackish colour of the drying petioles 24

b. Twigs drying brown, not or but contrasting little with the petioles 26

24a. Leaves membranous, drying brown or blackish brown, the lower surface somewhat paler. Perianth persisting under the fruit. *Mixed forest* .... **H. pallidicaula**[49]

b. Leaves usually chartaceous, drying bright brown or olivaceous, lower surface usually brown or chocolate. Perianth not persisting under the fruit 25

25a. Twigs slender, diam. towards the apex c. 2-3 mm. Leaves 7-16 cm long, on lower surface bright brown or chocolate, contrasting well with the grey-olivaceous upper surface. Fruit 1.8-2.7 cm long. *Kerangas forest, peat-forest* .... **H. oligocarpa**[82]

b. Twigs stouter, c. 3-10 mm diam. Leaves 13-35 cm long, the lower surface not conspicuously contrasting in colour. Fruit c. 1.5-2.0 cm long 28

26a. Tomentum of leaf bud and immature inflorescence very short, with hairs c. 0.1 mm long or less. Lateral nerves on upper leaf surface flat or sunken, or but little raised 27

b. Tomentum composed of hairs c. 0.1 mm long or more; lateral nerves raised or not above; if hairs only c. 0.1 mm long, then the lateral nerves, at least in the lower half, distinctly raised above 31

27a. Leaves on upper side dull, i.e. on drying the surface finely wrinkling 28

b. Leaves above not conspicuously dull, surface not finely wrinkling 29

28a. Leaves elliptic-oblong to oblong. Fruit c. 1.6-2.0 cm long. *Heath forest, peat swamp forest* .... **H. carnosa**[69]

b. Leaves elliptic-oblong to lanceolate. Fruit c. 1.5 cm long. *Mixed forest* .... **H tristis**[52]

29a. *Lowland species, up to c. 700 m alt.* Leaves membranous. Fruit 5-5.5 cm long, pericarp thick .... **H. obscura**[93]

b. *Mountainous species; c. 800-1800 m alt.* Leaves membranous or coriaceous. Fruit generally smaller 30

30a. Leaves on lower surface without distinct large hair-scars (lens!). Fruit 3-5 cm long .... **H. subalpina** subsp. **kinabaluensis**[92b]

b. Leaves on lower surface usually with distinct enlarged hair-scars. Fruit (immature) c. 1-1.5 cm long .... **H. xanthina**[94]

31a. Pedicels at base not articulate (this character best seen in male flowers).

Fruit with persisting perianth or not 32

b. Pedicel at base articulate. Perianth not persisting under the fruit 37

32a. Leaves generally large, 15-45 cm long. Fruit c. 6 cm long or more; perianth persisting for a long time under it. *Lowland or mountainous forest* 33

b. Leaves generally smaller, c. 5-20 cm long. Fruit c. 2-4 cm long; perianth not persisting. *Montane forest at 800-2000 m alt.* 35

33a. Nerves 11-22 pairs. *Sabah, Mt. Kinabalu at 1000-1500 m* .... **H. amplomontana**[88]

b. Nerves c. 20-30 pairs. *Forests up to c. 1000 m. alt* 34

34a. Female flower and fruit not known. *Hallier 624, Mt. Damoes, W. Kalimantan; apparently an undescribed species close to H. valida, see notes* .... **aff. H. valida**[84]

b. Female perianth 4-5 mm long. Fruit c. 6-8 cm long, pericarp 10-20 mm thick .... **H. fragillima**[86]

35a. Leaves membranous, apex acute-acuminate. Fruit 2.4-3 cm long .... **H. androphora**[87]

b. Leaves chartaceous to coriaceous, apex rounded to (sub) acute, not acute-acuminate 36

36a. Leaves chartaceous to coriaceous, lower surface without large hair scars (lens!). Female perianth c. 2 mm long. Fruit c. 2.0-2.7 cm long .... **H. montana**[89]

b. Leaves usually strongly coriaceous, usually with large and distinct hair scars on lower surface. Female perianth c. 2.5-3 mm long. Fruit c. 3-4 cm long .... **H. endertii**[83]

37a. Female inflorescence, female flower and fruit not known. Male inflorescence very stout, the rhachis towards the base 5-8 mm diam. *W. Kalimantan* .... **H. pachyrachis**[73]

b. Male inflorescence less stout 38

38a. Midrib on upper leaf surface towards the transition to the petiole c. 3 mm broad or more .... **H. laticostata**[79]

b. Midrib at base narrower 39

39a. Leaves 16-28 cm long, base short-attenuate to rounded; nerves 16-19 pairs. *Sarawak* .... **H. nervosa**[80]

b. Leaves 5-28 cm long, base either rounded or short- or long-attenuate; nerves c. 5-15 pairs 40

40a. Lateral nerves on upper leaf surface sunken or flattish, or but slightly raised 41

b. Lateral nerves distinctly raised above 42

41a. Leaf apex rounded. Fruit not seen .... **H. obtusa**[75]

b. Leaf apex acute-acuminate. Fruit c. 1.5-2 cm long .... **H. ridleyana**[74]

42a. Tomentum of leaf bud and young inflorescence with hairs c. 0.1-0.2 mm long. Leaves drying dull, greyish-brown, the colours of the upper and lower surface not much contrasting. Fruit c. 1.7-2.0 cm long .... **H. tenuifolia**[77]

b Tomentum of leaf bud c. 0.2 mm long or more; or if c. 0.1 mm long, then the olivaceous to dark brown colour of the dried leaf above much contrasting with the cinnamon colour beneath 43

43a. Twigs delicate, towards the apex c. 1-3 mm diam. Leaves generally membranous, 10-18 (-27) cm long. Fruit c. 2.3-2.4 cm long .... **H. macilenta**[78]

b. Twigs generally stouter, towards apex c. 2-5 mm diam. Leaves chartaceous, of various size. Fruits of various size 44

44a. Twigs early glabrescent; older bark ± longitudinally cracking. Leaf apex long acute-acuminate. Fruit c. 2.8-3.2 cm long; pericarp hard-woody, 8-10 mm thick. *Brunei* .... **H. disticha**[76]

b. Twigs usually rather late glabrescent; older bark striate, not cracking. Leaf apex acute-acuminate, the acumen not conspicuously long. Fruit variable, 1.9-6 cm long. *Whole of Borneo* .... **H. polyspherula**[81]

(6) PHILIPPINES, CELEBES, MOLUCCAS

1a. Leaves membranous, usually with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit perfectly globose, 1.5-2.0 cm diam., glabrous; pericarp 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Leaves various, usually not white-blotched. Fruit subglobose or ellipsoid; seed usually ellipsoid. *Plant coastal or not* 2

2a. Perianth 3-valved. Ovary and fruit glabrous 3

b. Perianth 2-valved 5

3a. Tomentum of leaf bud and inflorescence with hairs c. 0.2-0.6 mm long. Pedicel at base articulated. Fruit c. 2.0 (-2.5) cm long. *Philippines: Mindanao* ....**H. polyspherula** var. **polyspherula**[81a]

b. Tomentum composed of hairs c. 0.1-0.2 mm long. Pedicel not articulated 4

4a. Fruit 3.5-7 cm long; dry pericarp 8-15 mm thick. Leaves ± membranous, drying olivaceous to brown, midrib glabrous above; leaves sometimes with whitish marks as in *H. irya*. *Philippines, Celebes* .... **H. costulata**[91]

b. Fruit c. 4 cm long, dry pericarp 3.5-8 mm thick. Leaves membranous to thinly coriaceous, drying brown; midrib towards the base in younger leaves pubescent above. *C. Celebes* .... **H. coriacea**[96]

5a. Plant stout; twigs towards apex 4-14 (-20) mm diam., leaves c. 20-45 cm long, petiole short, 2-7 mm long. Tomentum of leaf bud and inflorescence with hairs c. 0.3-1.0 (-1.5) mm long. Female perianth c. 3.5-5 mm long, glabrous; ovary glabrous. Fruit c. 3.5-5.5 cm long, glabrous .... **H. sylvestris**[19]

b. Plant generally less stout, petiole relatively longer. Tomentum composed of hairs up to 0.2 mm long. Female perianth c. 3.0 (-3.5) mm long or less. Fruit up to 3 cm long, in *H. lancifolia* up to 3.5 cm long 6

6a. Leaves ± chartaceous, oblong-lanceolate to lanceolate. Female perianth at anthesis cleft to c. 1/4; ovary pubescent. Fruit often ± pear-shaped, 2.5-3.5 cm long, early glabrescent; dry pericarp 4-8 mm thick. *Celebes* .... **H. lancifolia**[37]

b. Leaves of various consistency, generally broader, oblong to oblong-lanceolate. Female perianth at anthesis cleft to c. 1/3 or more. Fruit c. 1.0-3.0 cm long 7

7a. Ovary and fruit pubescent; hairs on fruit may be very small and inconspicuous and only remaining at the very base near the insertion of the stalk (lens!). Pericarp thick or thin 8

b. Ovary and fruit glabrous; dry pericarp thin, c. 1-2 mm. (Female flower and fruit not known in *H. samarensis*[14] and *H. aruana*[28]) 11

8a. Female perianth c. 2.5-3 mm long, at anthesis cleft to c. 1/3-1/2. Fruit (1.6-) 1.8-2.8 (-3.0) cm long; dry pericarp 2-3 mm thick .... **H. laevigata**[35]

b. Female flower not known. Fruit smaller, pericarp thinner 9

9a. Fruit 1.5-1.6 cm long, short-ellipsoid. (Male perianth transversely ellipsoid, at anthesis cleft to c. 2/3-4/5). Leaves 8-30 cm long, membranous to chartaceous; nerves flat, inconspicuous. Twigs terete, not ridged. *Talaud Isls. possibly Celebes* .... **H. talaudensis**[13]

b. Fruit smaller, c. 1.1-1.3 cm long 10

10a. Fruit subglobose. Twigs towards apex ± flattened, usually lined or lowly ridged from petiole to petiole. Leaves c. 12-25 cm long, membranous; nerves flat, inconspicuous. (Male perianth ± pear-shaped, cleft to c. 2/3). *Moluccas* .... **H. decalvata**[38]

b. Fruit short-ellipsoid. Twigs terete, not lined. Leaves 5-14 cm long, chartaceous, nerves very inconspicuous on both surfaces. (Male perianth ± obtriangular, cleft to c. 1/2-way). *Philippines: Luzon* .... **H. obscurinervia**[11]

11a. Twigs towards apex angular or ridged. (Species distinctive only in male flowering specimens) 12

b. Twigs terete or subterete, neither angular nor ridged; twigs sometimes faintly angular or shallowly lined from petiole to petiole 13

12a. *SW. New Guinea, possibly Aru- and Tanimbar Isls.* (Female flower and fruit not known) .... **H. aruana**[28]

b. *Moluccas: Ceram, Banda, Dammar Isl., possibly Ternate.* (Ovary glabrous) .... **H. smithii**[15]

c. *Philippines* (Ovary glabrous or almost so) .... **H. ardisiifolia**[12]

13a. Bark of twigs drying pale, grey-brown, contrasting with the blackish colour of the drying petioles. Fruit drying blackish, 1.5-2.0 cm long. *Moluccas* .... **H. spicata**[7]

b. Twigs brown, in colour not contrasting with the petiole 14

14a. Fruit globose to subellipsoid, 0.9-1.2 cm long; drying blackish. *Aru Isls., New Guinea* .... **H. subtilis** var. **subtilis**[20a]

b. Fruit c. 1.1-1.6 cm long. Fruit not known in *H. samarensis* 15

15a. *Philippines: Samar Isls.* .... **H. samarensis**[14]

b. *Moluccas* 16

16a. Fruit ellipsoid, c. 1.5 cm long; drying blackish. *Morotai, Obi Isl.* .... **H. moluccana** var **moluccana**[9a]

b. Fruit subglobose or ellipsoid, 1.1-1.6 cm long, drying brown. *Celebes, Kabaena Isl., Ceram* .... **H. parviflora**[10]

(7) NEW GUINEA, SOLOMON ISLS., CAROLINE (PALAU) ISLS., AUSTRALIA

1a. Leaves membranous, often with irregularly shaped whitish blotches here and there. Female perianth 2-valved; ovary glabrous. Fruit perfectly globose, c. 1.5-2.0 cm diam., glabrous; pericarp c. 1-2 mm thick; seed globose. *Plant usually growing not too far from the coast* .... **H. irya**[6]

b. Leaves of various consistency, generally without whitish blotches. Fruit either ellipsoid or globose; if globose either only c. 1 cm diam. (*H. subtilis*), or the pericarp more than 2 mm thick, at least at one side; seed mostly ellipsoid. Fruit glabrous or pubescent. *Plant coastal or not* 2

2a. *Plant from Australia.* Female perianth 2-valved; ovary pubescent. Fruit ellipsoid, 1.8-2.2 cm long, drying orange to brown; pericarp 1-2 mm thick .... **H. australiana**[20]

b. *Plant not from Australia.* Fruit various 3

3a. Twigs towards apex distinctly angled or ridged from petiole to petiole. *Aru Isls., New Guinea* 4

b. Twigs terete, sometimes lined in between the bases of petioles but neither angled nor ridged. *New Guinea to Solomon Isls.* 9

4a. Leaves on lower surface with regularly scattered blackish-brown non-traumatic dots or cork warts originating from hair bases (lens!). Perianth 2-valved. *Vogelkop to W. Sepik Dist.* .... **H. inflexa**[8]

b. Leaves without blackish-brown dots 5

5a. Perianth 3-(or 4-) valved 6

b. Perianth 2-valved 7

6a. Ovary glabrous (?). Fruit 10-16 mm long, glabrous. Leaves chartaceous, 7-14 cm long; petiole relatively long and slender, 11-20 mm long. *SW. and S. New Guinea (Digul; Western Dist.)* .... **H. olens**[17]

b. Ovary pubescent. Fruit 17-20 mm long, pubescent at base. Leaves membranous to thinly chartaceous, 10-27 cm long; petioles 7-15 mm. *Vogelkop penins.* .... **H. angularis**[26]

7a. Female perianth depressed-globose, valves nearly 1 mm thick; ovary pubescent. Fruit 17-20 mm long, pubescent. Leaves membranous to thinly chartaceous. *Vogelkop penins.* .... **H. angularis**[26]

b. Female flower and fruit not known 8

8a. Leaves membranous. *SW. New Guinea; possibly Aru and Tanimbar Isls.* .... **H. aruana**[28]

b. Leaves thinly coriaceous. *SW. New Guinea* .... **H. iriana**[27]

9a. Perianth 3-(or 4-) valved; at anthesis cleft almost to the base. *East Sepik Dist.* ..... **H. sepikensis**[18]

b. Perianth 2-valved 10

10a. Ovary and fruit glabrous 11

b. Ovary and fruit pubescent; hairs on fruit either distinct or small and inconspicuous and only to be seen remaining at the base of the fruit near the insertion of the stalk (lens!). Fruit ellipsoid, sometimes in *H. sinclairii* globose 18

11a. Tomentum of leaf bud, apex of twig, and inflorescence, with hairs 0.3-1.5 mm long. Leaves large, 17-45 cm long, often ± parallel-sided, nerves 30-40 pairs. Fruit ellipsoid, 3.4-5.5 cm long, glabrous. *Moluccas and W. & C. New Guinea* ..... **H. sylvestris**[19]

b. Tomentum with hairs c. 0.2 mm long or less; hairs in *H. moluccana*[9] and *H. tuberculata*[39] c. 0.1-0.3 mm long. Leaves generally smaller, nerves fewer 12

12a. Fruit globose or subglobose, not beaked and without pseudostalk, c. 1.4 cm diam. or less 13

b. Fruit ellipsoid, c. 1.3 cm long or more 14

13a. Fruit drying brown; dry pericarp c. 1.5-3 mm thick. Female perianth at anthesis cleft nearly to the base. *Northern parts of Irian Jaya and of Papua New Guinea* ..... **H. basifissa**[31]

b. Fruit drying blackish; dry pericarp c. 1 mm thick. Female perianth at anthesis cleft to c. 1/3. *Aru Isls. Whole of New Guinea* ..... **H. subtilis** var. **subtilis**[29a]

14a. Fruit up to c. 2.0 cm long, drying blackish; top pointed/beaked or not, base without or with long or short pseudostalk 15

b. Fruit 1.3-3.7 cm long, drying brown or dark brown; top rounded, base without pseudostalk 16

15a. Pseudostalk of fruit (1.5-) 2-6 mm long. *Jayapura Dist. (Irian Jaya), W. Sepik Prov.* ..... **H. schlechteri**[30]

b. Pseudostalk absent or up to 3 mm long. *Whole of New Guinea* ..... **H. subtilis**[29]

16a. Twigs lined from petiole to petiole. Fruit 2.5-3.0 cm long; pericarp c. 2-3 mm thick, without coarse wart-like lenticels. *Palau Isls.* ..... **H. palauensis**[16]

b. Twigs lined or not. Fruit 1.3-3.7 cm long; pericarp thin or thick, with small or large wart-like lenticels or not 17

17a. Female perianth c. 2 mm long, cleft at anthesis to c. 1/2-4/5. Fruit 1.3-2.8 cm long, dry pericarp 1-2 mm thick. *Moluccas, W. New Guinea* ..... **H. moluccana**[9]

b. Female perianth 2-3 mm long, cleft at anthesis to c. 1/2-2/3. Fruits 1.5-3.7 cm long, pericarp 1-8 mm thick. *Caroline Isls. (incl. Palau), Bismarck Arch., Papuan Isls. and E. New Guinea (Milne Bay Prov.).* **H. tuberculata**[39]

18a. Arches of the submarginal nerve on the lower leaf surface distinct and very regularly looping; nerves often reddish brown. Leaves often ± parallel-sided. Tomentum of leaf bud composed of hairs c. 0.1-0.3 (-0.4) mm long. Female inflorescence and infructescence up to c. 7 cm long. Fruit 1.7-2.5 (-3.4) cm long, drying orange to brown; pericarp 1-2 mm thick. *Solomon Isls.* .... **H. whitmorei**[34]

b. Marginal nerve not very regularly looping. *Plant not from the Solomon Isls.* 19

19a. Tomentum of leaf bud, apex of twigs, and inflorescence short, composed of hairs c. 0.2 mm long or less; in *H. psilantha*[33] hairs c. 0.1-0.3 mm long 20

b. Tomentum long, with hairs c. 0.5-1.0 mm long; hairs 0.2-0.5 mm long in *H. ampliformis*[25]; tomentum not known in *H. ampla*[24] 28

20a. Tomentum of leaf bud composed of hairs c. 0.1-0.3 mm long. Infructescence (and ♀ inflorescence) large, much branched, 10-16 cm long. Fruit 1.7-2.2 cm long, pericarp thin, 1-2 mm thick, brown. *Bismarck Arch., Bagabag Isl., Long Isl.* .... **H. psilantha**[33]

b. Tomentum of hairs 0.1-0.2 mm long, or less. Female inflorescence and infructescence c. 10 cm long or less. Fruits various 21

21a. Female perianth incl. pedicel long-obconical. Fruit stalk tapering, thickened towards the fruit. Mature fruit not known. *E. New Guinea: Morobe Dist.* .... **H. crux-melitensis**[21]

b. Female perianth ± ellipsoid, well marked off from the slender pedicel. Fruit stalk not tapering 22

22a. Fruit 1.6 cm long or less; pericarp 1-3 mm thick. Perianth pubescent 23

b. Fruit 1.5 cm long or more; pericarp 2 mm thick or more; if fruit c. 1.5 cm long then almost globose and perianth glabrous 25

23a. Fruit without pseudostalk, top rounded .... **H. pilifera**[36]

b. Fruit with pseudostalk c. 1.5-5 mm long, top rounded or usually acute, sometimes rostrate 24

24a. Leaves drying olivaceous; midrib distinctly raised .... **H. clavata**[22]

b. Leaves drying dark brown; midrib slightly raised .... **H. squamulosa**[23]

25a. Female perianth c. 2-2.4 mm long, glabrous. Fruit (sub)globose, or short-ellipsoid, or obovoid, c. 1.5-2.5 × 1.5-2.0 cm; pericarp 4-6 mm thick. Leaves 6-14 cm long. *E. New Guinea (Papua New Guinea)* .... **H. sinclairii**[32]

b. Female perianth c. 2.5 mm long or more, pubescent or glabrescent. Leaves 10 cm long or more 26

26a. Fruit 1.6-3.0 cm long, usually with coarse pale-coloured wart-like lenticels; dry pericarp 2-6 mm thick. *Moluccas, New Guinea, and Bismarck Arch.; 0-1000 m alt.* (sometimes much resembling small-fruited *H. pachycarpa*[41]) .... **H. laevigata**[35]

b. Fruit (3.0-) 3.5-7.5 cm long; pericarp (4-) 5 mm thick or more. *New Guinea; (450-) 1000-2000 m alt* 27

27a. Perianth pubescent. Fruit 3.0-4.5 cm long; pericarp 4-10 mm thick .... **H. pachycarpa**[41]

b. Perianth glabrescent. Fruit 6-7.5 cm long; pericarp 10-20 mm thick .... **H. corrugata**[40]

28a. Tomentum of leaf bud and inflorescence composed of hairs c. 0.2-0.5 mm long. Female perianth c. 3 mm long, at anthesis cleft to c. 2/3. Fruit not known. Tomentum of leaf bud, female flower and fruit also not known in *H. ampla*[24] 29

b. Tomentum composed of hairs c. 0.5-1.0 (-1.5) mm long. Fruit usually conspicuously pubescent 30

29a. Inflorescence glabrescent. *Papua New Guinea: Sepik Prov.* ...... **H. ampla**[24]

b. Inflorescence pubescent. *Sepik and Morobe Prov.* .... **H. ampliformis**[25]

30a. Leaves coriaceous, beneath with harsh hairs, when hairs shed leaving thickened scars. Female perianth c. 4 mm long, at anthesis opening with a narrow pore-like slit at apex. Fruit 3.0-5.0 cm long, pericarp 4-7 mm thick. *New Guinea* .... **H. pulverulenta**[42]

b. Leaves membranous or chartaceous. Perianth at anthesis cleft to c. 1/4-1/2 31

31a. Flowers (only the male known) entirely pubescent. Fruit 2.0-2.4 cm long, pericarp 4-7 mm thick. *New Guinea* .... **H. leptantha**[43]

b. Flowers largely glabrescent 32

32a. Fruit 2.5-3.0 cm long. Female perianth c. 4 mm long. Leaves generally oblong-lanceolate, at apex caudate. *New Britain* .... **H. ralunensis**[45]

b. Fruit 1.2-2.8 cm long. Female perianth c. 3 mm long. Leaves oblong to oblong-lanceolate, at apex not caudate (always ?). *New Guinea and New Britain* .... **H. hellwigii**[44]

Enumeration and Description of Species

1. Horsfieldia iryaghedhi (Gaertn.) Warb. Figs. 1A(1); 2 I; 3.

Myristica iryaghedhi Gaertn., De Fruct. et Sem. Pl. 1 (1788) 196, t. 41, f. 4 — *Horsfieldia iryaghedhi* (Gaertn.) Warb., Mon. Myrist. (1897) 332, t. 21 fig. 1-4; Sinclair, Gard. Bull. Sing. 28 (1975) 68 — Type: Gaertner's drawing.

? *Phelima Noronha,* Verh. Batav. Genootschap Kunsten en Wetenschappen 5, art. 4 (1790) (3) et (edit. 1827) 66, *nom. nud.*

M. glomerata Thunb., Acta Holm. sive Vet. Akad. Nya Handl. (1799) 88, t. 2. f. 1 (*non* Miq., 1852) — Type: Herb. *Thunberg, n.v.;* microfiche: fragment of male inflor.

H. odorata Willd., Sp. Pl. (ed. 4) 4, 2 (1805) 872 — Type: not known (see Sinclair, l.c.).

M. horsfieldii (first spelling *horsfieldia*) Bl., Bijdr. 2, 11 (1826) 577; Rumphia 1 (1837) 192, t. 63; King, Ann. Roy. Bot. Gard. Calc. (1891) 296, pl. 122, 123 — *Pyrrhosa horsfieldii* (Bl.) Hasskarl, Cat. Pl. Hort. Bog. (1844) 174. — Type: *Blume s.n.,* Jave (L).

M. notha auct. non Wall. Koenig ex Bl., Rumphia 1 (1837) 192, *nom. nud. pro syn.*

Myristica (Cnema) glomerata Miq., Pl. Jungh. (1852) 170 (*non* Thunb., 1799) — Type: *Junghuhn s.n.,* Java (U; iso L).

Myristica odorata Reinw. ex de Vriese, Pl. Ind. Bat. Or. 2 (1857) 95 (*non odorata* Willd.), *nom. nud. pro syn.*

For further references see Sinclair, 1.c.

Tree 5-25 m. Twigs terete, not ridged, towards the apex 2-5(-14) mm diam., at first with woolly tomentum, of rust-yellow hairs c. 0.5 mm, twigs early to late glabrescent, bark grey-brown, rather coarsely striate, lower down coarsely striate or longitudinally cracking, rarely somewhat flaking; lenticels usually present but sometimes inconspicuous. Leaves in 2 rows, chartaceous, ovate-elliptic to oblong-lanceolate, broadest usually at about the middle, 10-28 × 4-12 cm, base rounded to attenuate, top acute-acuminate, upper surface glabrous, usually drying dark brown, or dark olivaceous, lower surface early or late glabrescent, without brown-black dots, the epidermis always finely papillose; midrib above often late-glabrescent, flat or slightly raised; nerves 9-16 pairs, above flat or sunken, the lateral arches not very distinct; tertiary venation forming a coarse network, usually ± trabeculate, above distinct to hardly visible; petioles late-glabrescent, 15-20 (-25) × 2-3 mm; leaf bud c. 10-15 x 3-4 mm, densely pubescent with hairs c. 0.5 mm long. Inflorescences densely woolly pubescent with hairs c. 0.3-0.5 mm, in ♂ : c. 6-15 × 4-10 cm, usually twice ramified, the branches rather few, thickish, common peduncle c. 0.3-2.0 cm, the flowers united into c. 10-25 subglobose dense clusters or capituli c. 5-10 mm diam., each with c. 80-100 flowers, the capituli being rather spaced along the branches; ♀ inflorescences smaller, little-branched, c. 1.54- × 1.5-2 cm, the flowers solitary or a few together; bracts broadly ovate or ± triangular to elliptic, the larger ones with distinct midnerve, c. 1-3 mm long, pubescent, caducous. Flowers in ♂ : 3 (or 4)-valved, in ♀ : 3 (or 2)-valved; perianth glabrous except towards the very base; pedicel short or absent, pubescent, at base not articulated. Male perianth narrowly ± obovoid-oblong or obconical, 3-5 (or 6)-angular, c. 2-2.5 × 1-1.6 mm, top broadly rounded, gradually tapering to the base, glabrous but with a few hairs c. 0.2 (-0.5) mm long at the transition to the pubescent pedicel: 0-0.2 (-0.3) mm long; perianth at anthesis cleft at first to c. 1/5-1/4, in adult usually up to c. 3/4; valves c. 0.2 (-0.3) mm thick. Androecium elongate, narrowly obconical or blunt ellipsoid-oblong, top ± truncate, base tapering, c. 1.0-1.2 × 0.4-0.5 mm; anthers 3-5 (i.e., 6-10 thecae), largely sessile, erect, free apices c. 0.2 mm, central column narrow, hollow to about half-way, androphore narrow, c. 0.2-0.5 mm long. Female perianth broadly ellipsoid, c. 3 × 2 mm, at anthesis cleft to c. 1/2-way, valves c. 0.3 (-0.5) mm thick; ovary broadly ellipsoid, c. 2.0 × 1.5 mm, densely short-pubescent, stigma minutely 2-4 (or more)-lobulate; pedicel absent or up to 0.2 mm. Fruits 3-8 in a cluster, ellipsoid to ellipsoid-oblong, top and base broadly rounded, c. 2.5-4.2 × 1.7-2.4 cm, densely rust-yellowish pubescent with stellate-dendroid hairs c. 0.5 mm, sometimes partly glabrescent, pericarp dark brown, not tuberculate, c. 1.5-2.0 (-3.0) mm thick; stalk 0.5-2 mm long; perianth not persisting under the fruit.

Distribution: Ceylon, introduced in Malaya (Penang Isl.), Singapore, Java.

CEYLON: *Balakrishnan NBK 935; Burman s.n., 33; Davidse* & Sumithraarachchi *8539;* herb. Hooker *s.n.; Huber s.n.; Jayasuriya & Bandaranaike 1869; Kostermans 23321; 24114, 26670, 27113; Meijer 268, 276; Nooteboom* (& *Huber) 3164, 3188;* herb. *Pallas 51;* herb. *van Royen s.n.; Thwaites C.P. 221; Waas 743, 892; Walker s.n.; White & Arnott s.n.; Worthington 2130, 2291, 2325, 2345, 2346, 2582, 3533, 3535, 4124, 4832, 5201, 5228, 6023, 6474, 6580.*

SINGAPORE (culta): *Walker 267.*

JAVA (culta, mainly W. Java): *Backer 36342; Bakhuizen van den Brink 7319, 7409; Blume s.n.; van Heurn s.n.; Junghuhn s.n. (42); Koorders 31019 β; Korthals s.n.; Martati (133); Radermacher 93;* herb. *Reinwardtianum 154; Teysmann s.n.; de Vriese s.n.; Zollinger 3263* (? *3268).*

Ecology. Lowland rain forest, wet evergreen forest, "intermediate" forest; also in disturbed forest; 0-500 m. Flowers and fruits throughout the year.

Vernacular names. Ruk, Rukghedhi and *Malaboda* (Ceylon); *Irie gaga* (Ceylon, König ms.); *Tjampaka sèlong* (Java, Soenda).

Uses. Formerly in Java a wax was obtained from cooking the fruits. The wood is moderately heavy and even-grained (see Sinclair, p. 72).

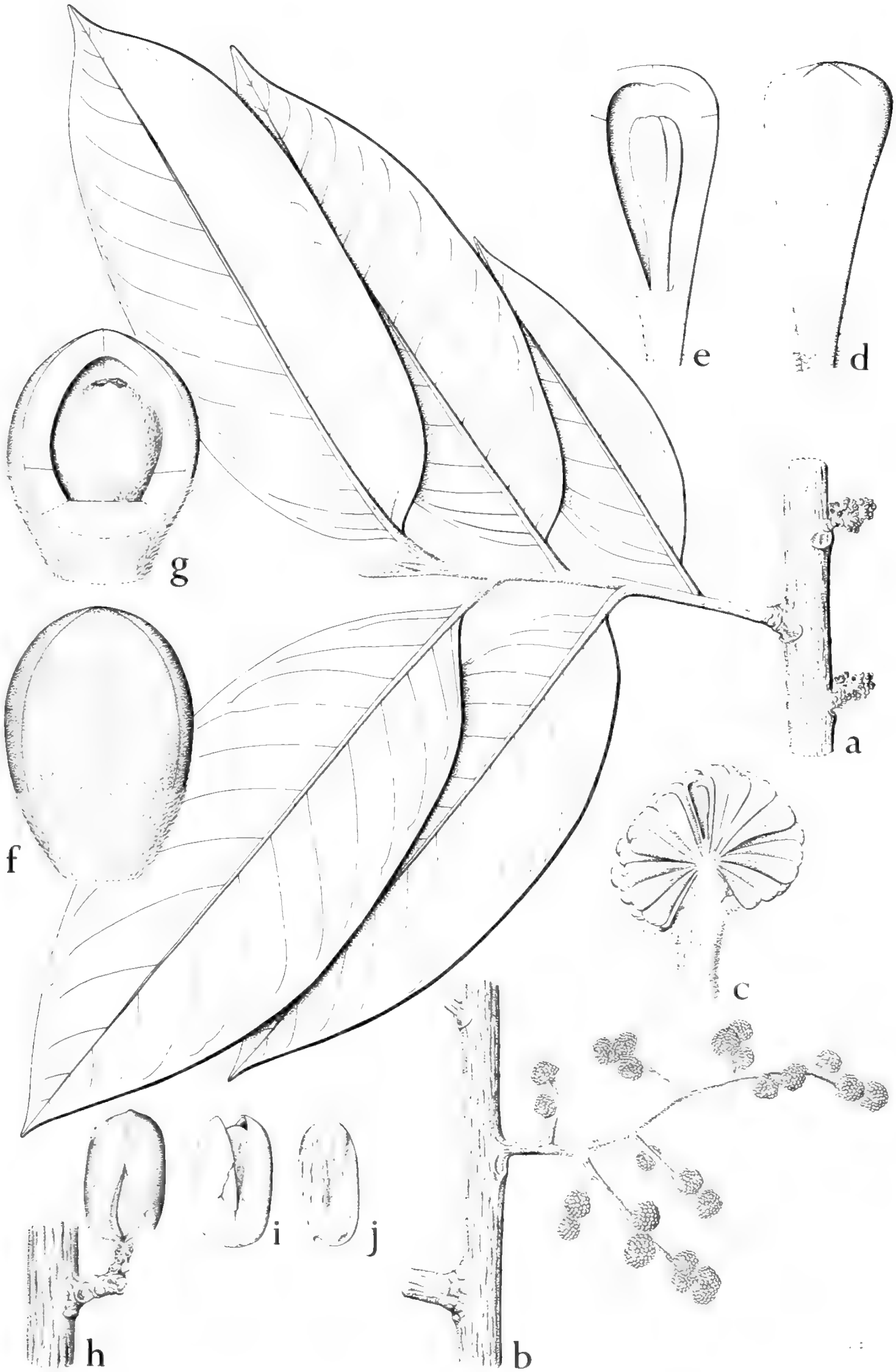

Fig. 3 *Horsfieldia iryaghedhi* (Gaertn.) Warb.
a. habit of twig with leafy shoot and female inflorescences, x 1/2; *b*. twig portion with male inflorescence, x 1/2; *c*. subspherical male flower head, flowers partly removed, one flower opened, x 3; *d*, mature male flower bud, lateral view, x 12; *e*, ditto, longitudinal section showing androecium, x 12; *f*, mature female flower bud, x 12; *g*, ditto, opened, showing pubescent ovary and sessile, minutely lobulate stigmas, x 12; *h*. infructescence, x 1/2, *i-j*. seeds with and without seed coat, x 1/2. — *a, f, g* from Anon., Hort. Bot. Sub. XIII-E-9; *b-e* from *Jayasurya & Bandaranaike 1869; h-j* from *Kostermans 26670.*

NOTES

1. *Fieldnotes.* Trees to c. 25 m tall, at base to c. 50 cm diam., branches drooping, sometimes branched from the base. Stilt roots sometimes present when growing in wet soil. Bark hard, outerbark light brown or black-brown or greyish-red, fissured or gritty, or peeling off in large pieces, or smooth; living bark 5-10 mm, beefy red or red brown, with white lines, exuding a clear light reddish brown sap; wood white to light yellow with red streaks. Leaves grey-green beneath. Perianth yellow or dark yellow, or orange brown; pistil with brown hairs. Fruits yellow or yellowish brown with rusty tomentum; aril complete, orange to deep red. Fresh male flowers c. 3 mm long; flowers strongly scented, reminiscent of that of *Michelia champaca,* according to Sinclair emanating again on boiling the dried flowers.

2. This species rather deviates from all other Horsfieldias, and is now placed by me in a separate section. It is mainly distinct by the leaves being papillate beneath, male flowers arranged in compact heads, rather-many-lobulate stigma; and according to Warburg (p. 334), the seed contains some starch, which seems to be unique for this species of *Horsfieldia.*

According to Sinclair (l.c.) its closest relative might be *H. wallichii* because in that species, before anthesis the flowers are almost sessile and clustered as well, and because of similar leaves. However, when mature, the flowers of *H. wallichii* are quite different, especially because of the much broader androecium; also, its leaves have typical minute dots and stripes beneath, but are not papillose.

Warburg placed *H. iryaghedhi* and *H. sylvestris* in a section *Orthanthera* because the flowers are similarly arranged into small dense capitula in the later species. At full anthesis, however, the flower heads of *H. sylvestris* loosen considerably and their inflorescences then link up with other Horsfieldias.

The arrangement of flowers in heads somewhat resembling dense capitula is found in the African genus *Pycnanthus* and the genus *Brochoneura* from Madagascar.

2. **Horsfieldia kingii** (Hook. f.) Warb. Figs. 1A(2); 4.

Myristica kingii Hook. f., Fl. Br. Ind. 5 (1886) 106; King, Ann. Roy. Bot. Gard. Calc. (1891) 300, pl. 127; Kanjilal & Das, I 1. Assam 4 (1940) 43; C.Y. Wu, Fl. Yunnanica 1 (1977) 10, fig. 4 (9-10); Tsiang Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 202, fig. 92 — *Horsfieldia kingii* (Hook. f.) Warb., Mon. Myrist. (1897) 308; Sinclair, Gard. Bull. Sing. 28 (1975) 74. — Type: *King s.n.* (Sikkim, 19th June 1881) (CAL, *n.v.;* K, iso; BM: G, *n.v.,* lecto); *Masters s.n.* CAL, *n.v.;* K, iso; L, P; BO, DD, M, PDA, *n.v.).*

H. hainanensis Merr., Lingnan Sc. J. 11 (1932) 43; Tsiang, Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 199, fig. 91 — Type: Tsang & Fung 17851 (NY, *n.v.;* iso K).

H. tetratepala C.Y. Wu, Acta Phytotax. Sin. 6 (1957) 218; Fl. Yunnanica 1 (1977) 12, fig. 4(1-8); Tsiang, Li & Li, Fl. Rep. Popul. Sin. 30, 2 (1979) 197, fig. 90 — Type: Exp. Sino-ross. Yunnan 2770 (KNN, PE, *n.v.*).

Tree 6-25 m. Twigs terete (not ridged) towards the upper 4-10 (-12) mm diam., bark dark brown, rather early glabrescent, tomentum grey-brown to light brown, hairs c. 0.2-0.4 mm long, bark lower down ± coarsely striate, not flaking; lenticels usually distinct. Leaves in (3-) 5 rows, membranous to chartaceous, (obovate to) elliptic-oblong to oblong-lanceolate, broadest at or usually somewhat above the middle, 12-35 (-55) × 5-17 (-22) cm, base attenuate, top acute-acuminate; upper surface drying dark olivaceous-brown to dark brown; lower surface largely early glabrescent but usually some tomentum vestigial for a while on and near the midrib, without brown-black dots; midrib flat above; nerves 13-18 pairs, flat or slightly sunken above, marginal arches indistinct; tertiary venation forming a coarse network generally faintly visible above; petioles (9-) 15-25 × (2-) 2.5-4 mm, glabrescent rather late; leaf bud c. 15-20 × 3-4 mm, densely grey brown to pale brown pubescent with hairs c. 0.2-0.4 mm. Inflorescences rather thinly woolly-pubescent with greyish to pale brown hairs c. 0.2-0.4 mm, in ♂ : rather slender to broad, 2-3 times ramified, flowers moderate to rather few, c. (5-) 7-16 × 3-8 (-12) cm, common peduncle c. 10-20 mm long; in ♀ : 1-2 times ramified, rather few-flowered, 2-8 cm long; bracts oblong to lanceolate, pubescent, 3-10 mm long, caducous. Flowers in male (see notes to the synonyms) 2- or usually 3- or 4- (or 5-) valved, in ♀ either 2- or 3-valved, in ♂ arranged in loose or dense clusters of 3-10, in ♀ c. 1-3 together; perianths pubescent with soft hairs 0.1-0.3 mm long, or partly glabrescent; pedicels pubescent to subglabrescent, at base not articulated. Male perianth in mature bud globose or subglobose, usually slightly angled on the valve-sutures, c. 2.5-3.5 × 3.0-4.0 mm, top rounded or slightly acute, base broadly rounded; pedicel stoutish, 1.0-2.0 (-2.5) mm long; perianth at anthesis cleft to 2/3-3/4, valves 0.5-0.8 mm thick, sometimes rather coriaceous. Androecium depressed-globose or depressed and broadly obovoid, top broadly rounded to subtruncate, c. 1.0-1.6 × 1.5-2.0 mm, in transverse section subcircular to bluntly 3- (or 4-) angular; anthers (12-) 14-16 (-20), largely sessile, free apices c. 0.1-0.3 mm, towards apex curved over and into the rather broad apical cavity, cavity c. 0.3-0.8 mm deep; androphore rather narrow, c. 0.1-0.3 mm long. Female perianth 2- or 3-valved, ovoid-ellipsoid, 3.0-4 (-5) × 3.0-3.5 mm, thinly pubescent or subglabrescent, at anthesis cleft to c. 1/2-way, valves c. 0.6 mm thick, ± coriaceous, ovary ellipsoid or obovoid, c. 2.0-2.5 × 2.0 mm, pubescent, stigma minutely 2-lobed, 0.1-0.2 mm long, pedicel 2-3 mm long. Fruits 1-6 per infructescence, ellipsoid to ellipsoid-oblong, top rounded to (sub) acute, base narrowly rounded to rather long-tapering, c. (3-) 4-6 × 2-2.7 cm, dry pericarp 3-4 mm thick with granulate-striate surface, drying dark brown, glabrescent early; stalk 3-8 mm; perianth persisting.

Distribution. India (Assam, Sikkim), E. Nepal, Bangladesh (?, no specimens seen), Burma (?, no specimens seen), China: Yunnan, Kwangsi (no specimens seen), Hainan.

INDIA. Bengal: *Haines 842* — Assam: *Masters s.n.;* herb. *Pierre 5462* — Sikkim: Gammie, *King's Coll. s.n.; King 2380; Rogers s.n.*

E. NEPAL: *Stainton 6436, 6880.*

CHINA. *Yunnan: Henry 12.234* — Hainan: *Tsang & Fung (317) L.U. 17851.*

Ecology. Lower montane forest, in gullies of evergreen forest; 300-1200 m alt. Flowers and fruits probably throughout the year.

Vernacular names. (See Sinclair, p. 75) *Amol* (Assam); *Mijing-ikum-asing* (Miri); *Pandikachoaphang* (Kach.); *Siltui* (Lushai); *Bolong, Bolouchi* (Garo).

Uses. Kernel used as a substitute for areca nut in betel chewing. The gum is good against mouthsores.

NOTES

1. *Fieldnotes.* Bark grey or brownish, somewhat rough, flaking in small square flakes, and longitudinally fissured; sap blood red. Male flowers recorded as orange-red, fruits as yellow.

2. *Synonyms.* In the *Flora of China* (Fl. Rep. Popul. Sin.) (1979), besides *H. kingii* two related species *H. tetratepala* and *H. hainanensis* are accepted. I have seen no material of *H. tetratepala* and *H. hainanensis* only the sterile isotype in K, and some separate flowers of the same collection kindly procured by the herbarium at Berkeley, but after studying the descriptions and the figures in the *Flora of Yunnan* (1977) and the *Flora of China* (1979) I see no reason to keep them separate. In the *Flora of China* the three species are keyed out on vegetation

characters *viz.*, the presence or absence of lenticels on the twigs, the degree of persistence of the tomentum on the lower midrib, the number of lateral veins (which strongly overlap), and the length of the infructescences: 6-12 cm in *H. tetratepala* and 2-4 cm in *H. hainanensis.*

However, the following remarks should be made.

1. *H. tetratepala:* in the *Flora of Yunnan,* figure 4, 3-4, a distinct cup-like disk under the androecium is visible, whereas in the figure of the same species in *Flora of China,* figure 91, this cup-like disk is absent. If, in fact, a disk is present, comparable to the one present in the Malayan *Knema plumulosa,* then this would be a strong argument to regard *H. tetratepala* as a distinct species.

2. *H. kingii.* In *Flora of China,* figures 92, 2, the male perianths were drawn as glabrous and 2-valved, whereas for *H. tetratepala* and *H. hainanensis* they are presented as pubescent and 3- or 4- (or 5-) valved. The perianths in the type of *H. kingii,* however, being also pubescent and 3-valved indicate this species be regarded as conspecific. If in the specimens used for the drawing of what is called *H. kingii* in *Flora of China* the male flowers are truly glabrous, and 2-valved, this would be a reason for further investigation on the status of these specimens, which might represent a new taxon.

3. *Henry 12.234* from Yunnan, a good male flowering collection, was identified by Sinclair as *H. macrocoma,* for reasons unclear to me, possibly because of the rather slender male inflorescences.

3. **Horsfieldia longiflora** de Wilde, *sp. nov.* Fig. 1A(3)

Horsfieldia amygdalinae affinis, differt foliis distichis, perianthiis masculis 2-valvibus, ± ellipsoideis parum compressis, c. 2-3 mm longis, androecio c. 2.0 × 1.3 mm, antheris 10-12, fructibus breviter ellipsoideis, c. 1.5 × 1.2 cm. — Type: *Eberhardt 3050* (P).

Tree 6-20 m. Twigs terete, not ridged, towards the top 2.5-6 (-10) mm diam., bark dark grey-brown to blackish brown, tomentum with hairs c. 0.1 mm long or less, grey-brown, early glabrescent, lower down the bark coarsely striate, not flaking, lenticels distinct. Leaves in 2 rows, membranous to chartaceous, elliptic-oblong to oblong-lanceolate, broadest at about the middle, 7-21 × 3-7.5 cm, base attenuate, top acute-acuminate; upper surface drying olivaceous brown to dark brown; lower surface glabrescent early, without larger dark brown dots; midrib flattish above to slightly raised; nerves 9-13 pairs, flat to slightly raised, or sunken above, marginal arches indistinct; tertiary venation forming a lax network, faint or invisible above, usually faint beneath; petioles 9-12 × 1.5-2.5 mm, glabrous; leaf bud slender, 10-14 × 2-3.5 mm, densely grey-brown pubescent with hairs c. 0.1 mm long or less. Inflorescences with sparse tomentum of hairs c. 0.1 mm or less, subglabrescent, in ♂: c. 3 times ramified, moderately- to many-flowered, c. 6-10 × 4-6 cm, common peduncle 6-20 mm; in ♀: 1-2 times ramified, c. 2-3 cm long; bracts ± elliptic, short-pubescent, 2-5 mm long, caducous. Flowers 2-, rarely with a few 3-valved, the ♂ in loose clusters of 3-6, the ♀ c. 1-3 together, glabrous; pedicels glabrous, at base not articulated. Male perianth in bud with frontal view broadly ellipsoid-obovoid, laterally somewhat flattened, 2.2-3.0 × 1.8-2.0 mm, 1.2-1.5 mm thick, top broadly rounded, base shortly rounded to subattenuate, outside faintly longitudinally ribbed or not; pedicel slender, 1-2 mm long; perianth at anthesis cleft to nearly 1/2-way, valves c. 0.2 mm thick. Androecium flattened, obovoid-ellipsoid, top broadly rounded to subtruncate, 1.7-2.0 × 1.0-1.3 × 0.6-0.8 mm, in transverse section ellipsoid; anthers 10-12, sessile, free apices c. 0.1 mm, suberect or little incurved; apical cavity narrow, 0.2-1.0 mm deep; androphore rather broad, tapering, c. 0.2-0.3 mm long. Female perianth ovoid-ellipsoid, c. 2.5 × 2.0 mm, glabrous, at anthesis cleft to nearly 1/2-way, valves c. 0.3 mm thick, ovary ovoid, c. 1.8 × 1.5 mm, glabrous, stigma minutely 2-lobed, c. 0.1 mm long, pedicel c. 1.0-1.5 mm long.

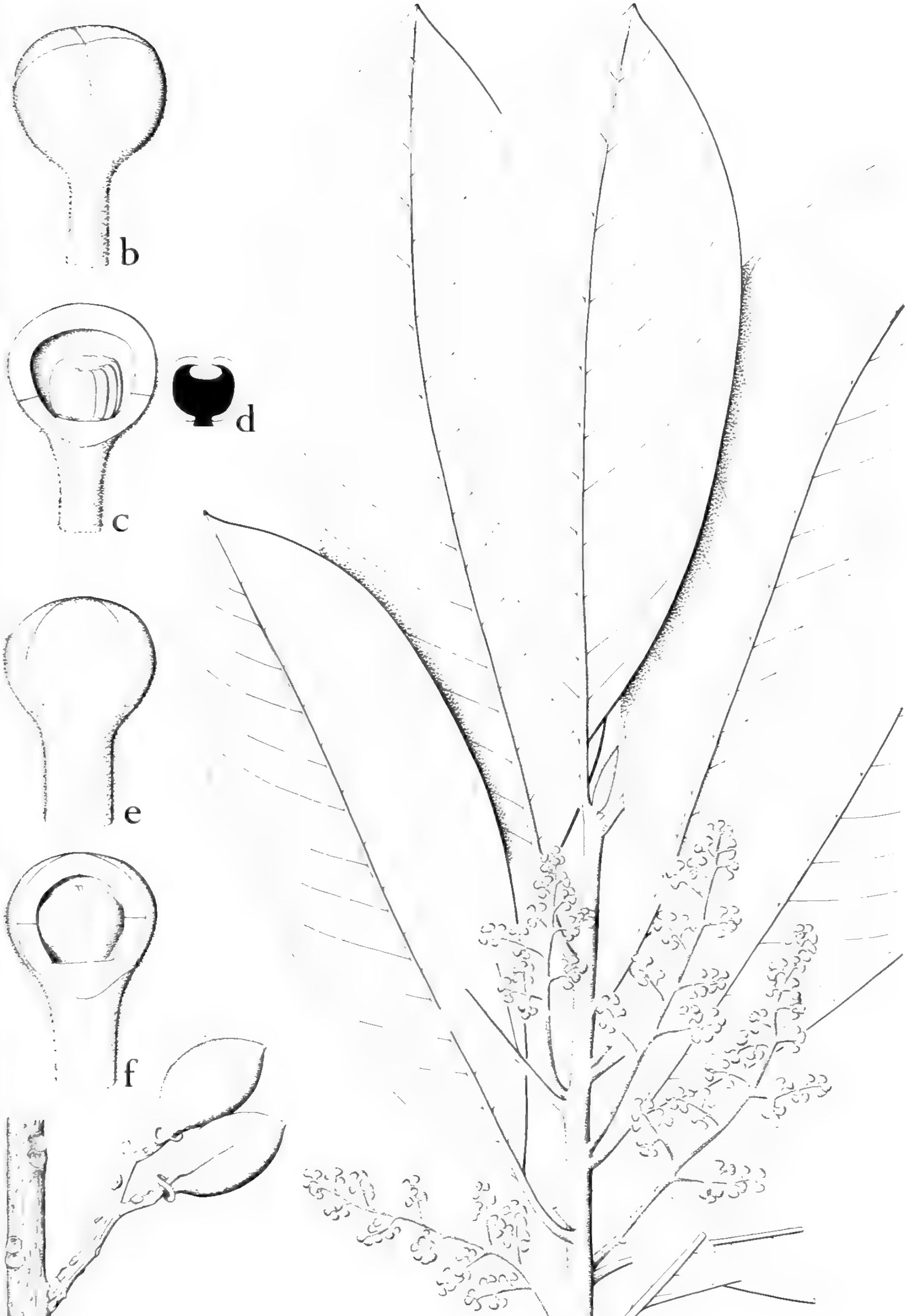

Fig. 4. *Horsfieldia kingii* (Hook. f.) Warb.
a, leafy twig with male inflorescences, note dispersed leaves, x 1/2; *b,* mature male flower bud, lateral view, x 6; *c,* ditto, opened, showing androecium, x 6; *d,* androecium, longitudinal section, schematic, x 6; *e,* mature female flower bud, x 6; *f,* ditto, opened, showing pubescent ovary with minute bi-lobed stigma, x 6; *g,* twig portion with infructescence, note persistent perianth under fruit, x 1/2. — *a-d,* from *Haines 842; e & f,* from *Tsang & Fung 317; g,* from *King's Coll. s.n.* (Sikkim).

Fig. 5. *Horsfieldia thorelii* Lecomte
a, twig with leaves and male inflorescences, note dispersed phyllotaxis, x 1/2; ***b,*** **mature male** flower, lateral view, x 12; *c,* ditto, opened, showing androecium, x 12; *d,* androecium, longitudinal section, schematic, x 12; *e,* twig portion with female inflorescences, x 1/2; *f,* mature female flower, laterla view, x 6; *g,* ditto, opened, showing glabrous ovary, x 12; *h,* twig portion with infructescence with immature fruits, x 1/2; *i,* mature fruit, x 1/2. — *a-c,* from *Poilane 19887; e-g,* from *Maxwell* 75-212; *h & i* from *Poilane 22394.*

Fruits 1-8 per infructescence, broadly ellipsoid, top and base rounded, c. 1.5 × 1.2 cm, surface granulate, not tuberculate, drying dark brown, glabrous, dry pericarp c. 1 mm thick; stalk 1.0-1.5 mm long; perianth not persisting.

Distribution: C. Vietnam (Annam)

VIETNAM. Annam: *Clemens 3474; Eberhardt 3050; Polane 10224, 13529, 29315.*

Ecology. Submontane evergreen forest, on rather poor soil; exact altitudes not recorded; flowers March to May, fruits May-July.

Vernacular names. Lan Ham, Coň na ham (Moi), Mĕ tŭóng.

Uses. Leaves are used for bathing after childbirth. The wood is recorded as soft and light.

NOTES

1. Flowers yellow, fruits red.

2. Closely related to *H. amygdalina* and *H. thorelii,* both differing by the shorter and smaller male flowers with differently shaped androecium (but see note 3 under *H. amygdalina),* and by the larger fruits. In *H. longiflora,* however, fruits are known only from one collection *(Clemens 3474).* All specimens of our present species have the leaves distichous; in *H. thorelii* all specimens have the leaves dispersed, in *H. amygdalina* both distichous and dispersed phyllotaxes can be found.

3. Sinclair included the specimens of the present new species in his broadly conceived *H. glabra.* The specimens were all collected after the treatment in the Flore Génerale de l'Indo-chine (1914).

4. **Horsfieldia thorelii** Lecomte

Figs. 1A(4); 5.

H. thorelii Lecomte, Not. Syst. 1, 4 (1909) 99; Fl. Gén. I-C. 5, 2 (1914) 100; Sinclair, Gard. Bull. Sing. 16 (1958) 422 (See note, in syn. of *H. amygdalina)* — Type: *Thorel s.n.* and 1186 (P) (some of the duplicates are *H. irya*).

Tree 4-20 m. Twigs terete, not ridged, towards the top 2.5-6 (-12) mm diam., bark dark grey-brown to dark brown, early glabrescent from a grey-brown to rusty tomentum with hairs c. 0.1-0.3 mm, bark lower down finely to ± coarsely striate, not flaking, lenticels small, generally inconspicuous. Leaves in 3-5 rows, membranous to chartaceous, elliptic-oblong to oblong, broadest at or somewhat above the middle, 9-23 × 3-9.3 cm, base attenuate, top acute-acuminate; upper surface drying olivaceous-brown to blackish brown; lower surface early glabrescent, without brown dots; midrib slightly to much raised above; nerves 9-13 pairs, flat to moderately raised above, marginal arches not distinct; tertiary venation forming a coarse network, usually faint to invisible on both surfaces; petioles 6-17 × 1.5-3.5 mm, glabrous; leaf bud slender to rather stout, c. 8-16 × 2-4 mm, densely greyish brown to rusty-pubescent with hairs c. 0.1-0.3 mm. Inflorescences ± thinly pubescent with hairs c. 0.2-0.5 mm, sometimes subglabrescent, in ♂ : 3-4 times ramified, many-flowered, 4-22 × 2-12 cm, common peduncle c. 10-30 (-75) mm; in ♀ : 1-2 times ramified, c. 2-6 cm long; bracts oblong to lanceolate, pubescent, c. 2-4 (?) mm, caducous. Flowers either predominantly 2-valved or in mixture of 2- and 3-valved, the ♂ in rather dense clusters of c. 5-12, the ♀ c. 1-4 together; perianths glabrous; pedicel glabrous, in ♂ at base not articulated, in ♀ articulated or not (see notes). Male perianth broadly obovoid to globose or depressed globose, top broadly rounded, base rounded to broadly rounded, outside faintly longitudinally ribbed or not, c. 1.0-1.5 (-1.7) × 1.2-2.0 mm; pedicel 0.4-1.0 (-1.5) mm, slender; perianth at anthesis cleft to c. 1/2-way, valves 0.1-0.2mm thick. Androecium depressed-obovoid to (depressed)globose, c. 0.6-1.0 × 0.6-1.1 mm, usually somewhat laterally flattened and hence subcircular to elliptic (not circular) in transverse section; anthers 7-9 (-10), sessile, free apices 0-0.1 mm, towards the apex incurved over a rather narrow central cavity c. 0.1-0.4 mm deep; androphore narrow, 0.1-0.2 mm long. Female perianth obovoid-ellipsoid, 1.8-2.5 × 1.6-2.2 mm , glabrous, at anthesis cleft to c. 1/3, valves 0.3-0.4 mm thick, ovary ellipsoid, 1.4-1.7 × 1.0-1.4 mm, glabrous, stigma minutely 2-lobed, c. 0.1 mm, pedicel 1-1.5 mm long, glabrous or thinly pubescent. Fruits 1-5 per infructescence, broadly ellipsoid, top and base broadly rounded, 1.8-3.2 × 1.5-2.4 cm, finely granulate, not tuberculate, drying dark brown, glabrous, dry pericarp c. 1.5-2.5 mm thick; stalk c. 1-2 mm; perianth not persisting.

Distribution. Vietnam (Annam, Cochin-China), Laos, Cambodia, S. and SE. Thailand (not in peninsula).

VIETNAM. Annam: *Poilane 8699, 18160, 18308, 18615, 19887, 22394* — Cochin-China: *Chevallier 39134, Pierre 14, 1812, 5434, Poilane (56), Thorel s.n., 1186.*

LAOS. *Poilane 13480.*

CAMBODIA. *Hahn 140, Pierre 680, Poilane 23253, 23341, Vidal 5044.*

THAILAND. *Maxwell 74-794, 75-212, 76-158, 76-429, Smitinand & Phengklai 10870.*

Ecology. Evergreen forest, regenerating forest; on rich red soil; 200-1100 m alt. Flowers and fruits throughtout the year.

NOTES

1. Latex from bark colourless. Leaves subcoriaceous. Flowers yellow; fruits greenish-yellow; aril thin, orange.

2. Female flowers have only been seen from two rather differeing collections, *viz.*, (1) an unnumbered specimen collected by Poilane (10) (Indo-China), which deviates somewhat in habit from the other specimens by its rather narrow lanceolate leaves c. 18 × 4.5 cm, and slender inflorescences of c. 6 cm long with immature flowers with the pedicels glabrous and articulated at the base; (2) *Maxwell 75-212*, from Thailand, with stouter and more condensed inflorescences, with stouter flowers of which the pedicels thinly pubescent towards the base and not articulated; possibly the articulation of the pedicels in the Poilane specimen is artificial and caused by the drying of the immature flowers.

3. *H. thorelii* is mainly characterized by the leaves being always dispersed in 3-5 rows, and by the very small globose male flowers c. 1.0-1.5 mm diam. It is closely related to the polymorphous *H. amygdalina*, a species with a larger distributional area and differing by having larger, male perianths (c. 1.5-2.3 mm long), generally more anthers (8-15), and slightly larger fruits (2.2-3.4 cm long); it is also closely related to *H. longiflora*, but the latter species differs by its larger and more elongate flowers, smaller fruits, and generally distichous leaves.

4. *Poilane 23252, 23341*, and *Vidal 5044*, from Cambodia, Prov. Kampot, alt. c. 200-300 m, are specimens deviating by the poor and short pubescence (hairs c. 0.1 mm) of the inflorescences; similar short-haired, glabrescent inflorescences have been collected in in Thailand e.g., *Maxwell 74-794.*

5. *H. thorelii* seems to replace *H. amygdalina* in Annam and Cochin-China (Central and S. Vietnam).

6. In 1956 Sinclair (p. 422) regarded *H. thorelii* as a synonym of *H. amygdalina;* in 1975 (p. 42) both these names were reduced to his wide conception of *H. glabra.*

5. **Horsfieldia amygdalina** (Wall.) Warb.

Myristica amygdalina Wall., Pl. As. Rar. 1, 4 (1830) 79, t. 90; Cat. (1832) No. 6797; Hook. f. & Th., Fl. Ind. (1855) 160, p.p.; King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 300, pl. 128. — *Horsfieldia amygdalina* (Wall.) Warb., Mon. Myrist. (1897) 310; Sincl., Gard. Bull. Sing. 16 (1958) 422 (in syn. and in notes to *H. bracteosa)*; C.Y. Wu (Ed.), Fl. Yunnan. 1 (1977) 12, fig. 3, 5-6 — Type: *Wallich.* Cat. 6797 (KW; K, iso; BM: CAL, G, *n.v.*).

Myristica floribunda Wall., Cat. (1832) no. 6805, *nom. nud.*

M. kurzii King, *nom. nud.* (sub *M. glabra auct. non* Bl.: King). — Type: *Kurz s.n.*, 984 (CAL, *n.v.;* iso, P).

Horsfieldia tonkinensis Lecomte, Not. Syst. 1, 4 (1909) 100; Fl. Gen. I.-Chine 5, 2 (1914) 101 — Type: *Bon 4272 (4302)* (P).

H. tonkinensis var. *multiracemosa* Lecomte, Not. Syst. 1, 4 (1909) 100; Fl. Gén. I.-Chine 5, 2 (1914) 102 — Type: *Bon s.n.* (4302) (P).

Myristica glabra auct. non Bl.: King, Ann. Roy. Bot. Gard. Calc. 3 (1891) 310, pl. 142 — *Horsfieldia glabra auct. non* (Bl.)- Warb.: Sinclair, Gard. Bull. Sing. 28 (1975) 35, p.p. (as for most of the specimens originating from continental Asia); Fl. Rep. Pop. Sin. 30, 2 (1979) 204, fig. 93.

H. prunoides C. Y. Wu, Yunnan Econ. Pl. (1973) 74, fig. 56, *nom. nud.* — Type: publication not seen; name cited in the synonymy of *H. glabra auct.* in Flora of China, 1979.

Tree 5-30 m. Twigs terete, not ridged, towards the top 1.5-3.5 (-8) mm diam., bark grey-brown to brown, tomentum greyish to brown, composed of hairs c. 0.1-0.2 mm (var. *amygdalina)* or c. 0.5-1.0 mm long (var. *lanata),* usually tomentum early glabrescent, lower down the bark rather finely striate, not flaking; lenticels small, ± conspicuous or not. Leaves either in 2, or 3, or 5 rows, or phyllotaxes mixed, membranous to subchartaceous, elliptic-oblong to oblong, broadest at about or slightly above the middle, 9-23 × 2.5-7.5 (-9) cm, base attenuate, tip acute-acuminate; upper surface drying olivaceous brown to dark brown; lower surface early glabrescent, without brown or blackish dots; above, midrib flat to moderately raised; nerves 7-14 pairs, thin, either sunken or flat, or moderately raised, marginal arches not distinct; tertiary venation forming a rather lax network, usually faint to invisible on both surfaces; petioles 10-20 × 1.5-3.5 mm, glabrous; leaf bud slender to stoutish, densely grey-brown to brown, pubescent with hairs 0.1-0.2 or 0.5-1.0 mm (see under the varieties), c. 10-15 × 1.5-4 mm. Inflorescences either very thinly pubescent with pale hairs c. 0.1 mm (var. *amygdalina*) to early glabrescent or early glabrescent and hairs densely set, rusty, c. 0.5 (-1.0) mm (var. *lanata*), in ♂: 3-4 times ramified, flower-number moderate to many, 6-18 × 3-12 cm, common peduncle 7-40 mm; in ♀ : 1-2 times ramified, 1-3 (-6) × 1-1.5 (-4) cm; bracts ± elliptic, tip rounded, pubescent, 1-2 (-3) mm long, caducous. Flowers either 2- or 3- (or 4-) valved, or ± an even mixture of 2- and 3-valved, in ♂ rather dispersed or in loose clusters of 4-10, in ♀ solitary or 2-3 together, glabrous; pedicels glabrous, at base not articulated, or in ♀ sometimes indistinctly articulated. Male perianth shortly obovoid or short-ellipsoid to globose, tip rounded, base rounded to ± tapering, outside often shallowly longitudinally ribbed, c. 1.5-2.3 × 1.7-2.0 (-2.2) mm; pedicel (0.8-) 1-2 mm; perianth at anthesis cleft to c. 1/2-way, valves c. 0.2 mm thick. Androecium globose or depressed-globose, sometimes truncate-ellipsoid (see notes), 0.8-2.0 × 0.8-1.3 mm, slightly laterally flattened or not and hence transverse section subcircular to ellipsoid; anthers 8-12 (-15), sessile, free apices 0-0.1 mm, towards apex curved over an apical cavity moderately broad to narrow, c. 0.2-0.4 (-0.5) mm deep; androphore rather narrow, c. 0.1-0.2 mm long; central column broad, solid. Female perianth ellipsoid, c. 2.5-3.0 × 2.0 mm, glabrous, cleft at anthesis to c. 1/3, valves 0.4 (-0.5) mm thick; ovary ovoid, glabrous, 1.5-1.7 × 1.2-1.5 mm, stigma minutely 2-lobed, c. 0.1 mm high; pedicel c. 1.0 mm long, glabrous, at base ± articulated or not. Fruits 2-6 (-16, see notes) per infructescence, ellipsoid, top and base (narrowly) rounded, 2.2-3.4 × 1.6-2.6 cm, glabrous, drying glaucous-brown to dark brown, finely granulate, not tuberculate, dry pericarp 2-3 mm thick; stalk 2-3 mm long; perianth not persisting.

Distribution. India to Indo-China, and S. China, not in Malaya.

Note. This species, and the closely related *H. thorelii* and *H. longiflora* (see also there) have similar fruits. These three are akin to *H. glabra* from West Malesia, the latter distinctive by a number of minor characters, but always easily ascertained by the presence of blackish dots on the lower leaf surface. *H. subalpina* from mountainous West Malesia is also closely related.

KEY TO THE VARIETIES

1a. Leaf bud, upper portion of twigs, immature inflorescences and immature leaves with rusty woolly tomentum with hairs 0.5-1.0 mm long .... b. var. **lanata**

b. Tomentum with greyish to dull brown hairs 0.1-0.2 mm long .... a. var. **amygdalina**

a. var. *amygdalina*

Leaf bud, young upper portions of twigs and immature inflorescences with tomentum of grey to dull brown hairs 0.1-0.2 mm long, or less. Mature Leaves usually membranous. Flowers in the same inflorescence either 2- or 3-valved or 2- and 3-valved mixed.

Distribution. India (Assam, Andaman Isl.), Bangladesh (E. Pakistan), Burma, S. China, N. Thailand, Laos, N. and C. Vietnam (Tonkin, N. and C. Annam).

INDIA (incl. E. Pakistan): *Hooker & Thomson* (coll. 11/50) *s.n.; Jenkins* (comm. Anderson) *s.n.; King's Coll.* 268; *Masters (coll. Simons) s.n.; Wallich 6804, 6805* (belonging to the material of *M. exaltata*, not the lectotype); *de Silva & Gomes, Wall. Cat. 6805.*

Andaman Isl. (S. Andaman(: *Balakrishnan 1033; Nair 843, 3641; King s.n., Kings Coll. s.n.* (several dates).

BURMA: *Beddome s.n.; Dickason 6556-bis, 6945; Falconer* (comm. Anderson) *5446; Helfer 4358; Keenan, Tun Aung & Rule* 1569; *Kurz s.n., 984; Wallich 6797.*

CHINA. Yunnan: *Huang Yun Wui 120;* also recorded S. Kwangsi, Hainan.

VIETNAM. Tonkin: *Bon 2669, 4272, 4302; Pételot 1070; Poilane 13041; W.T. Tsang 29198* — C. & N. Annam: *Chevalier 38164; Poilane 11106, 11119.*

LAOS: *Poilane 13700.*

THAILAND. North: *Hansen, Seidenfaden, Smitinand 11181, Put 796; Winit 1471.*

Ecology: Evergreen forest, recorded from sandy soil; 0-1000 m alt. Flowers and fruits throughout the year.

NOTES

1. Flowers greenish-yellow or yellow, evil-smelling; fruits yellow.

2. Rather variable in shape and size of the inflorescence, and size of the male flower, including the androecium.

Wallich 6805 (de Silva & Gomes), from Sylhet (Bangladesh) rather deviates by its large, longish, male flower, the perianth measuring c. 2.2 × 2.2 mm, with the androecium exceedingly elongate, c. 1.8-2.0 × 1.0 mm; this specimen resembles *H. longiflora,* a species with the leaves apparently always distichous and with still larger flowers, to c. 3 mm long, and with the androecium with broader and longer tapering androphore, c. 0.3 mm long.

3. The specimens *Poilane 11106, 11119* (from Annam), and *Poilane 13700* (Laos) seem to have a completely distichous phyllotaxis. Of these collections *Poilane 11119* somewhat deviates by its large infructescence bearing up to 16 (still immature) fruits; in most specimens only up to 6 fruits have been seen. In *Poilane 13700* the hairs on the leaf bud are relatively long for the variety, c. 0,2 mm.

4. Quite often the flowers in a specimen are in different stages of development; also fruits in the same infructescence are sometimes (e.g., *Balakrishnan 1033)* in different stages.

5. All specimens of both var. *amygdalina* and var. *lanata* were lumped by Sinclair in his large conception of *H. glabra.*

b. var. lanata de Wilde, *var. nov.* Fig. 1A(5)

A var. amygdalina differt tomento lanuginoso rufo-ferrugineo in foliorum gemmis et inflorescentiis juvenilibus valde distincto, pilis 0.5 (-1.0) mm longis — Type: *Kerr 8556* (L; iso BM, K, P).

Leaf buds, immature twig apices, immature leaves (partly), and young inflorescences with dense conspicuous rusty woolly tomentum composed of hairs 0.5 (-1.0) mm long. Mature leaves chartaceous. Male perianths either 2-, or 3- or 4-valved. Female flowers and fruits not seen.

Distribution. E. Thailand, Cambodia.

THAILAND (E.): *Kerr 8439, 8556.*

CAMBODIA: *Pierre 1812, 5469.*

Ecology. Evergreen forest; 0-200 m. Flowers in February.

Vernacular name. Lûat-nok (E. Thailand).

Note. The specimens *Pierre 1812* (P), *5469* (BM) from Cambodia slightly differ from the plants from Thailand by the somewhat shorter tomentum with hairs c. 0.4-0.5 mm long, and by the predominantly 2-valved perianths.

The Reproductive Biology of Rambutan, *Nephelium lappaceum* L. (Sapindaceae)

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Abstract

Nephelium lappaceum produces either male or bisexual flowers. The anther development in both types of flowers is the same but those in the bisexual flowers do not dehisce even though their pollen is viable. The anther is tetrasporangiate and its wall development conforms to the basic type. Cytokinesis in microspore mother cells is simultaneous, forming tetrahedral tetrads. The mature pollen grains are tricolpate and two-celled. Only pollen grains from the male flower germinate in the conventional media.

The ovule is anacampylotropous, bitegmic, crassinucellate and the micropyle is formed by the inner integument only. The embryo sac development is of the monosporic *Polygonum* type.

Flower anthesis is at 0900-1100 hours and pollination is entomophilous. Preliminary flower bagging experiments show that fruit formation is dependent on pollination. The average normal flower and fruit drop are 40% and 90% respectively.

The endosperm development is *ab initio* Nuclear and cell formation commences at the micropylar end, proceeding towards the chalaza. The outer layers of the outer integument differentiate into the edible flesh of the fruit. The testa is formed mainly from the inner part of the outer integument and the few remaining layers of the inner integument at the micropylar region.

The seed is non-endospermous and shows hypogeal germination. In fresh seeds, the average percentage germination is 96%, of which 2% of the seedlings give multiple shoots.

Introduction

In Malaya, several species of *Nephelium* produce edible fruits. Those common in cultivation are the Rambutan *(N. lappaceum L.)*, Pulasan (*N. mutabile* Bl.) and Mata kucing (*N. malaiense* Griff.).

Nephelium lappaceum L. is known as Rambutan to the Malays because of its hairy fruits; "rambut' in the Malay language means "hair". Whitehead (1959) recognised different clones based on size and taste of fruits, nature, colour and texture of the soft spines of the rind. The Rambutan is delicious when eaten fresh but it can also be canned or made into an excellent jam. A wine made from it was exhibited at the Colonial and Indian Exhibition in London in 1886 (Burkill, 1935) but the practice never seems to have caught on. The fruit wall, roots, leaves and bark are said to have medicinal value.

Materials and Methods

Field observations on phenology, floral anthesis and pollination, and collection of plant materials were undertaken at weekly intervals or more often as required, in the fruit-tree nursery of the Ministry of Agriculture in Serdang about 20 km from the University of Malaya campus. A voucher specimen *KLU 18610* was deposited in the Herbarium, Botany Department of the University of Malaya. The buds and flowers were fixed in formalin-propionic-alcohol while the fruits were fixed in Craf III. Routine methods of microtechnique were employed to obtain sections 8-15μ thick. Fruits in wax blocks had to be immersed for periods up to a month in a softening solution of Molifex (B.D.H. Co., U.K.) before they could be sectioned. The

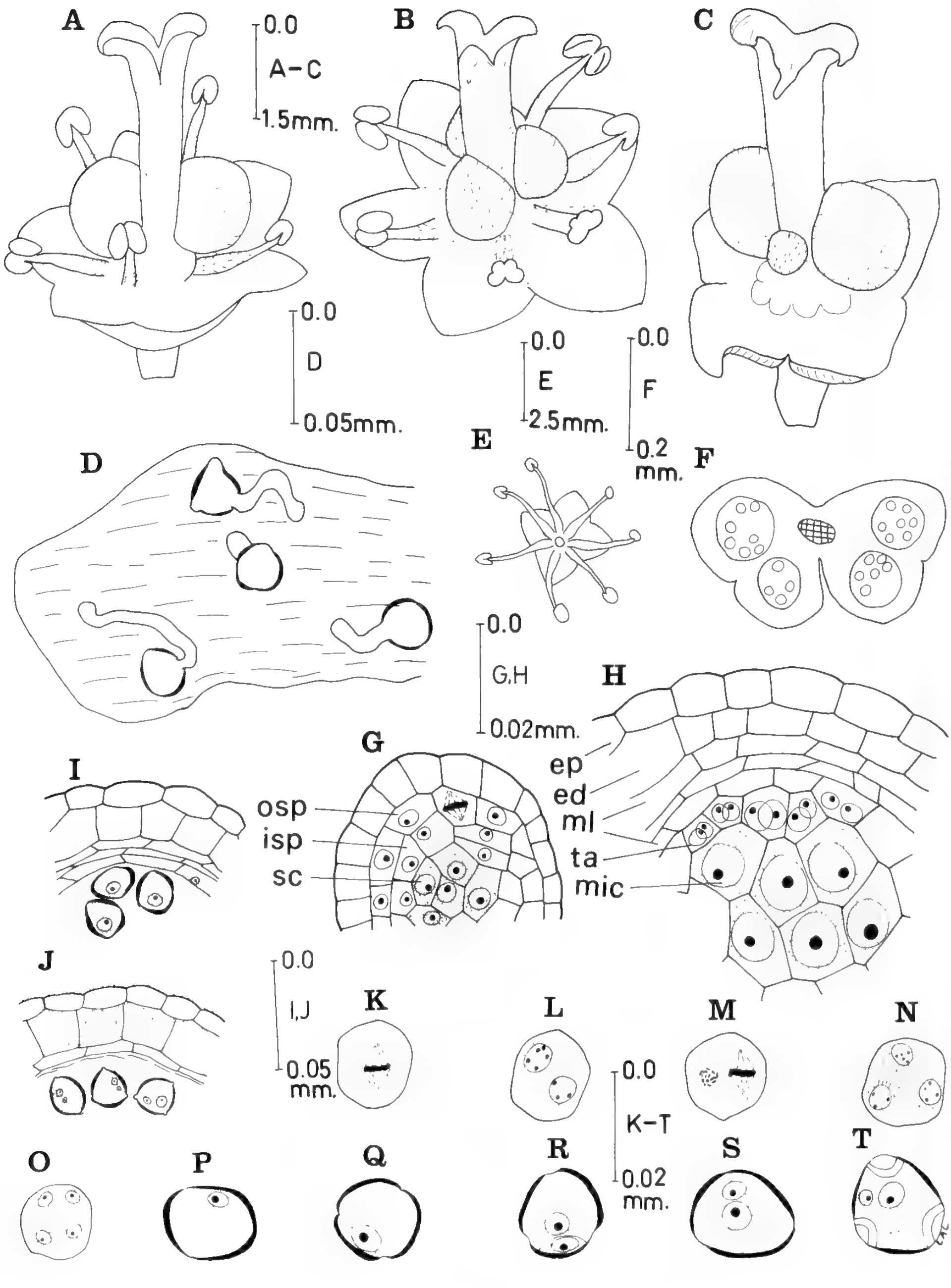

Fig. 1. Floral morphology, microsporangium, microsporogenesis and microgametophyte. (*ed*, endothecium; *ep*, epidermis; *isp*, inner secondary parietal layer; *mic*, microspore mother cell; *ml*, middle layers; *osp*, outer secondary parietal layer; *sc*, sporogenous cell; *ta*, tapetum).
A & B, bisexual flower; *C*, bisexual flower after pollination; *D*, pollen grains germinating on stigma; *E*, male flower, *F*, t.s. tetrasporangiate anther; *G-J*, anther wall at different stages of development; *K-O*, meiosis in microspore mother cells; *P-T*, microspore and a two-celled pollen grain.

mounted fruit sections had to be bleached in a solution made up of potassium dichromate (1 gm), chromic acid (1 gm), glacial acetic acid (10 c.c.) and distilled water (90 c.c.) before staining in safranin. Otherwise the whole embryo sac stains dark purple and this is caused by tannins and other cell inclusions, which mask the cellular organisation. Various concentrations of "Clorox", a commercial bleach, were tried but proved unsatisfactory.

To test pollen viability, the pollen grains from the bisexual and male inflorescences were germinated in various concentrations (2-20%) of sucrose and lactose solutions. The pollen grains from the male inflorescence were used immediately after anthesis while those from the bisexual flowers were released by cutting open mature anther sacs. The pollen grains were examined and pollen tubes measured at 12-hour intervals.

Seed germination and seedling morphology were studied by sowing fresh seeds in garden soil.

Observations and Results

Floral and Fruit Morphology

Flowers are borne on axillary or terminal panicles. The greenish flowers are minute (less than 3 mm wide), without petals (fig 1A, B) and have a pleasant scent. The trees bear either male or bisexual flowers (androdioecious). In a male flower, there are 5-8 anthers supported by white hairy filaments while the gynoecium is small and rudimentary (fig. 1E). In the bisexual flower, the anthers are 5-7 in number and the gynoecium is very well developed with a 2- or rarely 3-locular ovary (fig. 1A, B, C).

The bunched fruits are borne on woody stalks. Depending on the clone, each fruit is oblong to nearly round and it ripens to a red or, less commonly, yellow colour. The rind is covered with thick, soft spines (fig. 4D, F). The edible pulp is white and the taste ranges from sour to sweet. Sour taste and difficulty in detaching pulp from seed are considered poor qualities.

The non-endospermous seed is normally rounded at the micropylar end and pointed at the opposite end. It has a fibrous testa enclosing an embryo with two unequal cotyledons.

Phenology

Depending on the clone, as well as soil and climatic conditions, the tree starts to bear flowers and fruits after 3-5 years. Two distinct flowering seasons are observed in the Malay Peninsula. The first season starts at the beginning of April and the fruits are harvested at the end of July. The second begins mid-August and the harvest is mid-December. The seasonality of the fruits can easily be upset by any change in the pattern of wet and dry season. Most individual trees, however, produce fruits only once yearly; some during the first season and others during the second. Some trees in Serdang are peculiar in that while one side can be laden with ripe fruits, the other half can be just beginning of flower.

After the appearance of the inflorescence, the floral buds (average width 1 mm) take only 3 weeks to develop into mature flowers (average width 3 mm). They open acropetally. Both male and bisexual plants flower synchronously and the flowering period lasts 2-3 weeks. Anthesis is between 0900 and 1100 hours. Ten days after anthesis, the stamens in the bisexual flowers drop off and usually one of the ovules enlarges to form a young fruit (average width 4 mm) (fig. 3C). These fruits mature 12 weeks later and by then the average width is 3.5 cm and length 5.0 cm. The

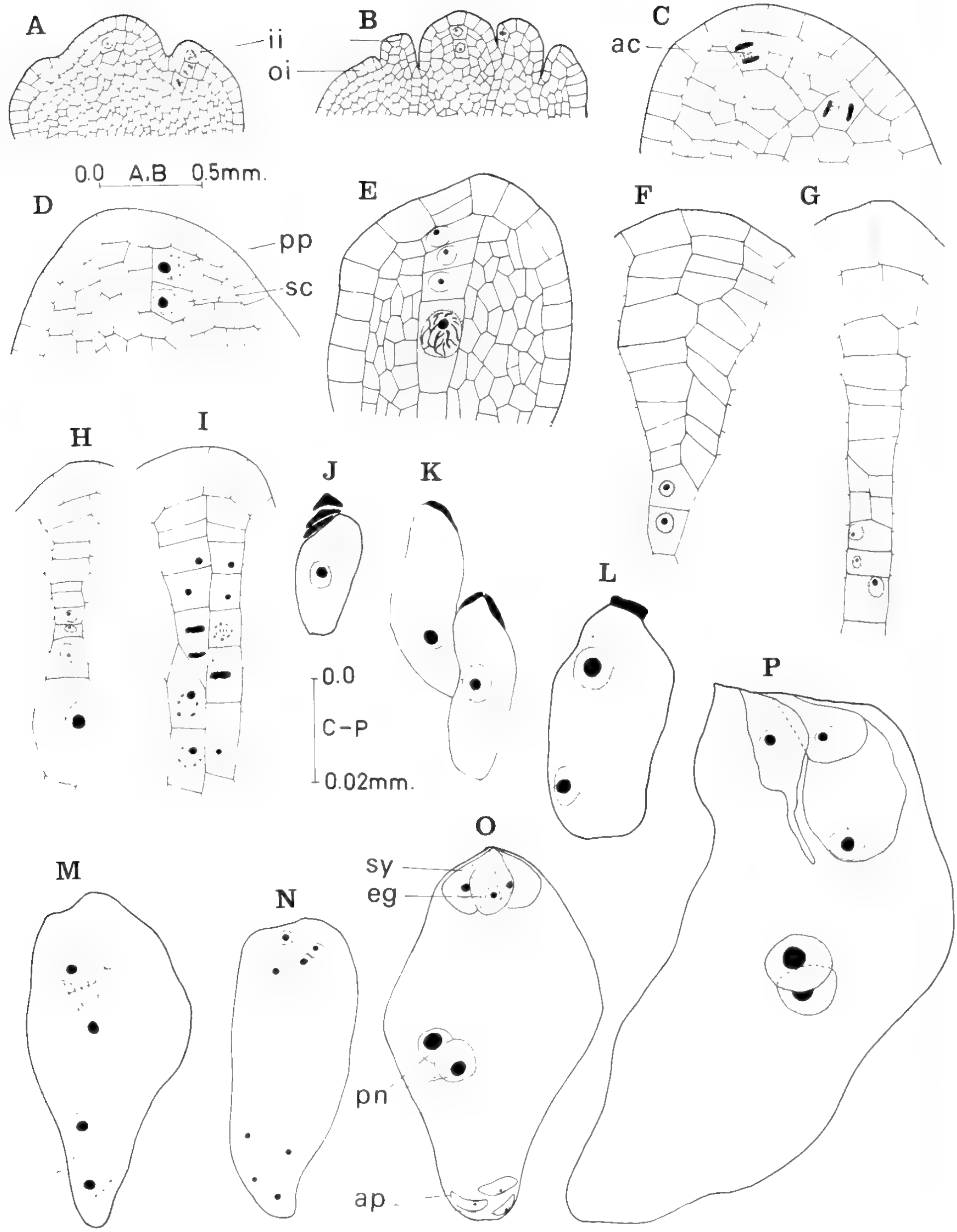

Fig. 2. Megasporogenesis and development of megagametophyte. (*ac*, archesporial cell; *ap*, antipodal; e.g., egg; *ii*, inner integument; *oi*, outer integument; *pn*, polar nucleus; *pp*, primary parietal cell; *sc*, sporogenous cell; *sy*, synergid).
A & B, development of integuments; *C, D*, formation of sporogenous cell; *E-H*, megasporogenesis; *I*, twin tetrads; *J*, functional megaspore; *K*, twin megaspores; *L-O*, development of megagametophyte; *P*, embryo-sac after the degeneration of antipodals.

observation of 10 samples of randomly tagged floral buds, 200 per sample, showed that the average flower abortion was 40% and fruit drop 90%.

Anther Development

The anther development in both male and hermaphrodite flowers is found to be similar except that dehiscence does not occur in the latter. Hence the bisexual flowers are found to be functionally female. The anther is tetrasporangiate and the anther-wall development conforms to the basic type of Davis (1966). The archesporial cells divide periclinally to form the primary parietal and sporogenous cells. The latter differentiate into microspore mother cells while the former divide to form the outer and inner secondary parietal cells. The endothecium and a middle layer are derived from the outer secondary parietal while the inner middle layer and the tapetum are derived from the inner secondary parietal (fig. 1G, H, I). The tapetum is secretory and includes at first uninucleate cells which become binucleate just before the microspore mother cells undergo meiosis.

Simultaneous cytokinesis accompanies meiotic divisions in the microspore mother cell (fig. 1K-O). The tetrads formed are usually tetrahedral but sometimes isobilateral. Stages of development varying from late prophase to microspore tetrad phase had been observed within the same flower. In addition, different locules of the same anther may exhibit different stages of development such as a locule with microspore mother cells at metaphase I while another locule shows microspore mother cells at anaphase II.

Soon after the tetrads are formed, the microspores separate out and at this time, the tapetum and middle layers begin to degenerate (fig. 1I). The nucleus migrates to the periphery of the microspore, giving the latter the characteristic signet ring shape (fig. 1P, Q). It then divides to form a small lenticular generative cell and a large vegetative cell (fig. 1R). At maturity, the pollen grain is binucleate (fig. 1S, T). By the time the microspores become mature pollen grains, the tapetum and the middle layers have degenerated, leaving only the fibrous endothecium and the epidermis in the anther wall (fig. 1J).

The mature pollen grains are smooth, triangular, tricolpate and measure 15-18 μ in diameter. Both male and bisexual flowers produce similar pollen grains. However, most pollen grains in the functionally female flowers are devoid of nuclei and hence are non-viable.

Pollen Germination

Pollen grains from functionally female flowers did not germinate in the conventional media of sucrose or lactose solutions. Those from male flowers showed maximum germination of 39% in 10% sucrose and 56% in 10% lactose solution. The control sample gave 19% germination in distilled water. Further, at optimum sugar concentrations (10% sucrose and 10% lactose), the pollen tubes were longer, i.e., an average length of 0.1 mm while after 24 hours' incubation the average pollen tube length in distilled water was 0.02 mm. Though the pollen grain is tricolpate, germination is monosiphonous.

Anthers from functionally female flowers were squashed to release the pollen grains, which were then dusted on to the stigma of another flower either of the same or a different tree. The inflorescences were bagged before and after the transference of pollen grains to prevent contamination by pollen grains from other flowers. This was performed on flowers *in vivo* because cut inflorescences tend to dehydrate very fast. After 4 hours the flowers were harvested, fixed in polyvinyl lactophenol and stained in lactophenol cotton blue. The nucleate pollen grains could be germinated on the stigmatic tissue (fig. 1D). However, the percentage germination was not calculated as the sample used was small.

Development in Ovule

Within each loculus of the ovary only one ovule, mounted on a thick funicle, is present. The ovular primordium develops from the placenta. The differentiation of the inner integument is followed by that of the outer (fig. 2A, B). Simultaneously one of the hypodermal nucellar cells enlarges to form the archesporial cell (fig. 2C).

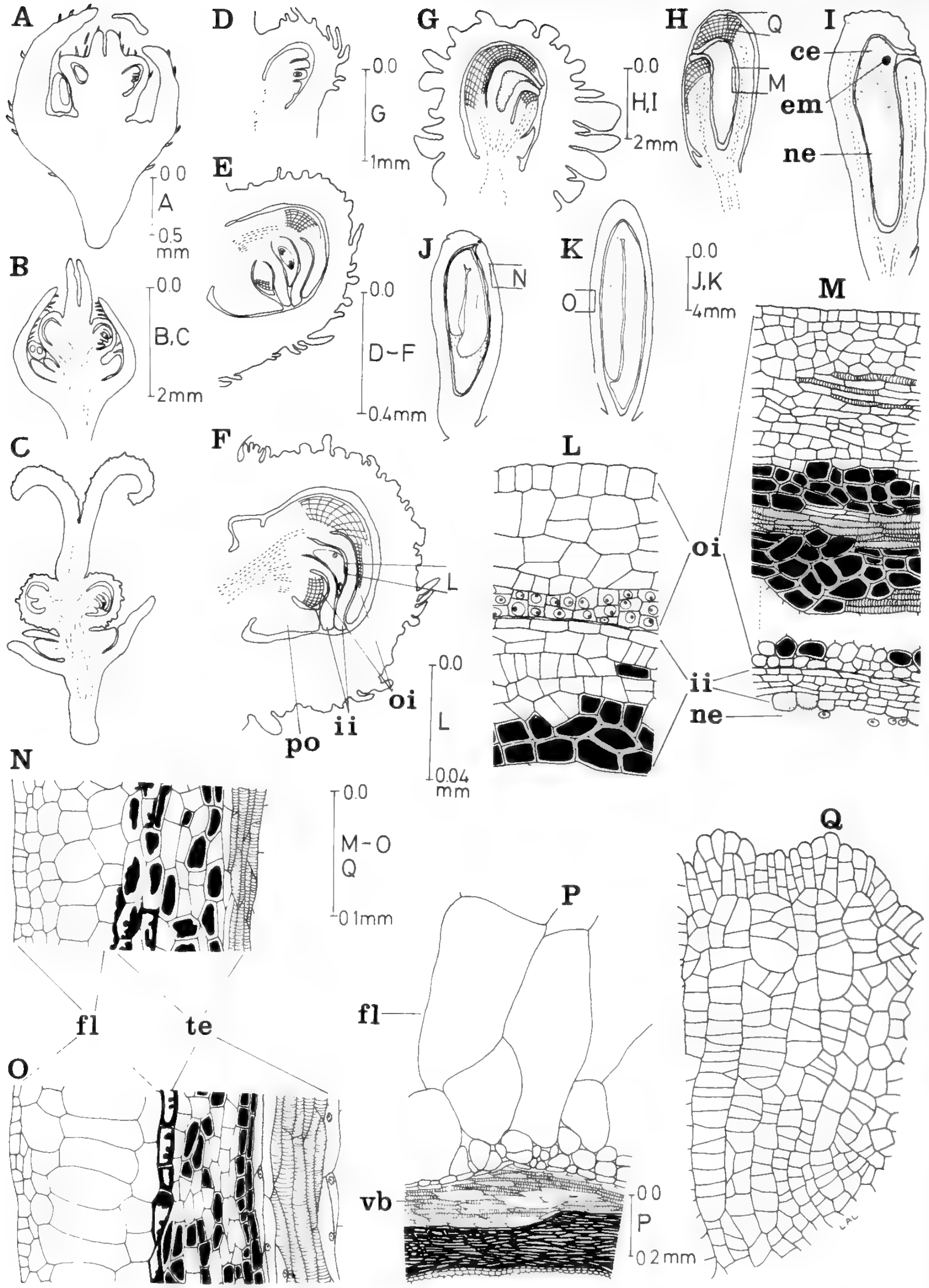

Fig. 3. Development of embryo, fleshy part of fruit, and testa. (*ce*, cellular endosperm; *em*, embryo; *fl*, fleshy part of fruit; *ii*, inner integument; *ne*, nuclear endosperm; *oi*, outer integument; *po*, placental outgrowth; *te*, testa; *vb*, vascular bundle).
A-C, l.s. flower showing ovule development; *D-F*, ovule development; *G & H*, seed differentiation; *I*, globular embryo in seed; *J*, *K*, dicotyledonous embryo; *L*, anatomy of integuments at mature embryo-sac stage; *M*, anatomy of integuments at globular embryo stage; *N-P*, differentiation of testa and fleshy region of seed; *Q*, anatomy of outer integument near micropyle of *H*.

The mature ovule is anacampylotropous, bitegmic, crassinucellate and the micropyle is formed by the inner integument alone (fig. 3E). A placental outgrowth is present at the chalazal end of the ovule (fig. 3F).

The archesporial cell divides periclinally, giving rise to the sporogenous cell and the primary parietal cell (fig. 2C, D) which undergoes further divisions resulting in the crassinucellate ovule. As its cytoplasm becomes denser and the nucleus enlarges, the sporogenous cell becomes the megaspore mother cell (fig. 2E). Following the first meiotic division in the megaspore mother cell, a pair of dyad cells are formed, of which the lower divides further to give a three-celled stage (fig. 2F, G). Later, the smaller, upper, dyad cell undergoes a second meiotic division to give a linear tetrad (fig. 2H). Within an ovule, usually only one embryo sac develops; however, exceptional cases of developing twin embryo sacs had been observed (fig. 2I, 2K). At the completion of meiosis, only the chalazal megaspore differentiates to form the female gametophyte while the other three megaspores degenerate soon after formation (fig. 2J). After three successive nuclear divisions, the megaspore gives rise to the mature eight-nucleate embryo sac (fig. 2L-N). Its development conforms to the monosporic *Polygonum* type. The free nuclei are at first arranged in two groups of four each at opposite poles of the embryo sac. One from each group migrates to the centre (the two polar nuclei) and the remainder organises into the egg, flanked by two synergids at the micropylar end, and by the three antipodals at the other end (fig. 2O). Soon after formation, the antipodals degenerate while the two polar nuclei fuse to form a large secondary nucleus (fig. 2P).

Pollination and Fertilization

N. lappaceum is entomophilous. Though the individual flowers are small, less than 4 mm wide, they are grouped into prominent panicles. Bees and butterflies are attracted by the nectar and presumably also by the sweet fragrance of the flowers. The visits of these insects had been observed to be most abundant during floral anthesis i.e., between 0900-1100 hours.

Preliminary bagging experiments, before and after anthesis, were conducted to determine whether fruit production is dependent on pollination. As the anthers in bisexual flowers do not dehisce, the inflorescences were bagged without the removal of anthers. The flowers are very small and several attempts to remove the anthers at the bud stage fatally damaged the buds. Ten random samples, each of 200 young floral buds (average diameter 1.0 mm), were bagged in butter-paper. All the flowers in these samples dropped off and no fruits were formed. Ten other random samples, each of 200 flowers (average diameter 3 mm), were bagged 5 days after anthesis. These samples did produce fruits and the average percentage of fruit abortion was 92%, very near to the average fruit drop (90%) in separate phenology studies. This shows that there is no significant difference between the fruit set from flowers bagged after anthesis and that from unbagged ones. Bagging thus has no marked deleterious effect on fruit development. In addition, flowers bagged before anthesis could not have been pollinated whereas those bagged after anthesis could have been pollinated by pollen grains from the male trees nearby. This strongly suggests that fruit production is dependent on fertilization or at least pollination stimulus.

Though actual pollen-tube growth and fertilization were not seen, the degeneration of one synergid occurs soon after the fusion of the polar nuclei. Later, only the egg and the secondary nucleus remain.

Endosperm

The development of the endosperm is of the *ab initio* Nuclear type. Just before the primary endosperm nucleus divides, the embryo sac enlarges (fig. 3F). The primary endosperm nucleus undergoes several mitoses and the resulting free nuclei occupy mainly the micropylar region and a position around the periphery of the enlarging embryo sac (fig. 4A). Corresponding to the increase in the number of endosperm nuclei, the embryo sac increases in size at the expense of the nucellus and later of the inner integument. When the embryo sac is about 2 mm long, there are only 3-4 layers of the inner integument at the sides but more at the micropylar

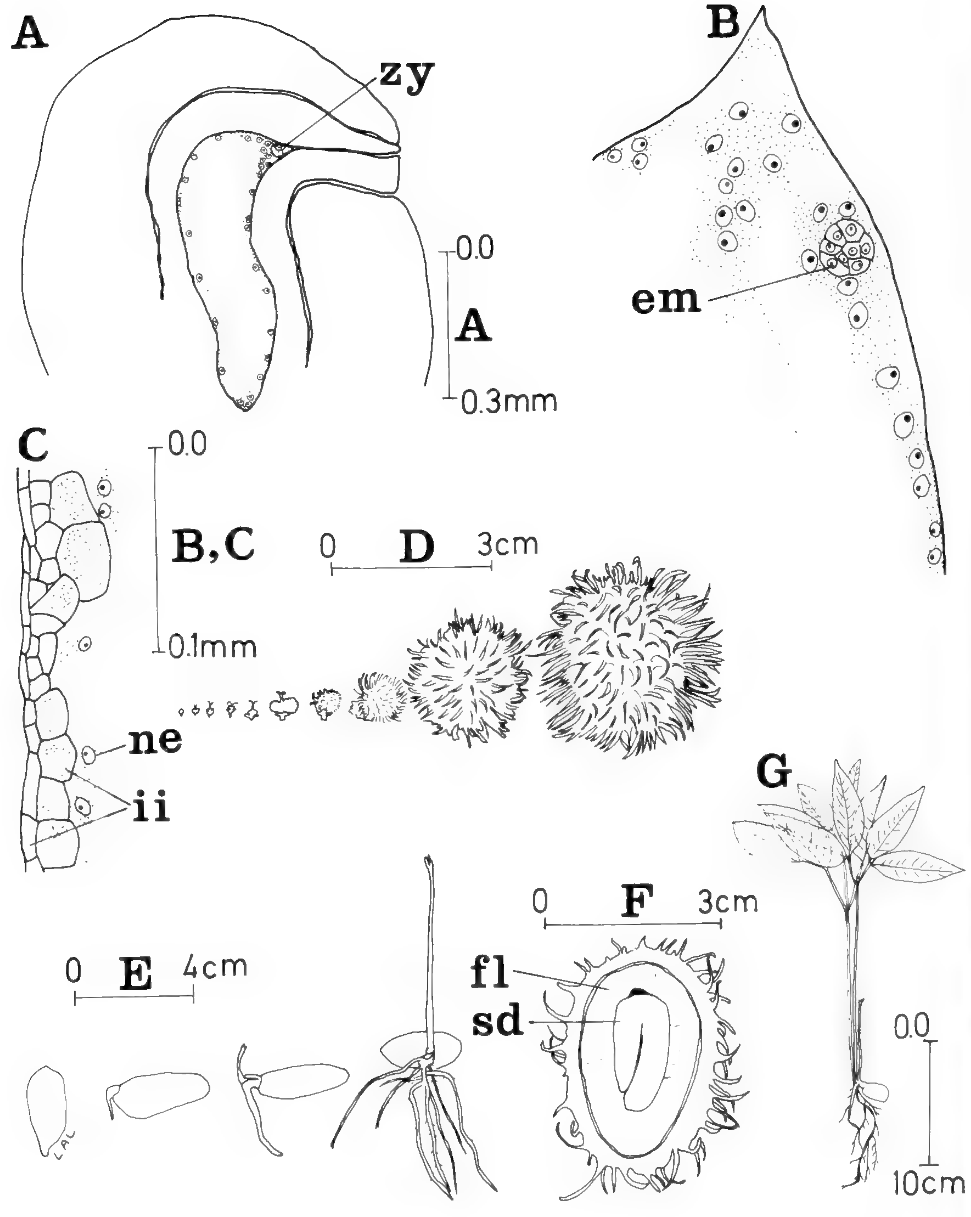

Fig. 4. Embryo, fruit development and seed germination. (*em*, embryo; *fl*, fleshy part of fruit; *ii*, inner integument; *ne*, nuclear endosperm; *sd*, seed; *zy*, zygote).
A & B, nuclear endosperm; *C*, degenerating inner integument cells; *D*, fruit development; *E*, seed germination, *F*, l.s. fruit; *G*, multiple-shoot seedling.

and chalazal regions (fig. 3H, M).

At the chalazal end of the embryo sac, a few cells of the inner integument enlarge to twice or thrice their normal size (fig. 4C). Some of these cells degenerate and release into the embryo sac the contents, which stain darkly with safranin and fast green. The contents are a mixture of tannin, resin and oil. When the embryo sac is 5 mm long, cell formation in the coenocytic endosperm commences at the periphery of the micropylar region and proceeds towards the chalazal end. At the young, globular embryo-stage (± 0.1 mm in width), only a quarter of the embryo sac is filled with cellular endosperm (fig. 3I). Most of the endosperm has become cellular when the embryo is dicotyledonous (fig. 3J), but it is completely absorbed when the embryo matures (fig. 3K).

Embryo

The division of the zygote occurs much later, compared with the formation of the nuclear endosperm. The earliest stage observed is a small globular embryo, 0.02 mm wide, surrounded by numerous endosperm nuclei (fig. 4B). The globular embryo increases in size and later differentiates into a heart-shaped embryo which then forms the mature straight embryo with two unequal cotyledons (fig. 3I-K). Degeneration of the embryo sacs was frequently observed. Often, the fruits increased in size while the embryo sacs remained small and eventually degenerated.

Seed Coat and Flesh of the Seed

The edible flesh of the fruit is derived from the outer integument while the testa is derived from both the outer integument and the remaining inner integument. The inner integument is initiated around the ovular primordium at the archesporial cell stage (fig. 2A), followed by the development of the outer integument (fig. 2B). Both integuments are already prominent at the megaspore mother-cell stage (fig. 3A, D). At the mature 8-nucleate embryo sac stage, the inner and outer integuments are respectively, 6-7 layers and 5-6 layers thick. The subepidermal cells of the outer integument near the chalaza and placental outgrowth have divided such that it is 10-12 cells thick (fig. 3B, E). The vasculature to the integuments is prominent and abundant.

After the degeneration of the antipodals and just before the division of the primary endosperm nucleus, meristematic activity spreads to the innermost cells on the lateral sides of the outer integument (fig. 3F, L). All these cells divide periclinally, hence they are arranged in rows which fan out radially. Simultaneously, cells of the inner integument also divide in that it becomes 10-13 layers thick. Periclinal meristematic activity of the outer integument continues from the chalazal to the micropylar region of the seed during nuclear endosperm formation (fig. 3G). The epidermis of the outer integument, so far, has only undergone anticlinal divisions.

Before the zygote divides, when the seed is about 1 mm long, the outer integument is 15-30 cells thick. The embryo sac has enlarged at the expense of the nucellus and the inner integument and by then the nucellus has been completely absorbed. The outermost cells of the inner integument elongate while those next to the embryo sac degenerate as this increases in size.

When the seed is about 5 mm long, the inner integument is only 3-4 cells thick along the periphery of the embryo sac though it is much thicker at the chalazal and micropylar ends. Meanwhile, rapid cell divisions, which may produce irregular folds, occur at the micropylar end of the outer integument (fig. 3H, Q). The epidermis of the outer integument now divides both anticlinally and periclinally. These cells contain tanniniferous materials. They then enlarge, become turgid with a juicy fluid and the tannin content disappears during ripening.

The seed continues to grow at the expense of the inner integument which is now only 2-3 layers along the wall of the embryo sac, and 5-6 layers at the micropylar end. When the seed measures to 6-8 mm long (at the globular embryo stage) the cells of the outer integument differentiate into an outer region of thin-walled parenchymatous cells and an inner region of sclerenchyma cells, traversed by vascular tissues (fig. 3I). The outer 6-7 layers of cells increase in size and differentiate into the fleshy part of the fruit (fig. 3M-P). The inner layers of the outer integument and the remaining inner integument become compressed to form the long fibres, tanniniferous cells and vasculature of the testa (fig. 3P).

The placental outgrowth of the ovule, very prominent at the mature embryo-sac stage, contributes neither to the formation of the testa nor to the fleshy part of the fruit.

Seed Germination

Fresh seeds take only 7-10 days to germinate and germination is hypogeal, in which the hypocotyl is undeveloped and the cotyledons remain within the testa. The first sign of growth is detected when the cotyledons split and the radicle emerges, growing downwards, while the plumular shoot emerges above the soil level (fig. 4E). It is recurved at first, later growing upright. Two axillary shoots develop from the base of the shoot system but these die off one month after germination. When the seedlings are about 2 weeks old i.e., when the stem is about 8 cm long, the first pair of leaves unfold.

The average percentage of germination of 200 fresh seeds sown in garden soil is 96%. Of the seedlings, 2% possess 2 or 3 shoots which emerge from the same point of the seed and they share one root system (fig. 4G). Probably more than one shoot apex are in the embryo.

Discussion

Nephelium lappaceum is a common, indigenous Malaysian fruit tree with great economic potential. The external morphology has been described by Corner (1952) and Allen (1967).

The plants are functionally dioecious and are either male or bisexual. The stamens in the bisexual flowers have been called 'staminodes' (Ochse, 1961). The term seems inappropriate since the present study shows that though the anthers do not dehisce, they do produce viable two-celled pollen grains which could germinate on a living stigma.

Corner (1952) reports that in *Nephelium,* the relation between the male and bisexual trees is not known. He states "it seems therefore that the male trees are useless though it is possible that the bisexual flowers must be cross-pollinated from the male trees to set fruit". This present study on the bagging of the flowers before and after anthesis strongly suggests that fruit production in *N. lappaceum* is indeed dependent on fertilization or at least pollination. Self pollination cannot occur as the anthers of bisexual flowers are not able to release its viable pollen grains. This seems an effective barrier against inbreeding of the species.

Heterostyly is more elaborate in *Cardiospermum halicacabum* (Nair and Joseph, 1960) and *Litchi chinensis* (Banerji and Chaudhuri, 1944). Both bear 3 types of flowers, which differ from each other mainly in the degree of sexual development. These flower types appear consecutively on the same panicle and are designated as Type I, II and III according to the chronological order of the development (Mustard, 1960). Type I functions as male since the gynoecium is rudimentary, Type II as female as the androecium is underdeveloped and Type III, an intermediate of the two, normally functions as male. The only difference between *N. lappaceum* and *L. chinensis* is that in *N. lappaceum,* the 2 types of flowers are borne on different trees. Yet Whitehead reports (1959) that "the cultivated rambutan is usually monoecious, flowers of both sexes being borne on the same inflorescence".

A large proportion of the flowers and fruits of the Rambutan degenerate during development. Khan (1939) and Mustard (1960) also noted such high percentages of flower and fruit abortion in *L. chinensis.* Khan (1939) reported that only a very small ratio (1:78) of female flowers set fruit. Mustard (1960) was able to reduce total degeneration of embryo sac from 63.1% to 41.0% by partial defloration. The decrease in degeneration in partially deflorated as compared to non-deflorated panicles indicates a competition among flowers. She suggested that water and nutrient deficiencies may be contributing factors, not only to the degeneration of megagametophytes but also the problem of fruit set in *L. chinensis.*

Studies on the embryology of the members in the Sapindaceae are scanty and incomplete except in *L. chinensis* and *Cardiospermum halicacabum.* This present study shows that the anther of *N. lappaceum* is tetrasporangiate and the wall development conforms to the basic type. In the functionally female flowers, degeneration of the pollen grain is common at the various stages of development.

The ovule is bitegmic and crassinucellate and the embryo sac development conforms to the monosporic *Polygonum* type as in other species in the family already studied (Davis, 1966).

The details of embryogeny in *N. lappaceum* are masked by the dense, free-nuclear endosperm and the darkly staining resinous and tanniniferous content of the embryo sac. Within the family the embryogeny of *C. halicacabum* only has been investigated and reported as the Asterad type by Nair and Joseph (1960) but as the Onagrad type by Kadry (1946).

The fleshy pulp of the fruit in Sapindaceae has generated much controversy over the years. Radlkofer (1933) said that the edible fleshy part of *N. lappaceum* is an aril which adnates to the testa. Van der Pijl (1957) and this study show that the fleshy layer is the swollen outer integument and the dry, protective seed coat originates from the innermost layers of the outer integument and the inner integument. In contrast, the edible, fleshy layer of *Nephelium longana* and *L. chinensis* are considered as a free aril (Radlkofer, 1933) or an arillode (Van der Pijl, 1957). The differentiation of the flesh around the micropyle observed here is the same as the exotestal patch described by Corner (1976).

Acknowledgements

I express my sincere thanks to the Vice-Chancellor of the University of Malaya for research facilities and grant which made this study possible. I am grateful to Dr. N. Prakash, University of New England, Australia, for advice and comments.

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A Revision of *Rennellia* (Rubiaceae) in the Malay Peninsula

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EFFECTIVE-PUBLICATION DATE: 7 MAR. 1985

Abstract

Rennellia (Rubiaceae) is revised for the Malay Peninsula. Four species are recognised, *viz.*, *R. elongata* (K. & G.) Ridl., *R. paniculata* K. & G., *R. speciosa* Hk. f. and a fourth, which resembles, but cannot be matched with certainty to, *R. morindiformis* (Korth.) Ridl. A key to the species and varieties is provided, and the taxa are enumerated with descriptions. *R. paniculata* var. *condensa* Wong is newly described.

Introduction

Rennellia Korth. is a small genus native to SE. Asia, with seven recorded species. In the Malay Peninsula, it is represented by four species. *Rennellia* is most closely related to *Morinda* L.; the two genera belong to the tribe Morindeae and share the following characters: inflorescences terminal in origin; flowers 4-5-merous, connate by their calyx tubes and arranged in non-involucrate heads; corolla aestivation valvate; ovary 2-celled, each cell with one ovule; fruits syncarpous.

In the Malay Peninsula, *Rennellia* can be distinguished from *Morinda* by the following key:

Shrubs, trees or lianes; flowering heads individually stalked, arranged in clusters of a few or as a pseudoumbel (but never arranged along a main rachis); flowers many (more than 6) in each flowering head; ovules inserted sub-basally in each locule .... *Morinda* L.

Shrubs or trees, never lianes; flowering heads sessile or individually stalked, arranged in clusters along a main rachis; flowers few (3-6) in each flowering head; ovules inserted on the septum in each locule .... *Rennellia* Korth.

Rennellia was first recorded from the Malay Peninsula by Hooker (in Bentham & Hooker, 1873), who recognised that a plant listed by Wallich as *Morinda speciosa* (Wall. *Cat. 8436,* from Tenasserim in Burma) was identical with a species with several collections from the Malay Peninsula, and that this species in fact belonged to *Rennellia.* Subsequently, Hooker (1880) formally described it as *R. speciosa,* and listed it as occurring in the Malay Peninsula. Later, King & Gamble (1904) described a second species (*R. paniculata* K. & G.) for the Malay Peninsula and Ridley (1939) elevated the status of *R. speciosa* var. *elongata* K. & G. to that of species, *R. elongata* (K. & G.) Ridl.

However, because the keys presented in the accounts of King & Gamble (1904) and Ridley (1923; 1939) rely mainly on the characters of habit and inflorescence structure, the concept of *R. speciosa* came to be based on a mixture of species, and thus the keys were difficult to use.

A fourth species represented by one specimen is here designated only as *Rennellia* sp.; the difficulty in naming it precisely is discussed under the species enumeration.

Characters Useful to the Taxonomy of *Rennellia*

All four species in the Malay Peninsula have a habit ranging from shrub to treelet. There is variation between species in the inflorescence structure, the number of flowers in each flowering head, floral size and leaf venation.

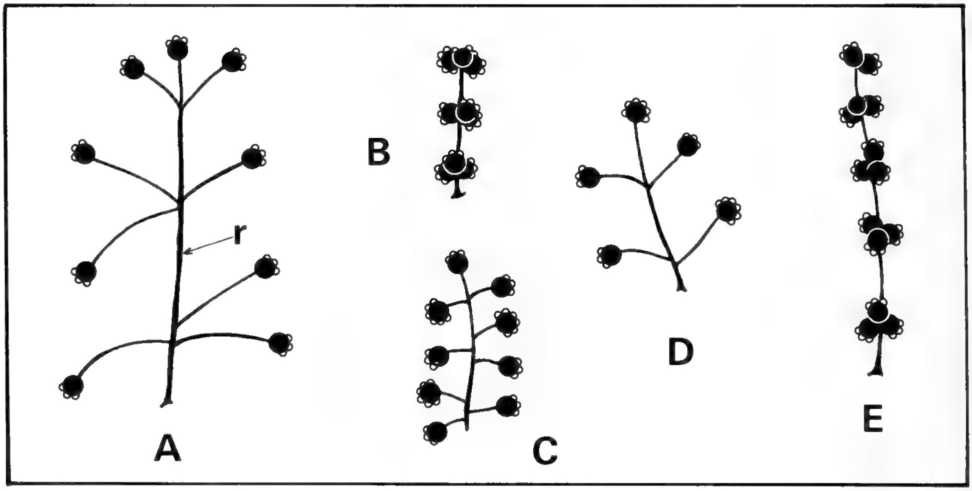

Fig. 1. Inflorescence structure in *Rennellia*.
A, R. paniculata var. *paniculata* (3 flowers per head). *B, R. paniculata* var. *condensa* (3-6 flowers per head). *C, R. speciosa* (3-6 flowers per head). *D, Rennellia* sp. (3-6 flowers per head). *E, R. elongata* (3 flowers per head). *r:* inflorescence rachis.

Plate 1. *Rennellia elongata* in flower *(FRI 32013)*

The flowering heads are individually stalked in *R. paniculata* var. *paniculata, R. speciosa* and the species here designated as *Rennellia* sp., but are sessile on the rachis in *R. elongata* and *R. paniculata* var. *condensa.* The heads are arranged loosely in clusters, recognizable as tiers along the rachis (Fig. 1).

The number of flowers within each flowering head is consistent, 3 for *R. elongata* and *R. paniculata* var. *paniculata* and 3-6 for *R. paniculata* var. *condensa, R. speciosa* and the unnamed *Rennellia* species.

Floral dimensions distinguish the different species reliably. In *R. paniculata* the corolla tube is 6-12 mm long, with lobes 4-9 mm long, while in the unnamed *Rennellia* species the tube is 9-15 mm long with lobes 9-11 mm long. In *R. elongata* and *R. speciosa,* the corolla tube length is 15 mm or longer, the lobes exceeding half its length in *R. elongata* and not half as long in *R. speciosa.*

The species are functionally dioecious. In male flowers, the anthers are normally formed and protrude slightly from the corolla throat while the style is reduced, hardly reaching half the length of the corolla tube. In female flowers, the anthers are smaller, empty, and are completely included within the corolla tube, while the style is slightly exserted from the corolla throat and bears a bifid stigma.

For leaf venation, *R. paniculata* has tertiary veins that are distinctly raised and prominent as a dense network on the leaf undersurface. In *R. elongata, R. speciosa* and the unnamed *Rennellia* species, the leaf undersurfaces have sparse tertiary veins that are hardly distinct.

Key to the Species and Varieties of *Rennellia* in the Malay Peninsula

Leaf undersurfaces with a dense network of prominently raised tertiary veins; secondary veins 11-13 pairs

  Inflorescence rachis 6-9 cm long, flowering heads with stalks 2-3 cm long, with 3 flowers per head, arranged as 2-3 tiers along the inflorescence rachis .... *Rennellia paniculata* var *paniculata*

  Inflorescence rachis 1-3 cm long; flowering heads sessile, with 3-6 flowers each, arranged as 1-3 tiers along the inflorescence rachis .... *Rennellia paniculata* var. *condensa*

Leaf undersurfaces with sparse, hardly distinct tertiary veins; secondary veins 6-11 pairs

  Inflorescence rachis 1.5-3.5 cm long; flowering heads stalked, with 3-6 flowers each

    Flowering heads with stalks less than 1 cm long, arranged as 1-4 tiers along the inflorescence rachis; corolla with tube 15-23 mm long, the lobes less than half the tube length .... *Rennellia speciosa*

    Flowering heads with stalks 1-3 cm long, arranged as 2-3 tiers along the inflorescence rachis; corolla with tube 9-15 mm long, the lobes more than half the tube length ....*Rennellia sp.*

  Inflorescence rachis 8-15 cm long: flowering heads sessile, with 3 flowers each, (flowering heads arranged as 2-12 tiers along the inflorescence rachis) .... *Rennellia elongata*

Systematic Enumeration of Taxa

In the following enumeration, a list of specimens examined for each taxon is provided wherein male and female specimens are marked ♂ and ♀, respectively and specimens with flowers too immature for sex determination are asterisked.

1. **Rennellia elongata** (King & Gamble) Ridley, Kew Bull.: 608 (1939) Plate 1

   Basionym: *R. speciosa* var. *elongata* K. & G., J. As. Soc. Beng. 73: 90 (1904); Ridley, Fl. Malay Pen. 2: 120 (1923).

   Synonym: *R. speciosa sensu* Corner, *pro parte,* Wayside Trees of Malaya 1: 558 (1952).

   Lectotype (here chosen): *Ridley 5834,* Pahang, Tahan River (SING!).

Distribution & Ecology. Sumatra, Malay Peninsula, Borneo (Sarawak). Lowlands to montane forest above 1200 m alt.

Shrub or treelet to 5 m tall. Leaves obovate to elliptic, (3-14) × (10-32) cm, with 6-10 pairs of secondary veins and sparse, hardly distinct tertiary veins. Inflorescence rachis 8-15 cm long, with 2-12 tiers of sessile flowering heads. Each flowering head with 3 flowers. Mature open flowers with corolla tube 15-19 mm long, and corolla lobes 10-15 mm long.

Specimens examined

PERAK: *Curtis s.n.* 25. xii. 1901, Larut Hill (SING!, ♀); *Sow KEP 47232,* Sg. Penuh (KEP!, ♀). SELANGOR: *Ahmad KEP 94290,* Ulu Gombak (KEP!, K, ♀); *Gadoh & Millard K.L. 494,* Ulu Langat (KEP! ♀); *Gadoh & Millard K.L. 2247,* Ulu Langat* (KEP!); *Hume 8980,* Genting Simpah* (SING!); *Stone 5986,* Fraser Hill (SING!, ♂); *Whitmore FRI 15721,* Ulu Gombak (KEP!, ♀); *Wong FRI 32013,* KEP F.R. grds (KEP!, ♀); *Wong,* s.n., 4. iii. 1981, Bt. Lagong (KEP!, ♂); Wyatt-Smith *KEP 60635,* Bt. Lagong (KEP! ♂); *Wyatt-Smith KEP 79199,* Ulu Gombak (KEP!, ♂). NEGRI SEMBILAN: *Everett KEP 104912,* Jelebu (KEP!, K, ♀). KELANTAN: *Whitmore FRI 4081,* Sg. Nenggiri nr Kg. Jenera (KEP!, K, ♀). TRENGGANU: *Moysey & Kiah SFN 33827,* Ulu Brang (SING!, ♀). PAHANG: *Ang FRI 23312,* Taman Negara (KEP!, K, ♀); *Henderson FMS Mus. 10548,* Temerloh, Titi Bungor (SING!, ♀); *Md. Shah MS 1517,* K. Kenyam (KEP!, K, ♂); *Md. Shah & Md. Noor MS 1768,* Ulu Sg. Sat nr Kelepah (KEP!, ♀); *Ng FRI 27272,* Tekam F.R. (KEP!, ♀); *Ng & Beltran FRI 6447,* Jerantut, Ulu Tekam (KEP!, K, ♀); *Ridley 5834,* Tahan River (SING!, ♀); *Ridley, s.n.,* 1891, Tahan (SING!, ♀). JOHORE: *Corner, s.n.* 9. ix. 1934, Mawai (SING!, ♂); *Vethevelu FRI 25287,* Kota Tinggi (KEP!, K, ♀); *Whitmore FRI 8764,* NW. G. Blumut (KEP!, K, ♂).

2(a) Rennellia paniculata King & Gamble, var. *paniculata.*
J. As. Soc. Beng. 73: 89 (1904); Ridley, Fl. Malay Pen. 2: 119 (1923).
Synonym: *R. speciosa sensu* Corner, *pro parte,* Wayside Trees of Malaya 1: 558 (1952).

Lectotype (here chosen): *King's Coll. 2592,* Perak, Larut, 3000-4000 ft. (K!).

Distribution & Ecology. Malay Peninsula (endemic). Montane forest at about 1000-1300 m alt.

Shrub or treelet to 8 m tall. Leaves obovate to elliptic, (4-9) × (10-22) cm, with 11-13 pairs of secondary veins and a dense network of distinctly raised tertiary veins on the undersurface. Inflorescence rachis 6-9 cm long, with 2-3 tiers of stalked flowering heads (the stalks 2-3 cm long). Each flowering head with 3 flowers. In mature open flowers, corolla tube 6-12 mm long, and corolla lobes 4-9 mm long.

Specimens examined

PERAK: *King's Coll. 2164,* Larut, 3000-3500 ft. (K! ♀); *King's Coll. 2592,* Larut, 3000-4000 ft.* (K!); *King's Coll. 5432,* Larut, 3000-3500 ft. (SING! K ♀).

(b) Rennellia paniculata var. *condensa* Wong, **var. nov.**
Synonym: *R. speciosa sensu* K. & G., *pro parte,* J. As. Soc. Beng. 73: 89 (1904); *sensu* Ridley, *pro parte,* Fl. Malay Pen. 2: 120 (1923).

Varietas affinis *Rennellia paniculata* var. *paniculata* sed inflorescentia 1-3 cm longis, capitulis floriferis sessilis, 3-6 floribus, in 1-3-fasciculatis disposita differt.

Holotype: *Curtis, s.n.,* Dec. 1895, Perak, Bujong Malacca (SING!).

Distribution & Ecology. Malay Peninsula (endemic). Lowlands to hill forest at about 300 m alt.

Shrub or treelet to 5 m tall. Leaves obovate to elliptic, (4-10) × (16-32) cm, with 11-13 pairs of secondary veins and a dense network of distinctly raised tertiary veins on the undersurface. Inflorescence rachis 1-3 cm long, with 1-3 tiers of sessile heads. Each flowering head with 3-6 flowers. Mature open flowers with corolla tube 6-12 mm long, and corolla lobes 4-9 mm long.

Specimens examined

KEDAH, *Kochummen FRI 2021,* G. Inas F.R. (KEP! K, ♀). PENANG, *Abrams s.n.* vi. 1890 (SING! ♀). PERAK, *Curtis 3345,* Ipoh (SING!, ♀); *Curtis s.n.* xii. 1895, Bujong Malacca (SING! ♀); *Haniff & Nur SFN 6985,* Sg. Siput (SING!, ♀); *Hashim KEP 9663,* Ijok F.R. (SING!, ♀); *Ng FRI 6083,* Bubu F.R., Sg. Wang (KEP!, ♀); *Ogata KEP 110224,* Tapah, Changkat Jong F.R.* (KEP!); *Wray 2897* (SING!, ♀); *Wray 4008,* Larut, Relau Tujor (SING! ♂).

3. **Rennellia speciosa** Hk. f., Fl. Brit. Ind. 3: 158 (1880); King & Gamble, *pro parte,* J. As. Soc. Beng. 73: 89 (1904); Ridley, *pro parte,* Fl. Malay Pen. 2: 120 (1923); Corner, *pro parte,* Wayside Trees of Malaya 1: 558 (1952).

Holotype: *Wallich, Cat. 8436,* Burma, Tenasserim, Chappadong Hill (K!).

Distribution & Ecology. Burma, Thailand, Malay Peninsula, Borneo (Sarawak). Lowlands to hill forest at about 500 m alt.

Shrub or treelet to 7 m tall. Leaves obovate to oblanceolate to elliptic, (3-12) × (10-30) cm, with 8-11 pairs of secondary veins and sparse, hardly distinct tertiary veins. Inflorescence rachis 1.5-3.5 cm long, with 1-4 tiers of stalked flowering heads (the stalks less than 1 cm long). Each flowering head with 3-6 flowers. Mature open flowers with corolla tube 15-23 mm long, and corolla lobes 6-7 mm long.

Specimens examined

LOWER THAILAND: *Curtis 3000,* Poongah (SING!, ♀). KELANTAN: *Cockburn FRI 7187,* Ulu Sg. Aring (KEP!, K, ♀); *Cockburn FRI 7462,* Ulu Kelantan, Sg. Jenal (KEP!, K, ♀); *Md. Shah & Ahmad MS 3211,* Machang, Bt. Baka, Sg. Jeram Tinggi* (KEP!, SING!); TRENGGANU: *Corner s.n.,* 31.x. 1935, Kemaman, Bt. Kajang (SING!, ♀); *Md. Shah & Samsuri MS 3549,* Jerteh, Bt. Yong, Sg. Tok Barak* (KEP!, SING!); *Md. Shah & Samsuri MS 3805,* path to Bt. Bongkok, via Kg. La* (KEP!, SING!); PAHANG: *Md. Shah MS 1315,* K. Tahan (KEP!, SING!, K, ♀); *Md. Shah MS 1348,* Sg. Teku (KEP!, SING! ♀); *Whitmore FRI 4805,* K. Teku (KEP! K, ♂); *Wong & Wyatt-Smith W 47,* Ascent G. Tahan (KEP!, ♀). MALACA: *Alvins 562** (SING!); *Alvins, 710,* Selandar* (SING!) *Alvins 2038,* Merlimau (SING!, ♀); *Alvins s.n.* 18.iv. 1886, Merlimau (SING!, ♀); *Alvins 2101,* Chabau (SING!, ♀); *Alvins s.n.* 9. ii. 1886* (SING!); *Hervey s.n.,* 1891 (SING!, ♀); *Ridley s.n.,* 1891, Ayer Panas (SING!, ♀); JOHORE: *Corner SFN 29030,* 14 m. Mawai-Jemaluang Rd (SING!, K, ♀); *Fox s.n.,* 1902, Muar (SING!, ♀); *Hardial & Samsuri H.S. 1008,* Datok Sawah* (SING!); *Kiah SFN 32309,* Sg. Kayu (KEP!, ♀).

4. **Rennellia** sp.

Shrub or treelet to 6 m tall. Leaves obovate to elliptic, (4-9) × (6-22) cm, with 8-10 pairs of secondary veins and sparse, fine tertiary veins. Inflorescence rachis 1.5-3 cm long, with 2-3 tiers of stalked flowering heads (the stalks 1-3 cm long). Each flowering head with 3-6 flowers. Mature open flowers with corolla tube 9-15 mm long and corolla lobes 9-11 mm long.

Specimen examined

PAHANG: *Purseglove P. 4311,* Fraser's Hill, Ring Road, 4000 ft. alt. (K! SING! ♀).

This species, represented only by one specimen in the Malay Peninsula, is possibly the same as *R. morindiformis* (Korth.) Ridl. (Ridley, 1939), typified by the specimen *Korthals, s.n.,* from Mt. Singalang in Sumatra (holotype at Leiden, isotype at Kew).

The Korthals specimen which typifies *R. morindiformis* has flowers represented only in the bud stage and it is not possible to ascertain the dimensions of mature flowers without further collections of this species from the type locality in Sumatra. The Purseglove specimen from the Malay Peninsula (where it is the only collection of its kind) has mature flowers and matches the Korthals specimen in vegetative and inflorescence structure. One disparity is the labelling of the Purseglove specimen as a treelet and the labelling of the Korthals specimen as *"pseudo-parasiticus."* However, the habit of species of *Rennellia* ranges from shrublets to treelets and I have personally observed *R. elongata* to grow from hollows of tree boles as well as to stand independently as treelets; the habit may therefore be confusing to the collector at times. I am not willing to name the Purseglove specimen as a distinct species as present evidence allows this to be matched to *R. morindiformis.* Still, it is worthy to remember that the structure of mature flowers of *R. morindiformis* can only be elucidated with further collections from its type locality. Purseglove's label on his specimen identifies it as "R. longiflora Ridl." but that is an unpublished name.

Acknowledgements

I wish to thank the Keepers of the herbaria at Bogor, Kew and Singapore who have generously made available photographs of reference specimens and herbarium loans for study. I am grateful to Diane Bridson at Kew, and Ruth Kiew at the Agricultural University of Malaysia for their criticisms.

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Keys to the Cultivars of Keladi *(Colocasia esculenta* — Araceae) in Peninsular Malaysia

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Abstract

Colocasia esculenta (Araceae), the Keladi or *taro,* is an ancient staple food crop of the Asian and Oceanic Pacific populations. In Peninsular Malaysia, collections have reached 50 cultivars but only two of them are commercially cultivated. Confusion exists in the identification of these cultivars, which is attributed to loose usage of vernacular names. In this study a key to these cultivars is presented, one which has been worked out from plants grown *in situ* and replanted in experimental plots. Only stable morphological and behavioural characteristics have been used in differentiating the cultivars.

Introduction

The Araceae, a family of about 115 genera and over 2000 species, is of worldwide distribution, but 92% of the species are native to the Asiatic and American tropics. The centres of greatest diversity are Brazil and the Indo-Malaysian region (Watt, 1889; Burkill, 1935; Chang, 1958; Keleny, 1962; Leon, 1976). In Peninsular Malaysia alone there are some 23 genera and 120 species (Henderson, 1954).

The family is often an important component of tropical forests especially the rainforest. There is considerable diversity of form in the family, as well as evident adaptation to several rather different habitats. Some genera have become well-known in cultivation either as ornamental plants, such as *Aglaonema, Dieffenbachia, Caladium, Scindapsus, Syngonium, Philodendron, Raphidophora,* and genera with colourful inflorescences such as *Anthurium, Spathiphyllum, Typhonium,* and *Zantedeschia* or as useful plants providing food, occasionally the fruit (as *Monstera)* or, more usually, the enlarged subterranean storage organs or corms (*Alocasia, Amorphophallus, Colocasia, Cyrtosperma,* and *Xanthosoma*). One genus, *Pistia,* has become highly specialized as a floating aquatic plant.

The Araceae are divided into eight subfamilies on morphological and anatomical grounds (Engler & Prantl, 1889; Engler & Krause, 1920). Each subfamily is in turn subdivided into tribes. The genera with edible subterranean corms are in two subfamilies, *Lasioideae* and *Colocasioideae.* The first of these consists of terrestrial or paludose shrubs with sagittate, multiparted leaves with reticulate venation. They have either bisexual or unisexual flowers, anatropous ovules, and ex-endospermous seeds. The fibrovascular bundles have superposed simple laticiferous cells. *Cyrtosperma* and *Amorphophallus* are included in the *Lasioideae.*

The *Colocasioideae* contains the useful genera *Colocasia, Alocasia,* and *Xanthosoma.* The first two are Asiatic, the last is an American genus. These plants are usually found in wet or swampy ground, have spirally arranged long-petiolate leaves with a sagittate lamina or with a pair of posterior lobes, and with reticulate venation. The petiole is peltately attached to the lamina. The flowers are unisexual and the plants are monoecious, the ovules anatropous or orthotropous. The laticiferous cells are fused, anastomosing in the fibrovascular bundles.

The genus *Colocasia* is one of the most important useful genera. There are seven species, according to Engler & Prantl (1889), all indigenous in Asia (Bentham

& Hooker, 1883; Conner, 1908). The best known species, *Colocasia esculenta,* was first described as *Arum esculentum* by Linnaeus in 1775 (Hill, 1952), who also described simultaneously *Arum colocasia.* Schott established the genus *Colocasia* in 1832 and renamed Linnaeus's species as *C. antiquorum* and *C. esculenta.* While some disagreement remains over these "species" many botanists now recognize one species, though some divide this into subspecies or varieties (Purseglove, 1975). For example, *Colocasia esculenta* may be regarded as consisting of two varieties, var. *esculenta* (syn. var. *typica* A. F. Hill) and var. *antiquorum* (Schott) Hubb. & Rehd.

At the cultivar level, however, there are many more entities, and there has never been a complete classification of the cultivars. Since *Colocasia* plants are normally propagated vegetatively, each region or country tends to have and perpetuate its own "forms" of which at least 1000 are thought to exist (Kay, 1973).

Owing to the plasticity as well as the morphological and behavioural diversity of these plants, and to a prior lack of collections and descriptions, there are very few adequate references to permit the accurate identification of cultivars.

Cytological and karyological studies of the Keladi have been carried out to some extent but, although several workers have been involved, their findings are inconclusive (Ito, 1942; Rao, 1947; Delay, 1951; Yen & Wheeler, 1968; Marchant, 1971).

Local Cultivars of *Colocasia esculenta*

In Peninsular Malaysia the common name "Keladi" refers not only to *Colocasia* but to all similar tuber- and corm-bearing plants including species of *Alocasia, Amorphophallus,* and even unrelated plants such as *Eichhornia crassipes* (Water Hyacinth; Watson, 1896; Burkill 1935; Furtado 1937, 1940). However, in the present paper, "Keladi" is used strictly for referring to *Colocasia.*

Cultivars are usually provided with vernacular names and they are propagated by vegetative means; hence each is a clone (Allen 1940; Chee and Low 1976; Ghani 1979). The cultivar name may be descriptive or not, and may be known only regionally.

Though local names have proved helpful, much confusion exists because of the numerous cultivars, their diversity and plasticity. It is believed that strict definitions and careful use of the cultivar names is worth achieving, thus permitting better communication between growers and research workers.

Collection and Identification

All plants located during collection trips were first observed *in situ,* and descriptions of them drawn up. Later they were transferred to prepared experimental plots. Repeated visits were made to the original collection sites to observe growth, and these observations formed a basis for comparison with similar ones made on the plot-grown plants.

Identifications were made using reference specimens preserved in the Herbarium of the Botanic Gardens, Singapore (SING). From these, and primarily from the living plants, the identification key was prepared. Characters were tested for consistency and reliability over a four-year period of study.

A model for the key and characteristics used has been the classic study by Whitney (Whitney *et al.,* 1939) on Hawaiian taro varieties. Characteristics of the developmental stages of the crop, descriptions of the inflorescences (where available) and longevity have all been utilised.

The crop cycle of the cultivars is important in identifying the maturity phase i.e. the mid-crop period. At this stage the colour and markings of the leaf lamina, petioles, corm flesh, leaf shape and size, number, length and colour of stolons and rhizome are stable characters for identification purposes.

During the first few months of growth, while the plant attains height and enlargement of corm size, and produces new leaves in increasing numbers, the morphological characters are in a state of flux. At mid-crop, maximum plant height, leaf number and leaf size are attained, after which there is a decline, until at harvest when leaf number is reduced to 2-3 and plant height reaches between 30 and 40 cm.

Corms of the Keladi cultivars observed over the 4-year experimental period exhibited consistent differences in configuration, which are useful in grouping the cultivars *viz.*, corm occurring singly and surrounded by cormels of the same size or different sizes, shapes of branching corms, and presence or absence of stolons.

These characters have been used to initiate a preliminary key for identifying the Malaysian Keladi cultivars. Ongoing research and observations could be used to update useful characters and contribute towards a better key.

Grouping of Cultivars

GROUP I. Crop cycle 9 to 11 months: — plants tall, 80-110 cm; petioles upright or spreading, thick; leaves sagittate.

Subgroup Ia:— corms single, cylindrical with ends tapered; plants producing stolons.

Subgroup Ib: — corms single, cylindrical or globose, surrounded by cormels.

GROUP II. Crop cycle 6 to 8 months: — plant-height medium, 50-70 cm; petioles upright or spreading, slender, leaves sagittate or cordate.

Subgroup IIa:— parent corm globose, with stolons producing plants close to the parent corm, giving rise to "thick" clumps of plants of uniform height. Stolon plants produce 10-12 smaller globose cormels closely arranged around the parent corm.

Subgroup IIb:— corms cylindrical, single, without stolons.

GROUP III. Crop cycle 5-6 months: — plants short, 30-50 cm tall, petioles slender, outspreading, leaves small and cordate.

Subgroup IIIa:— parent corm single, not branching, surrounded by 6-8 cormels of similar size and shape.

Subgroup IIIb:— corm branching, appearing like clump of 6-8 corms.

GROUP IV. Crop cycle indefinite:— leaves and petioles not acrid (edible). Corms reduced (rhizomatous), acrid (inedible).

Plates 1 & 2. Vegatative characters of some cultivars of *Colocasia esculenta*. *1, left,* Keladi cina; *2, right,* Keladi udang.

Plates 3 & 4. Vegetative characters of some cultivars of *Colocasia esculenta.* 3, *left,* Keladi minjak, 4, *right,* Keladi banjar.

KEY TO PENINSULAR MALAYSIAN Keladi CULTIVARS

Key to Groups I — IV

1. Crop cycle 5-6 months .... GROUP III

1' Crop cycle longer or indefinite

  2. Crop cycle 6-8 months .... GROUP II

  2' Crop cycle longer or indefinite

    3. Crop cycle 9-11 months .... GROUP I

    3' Crop cycle indefinite .... GROUP IV

Key to Keladi Cultivars of Group I

1. Parent corms 20-24 cm long, 10-12 cm wide, single, cylindrical, tapered at both ends, producing numerous (8-10) stolons

  2. Leaf lamina not variegated or mottled over entire surface in white, yellow and green

    3. Main veins on the under-surface of lamina not purplish black. Lamina in shades of green

      4. Laminar sinus purplish black-pink, the colour extending only to the petiole, the piko* green, lamina sagittate .... **Keladi cina (Plate 1)**

      4' Laminar sinus deep red, the colour extending to all main veins on lower surface, the piko reddish green, lamina not sagittate .... **Keladi udang (Plate 2)**

    3' Main veins on under-surface purplish black .... **Keladi batang hitam**

  2' Leaf lamina variegated or mottled in white, yellow and green .... **Keladi air**

1' Parent corms 15-18 cm long, 8-9 cm wide, single, cylindrical, surrounded by 5-7 smaller cormels, without stolons at maturity

  5. Lamina with upper surface glaucous dark green and lower surface green; veins and undulating margin purplish red .... **Keladi nibong merah**

  5' Lamina with upper and lower surface and margin otherwise

    6. Lamina with upper surface waxy green and lower surface light green; veins conspicuously ridged, white to cream .... **Keladi minyak (Plate 3)**

    6' Lamina surfaces not as above and veins not ridged

      7. Petioles purplish black throughout except for the white base .... **Keladi serakit hitam**

      7' Petioles not entirely purplish-black

        8. Petioles pale green throughout except for the greenish-yellow base .... **Keladi batang hijau**

        8' Petioles otherwise

          9' Corm flesh yellow, flecked with pale brown fibres .... **Keladi serakit putih**

          9' Corm flesh creamy white, flecked with brownish yellow fibres .... **Keladi banjar (Plate 4)**

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*Centre of the leaf lamina

Key to Keladi Cultivars of Group II

1. Parent corm globose, 10 cm diameter, surrounded by cormels (6-8) of same size

    2. Leaf cordate and pendant

        3. Lamina: upper surface wrinkled, piko green .... Keladi cincang wangi

        3' Lamina: upper surface not wrinkled, piko black splashed .... Keladi pinang (Plate 5)

    2' Leaf not cordate and not pendant, lamina broad sagittate and cupped .... Keladi putih

1' Parent corm not globose, 8-10 cm diameter, 15-18 cm long; tapered at both ends, surrounded by 6-8 smaller cormels or stolons

    4. Lamina: upper surface glaucous dark green; margin undulating and blackish purple; veins on the lower surface purplish red .... Keladi bantan (Plate 6)

    4' Lamina: surfaces, margin and veins not as above

        5. Petiole reddish purple and with green longitudinal stripes throughout except for the purplish base .... Keladi songket ungu

        5' Petiole not reddish purple

            6. Petiole creamy white with green longitudinal stripes .... Keladi songket hijau

            6' Petiole otherwise

                7. Corm flesh lilac purple, without fibres .... Keladi dara

                7' Corm flesh reddish orange, with brown fibres .... Keladi kelapa

Key to Keladi Cultivars of Group III

1. Parent corm non-branching, cormels small, 10 cm diameter, globose (or cylindrical, 10 cm wide, 10-12 cm long)

    2. Petiole light green with dark green striations

        3. Petiole base and collar ring yellow or brown .... Keladi lilin

        3' Petiole base and collar ring pinkish purple .... Keladi dara

    2' Petiole not entirely green, with purple and white striations .... Keladi tongsan

1' Parent corm branching at apex .... Keladi peladang

Key to Keladi Cultivars of Group IV

1. Tall plants 80-100 cm high; rhizome underground

    2. Petiole greenish yellow throughout, with the basal zone white

        3. Leaf sagittate, the upper surface wrinkled .... Keladi huma

        3' Leaf not sagittate, the upper surface smooth, glossy .... Keladi air

    2' Petiole colour not as above, but with purplish green streaks; petiole-lamina junction pinkish .... Keladi belang hijau

1' Shorter plants, less than 80 cm high; rhizome underground, acrid

        4. Petiole with alternate bands of blackish green and light green

            5. Leaf narrowly sagittate; lamina margin undulating .... Keladi hutan

            5' Leaf not narrowly sagittate; lamina margin smooth .... Keladi liar

Plates 5 & 6. Vegetative characters of some cultivars of *Colocasia esculenta* 5, *left*, Keladi pinang; 6, *right* Keladi bantan.

4' Petiole without markings, light green throughout, the basal zone white and the collar ring dark green .... Keladi kubis

Acknowledgements

I wish to thank En. Hassan Basir, En. Abd. Rahim Osman, En. Saad Hamid of the Botany Department, Universitit Kebangsaan Malaysia for their assistance during the numerous collection trips; Cik Normadiah Omar for typing this manuscript; and Dr. Abd. Latiff Mohamed of the same Department for his valuable comments. I am grateful to Dr. B. C. Stone for his constant encouragement and willing advice.

This work is supported by the International Foundation for Science, Sweden (Grant R269).

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Notes on the Systematy of Malayan Species of *Chionanthus* (Oleaceae)

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Abstract

Examination of Blume's type specimens shows that *Chionanthus platycarpus* (K. & G.) Kiew is synonymous with *C. callophyllus* Bl. and *C. elaeocarpus* (Stapf) Kiew is synonymous with *C. macrocarpus* Bl. Two new records of *Chionanthus* for Malaya are *C. grandifolius* (Elmer) Kiew (previously only recorded from the Philippines) and *C. curvicarpus* **sp. nov.** (formerly known as *C. cuspidatus* Bl. *sensu* Merrill).

Sabbatical leave gave me the opportunity of examining at the Rijksherbarium, Leiden, Blume's types (and other specimens determined by him) of *Chionanthus*, which show that several of the names of Malayan species need to be changed.

1. **Chionanthus macrocarpus** Blume

Mus. Bot. Lugd. Bat. 1 (1850) 319. Typus: Java, Herb. Lugd. Bat. 908. 161... 213 (L, lecto, here chosen).

Linociera macrocarpa (Bl.) Knobl. Bot. Centralbl. 61 (1895) 87; King & Gamble J. As. Soc. Beng. ii 74 (1905) 267; Back. & Bakh. f. Fl. Java 2 (1965) 214, *non* (*C. macrocarpus sensu Kiew* Mal. For. 42 (1979) 271).

Chionanthus insignis Miquel Fl. Ind. Bat. Suppl. (1862) 559.
Typus: *Teysmann*. Palembang, Sumatra (BO, K, L, syntypes); *pro parte* *Linociera insignis* (Miq.) C.B.Cl. in Hooker f. Fl. Brit. Ind. 2 (1882) 610; *pro parte* Ridley Fl. Mal. Pen. 2 (1923) 316.

Linociera elaeocarpa Stapf Kew Bull. (1915) 115; Typus: *Beccari PB 725* (K, holo). Merrill J. Str. Br. R. As. Soc., Spec. No. (1921) 488. *Chionanthus elaeocarpus* (Stapf) Kiew var *elaeocarpus* Mal. For. 42 (1979) 267; 43 (1980) 373; 44 (1981) 150.

Notes

Examination of the specimens of *Chionanthus macrocarpus* at Leiden annotated by Blume shows no differences between *C. macrocarpus* from Java and the Bornean type specimen of *Linociera elaeocarpa* Stapf. Specimens cited as *C. elaeocarpus* (Stapf) Kiew (Kiew 1980, 1981) are therefore also those of *C. macrocarpus.*

Backer & Bakhuizen f. (1965) described the fruit as more or less angular. Fruits sometimes dry with sides flat but the angles are not ridged and these fruits would not be confused with *Linociera beccarii* Stapf (from Sumatra) or *C. porcatus* Kiew (from Borneo), which have ridged fruits where the ridges correspond to those on the woody endocarp. The endocarp of *C. macrocarpus,* although hard and thick, is not woody.

The geographic distribution of *C. macrocarpus* covers Java, Sumatra, Borneo and Malaya (although it is less common in Malaya than elsewhere). It has been collected from lowland and hill forest up to 1500 m, sometimes from freshwater swamp or areas that flood periodically. In Malaya only the typical variety with ovoid fruits is found; the variety with a globose fruit, var *globosus* Kiew, is restricted to Borneo (Kiew, 1980).

Chionanthus insignis was originally described from Sumatra by Miquel who cited Teysmann's specimen from Palembang. This specimen has leaves, infructescences and fruits of the same size and shape as *C. macrocarpus* with which *C. insignis* is thus synonymous. However, Clarke based his description of *Linociera insignis* on specimens from Burma (*Helfer 3688,* K, L) which differ from those of *C. macrocarpus* Bl. in their smaller fruits (1 cm long) and glossy leaves. These non-Sumatran specimens are therefore not specimens of *C. macrocarpus* and must be excluded from *C. insignis* Miquel, which is a synonym of *C. macrocarpus.*

2. **Chionanthus callophyllus** Blume

Mus. Bot. Lugd. Bat. 1 (1850) 319. Typus: Korthals s.n. Borneo Herb. Lugd. Bat. 908. 158... 933 (L, lecto — here chosen). *Linociera callophylla* (Bl.) Knobl. Bot. Centralbl. 61 (1895) 319.

Linociera paludosa King & Gamble J. As. Soc. Beng. ii 74 (1905) 268. Typus: *Wray 2424* (SING), Ridley Fl. Mal. Pen. 2 (1923) 316.

Olea platycarpa King & Gamble l.c. 271. Typus: *King's Coll. 5541* (K), Ridley l.c. 319. *Chionanthus platycarpus* (K. & G.) Kiew Mal. For. 42 (1979) 272 & Fig 5, 44 (1981) 149.

Notes

Chionanthus callophyllus is a distinctive species with large, obovate leaves (23-38 by 7-13 cm) with a particularly thick petiole, the veins impressed above and prominent below. In addition, it has short ramiflorous inflorescences and the base of the fruit is flattened, the latter is a unique character for Malesian species of *Chionanthus.* In addition, the fruit is often covered with a white bloom. Ramiflory is known in only one other Malesian species *viz., C. gigas* (Lingelsheim) Kiew from New Guinea. Blume described the inflorescence as equal to or longer than the petiole (which they are) and as axillary or lateral. In fact the inflorescences are extra-axillary i.e., ramiflorous.

Chionanthus callophyllus is more common in Malaya (18 collections) than in Borneo (3 from Sabah and 3 from Kalimantan) or in East Sumatra (one collection, *Krukoff 310,* US).

3. **Chionanthus grandifolius** (Elmer) Kiew **comb. nov.**

Linociera grandifolia Elmer Leaflets Philip. Bot. 5 (1913) 1657. Typus: *Elmer 13425* (with fruits) Mindanao, Philippines (K, lecto — here chosen, BM, Gray, L; US, isolecto).

Chionanthus macrocarpus non Blume *sensu* Kiew Mal. For. 42 (1979) 271.

Malayan specimen: *Cockburn FRI 10578* (with flowers) Batu Biwa, Trengganu (K, KEP, L, SING).

Notes

The specimen *FRI 10578* is outstanding among Malayan *Chionanthus* species for its indumentum: no other species has leaves where the lamina is softly and densely hairy below. In this character it matches the single specimen of *Linociera grandifolia* from Mindanao, Philippines. Both these specimens have oblong leaves with a rounded to acuminate apex and a cuneate base, the leaf is subcoriaceous and slightly shiny above, the veins are impressed above and are prominent below and the twigs are flattened at the node. The Malayan specimen is therefore considered to be the same as *Linociera grandifolia* based on vegetative characters, as unfortunately the Malayan specimen is in flower and the Philippine one in fruit. *Linociera* is now considered synonymous with *Chionanthus* (Stearn, 1971) and the appropriate combination is made above.

Amended description

Small tree to 7 m. Twigs pale grey, flattened at nodes, pubescent. Leaves chartaceous to subcoriaceous, drying deep reddish brown, elliptic oblong, 22-33 by 9-13.5 cm, apex obtusely rounded to acuminate, base acute. Lower surface of lamina and veins densely covered by long unicellular hairs, upper surface with sparse, short unicellular hairs. Veins 11-13 pairs, slightly impressed above, prominent below, tertiary veins inconspicuous. Petiole 1.5 cm long, 5 mm thick, shortly pubescent. *FRI 10578* — Inflorescence paniculate, 13-17 cm long, densely hairy, axillary clustered, branched from base. Flowers sessile, yellow with pleasant scent. Calyx lobes acute, 1.5 mm long, densely pubescent. Corolla 3.5 mm long, lobes joined in 2 pairs for 1 mm at the base, lobes narrowly linear, pubescent, valvate. Stamens almost sessile, anthers 1 mm long. Ovary conic, stigma obscurely lobed. *Elmer 13425* — Infructescence 3-5 cm long, pubescent. Fruits ovoid to subglobose, 17 by 19 mm, subsessile. Pericarp thin and brittle. Seed 1, endosperm copious.

4. **Chionanthus curvicarpus** Kiew **sp. nov.**

Typus: *A. Gibot SAN 35826* (SAN — holo, K, UPM — iso).
Linociera cuspidata (Bl.) Knobl. *sensu* Merrill J. Str. Br. R. As. Soc. Spec. No. (1921) 488, Univ. Cal. Publ. Bot. 15 (1929) 249; *non Chionanthus cuspidatus* Bl. *sensu* Kiew Mal. For. 43 (1980) 372 & Fig 2J, 44 (1981) 152. Non *Chionanthus cuspidatus* Bl. Mus. Bot. Lugd. Bat. 1 (1850) 319. Typus: *Muller,* Gunung Bahay Herb. Lugd. Bat. 908. 158... 996 (L, lecto — here chosen).

Chionanthus curvicarpus sp. nov. propter habitum arboris minoris cortice ramorum albo, folios chartaceos lanceolatosque, nervis subtus prominentibus, *C. oligantho* (Merrill) Kiew affinis sed nervis numerosioribus (8-15 paribus vice -9), inflorescentiis longioribus (1.5-6 cm vice 0.5-1.5 cm) et forma fructu differt; fructus *C. curvicarpi* egregius, anguste-ellipsoideus, 2.5 × 1.75 cm, curvatus et porcatus vice in *C. oligantho* globosus.

Notes

Chionanthus curvicarpus is common in Borneo where Merrill (1929) identified specimen *Elmer 21047* (BO) near Tawao as *Linociera cuspidata* (Bl.) Knoblauch. This interpretation was followed by Kiew (1980, 1981). However, Blume's type specimen of *C. cuspidatus* although similar in leaf shape and size, differs in possessing a shorter inflorescence (1.3 cm long as opposed to 1.5-6 cm in *C. curvicarpus),* and the petals are longer (6 mm long as opposed to 2-3 mm long). The most striking difference is that the leaves dry chestnut-brown (in *C. curvicarpus* the leaves of all specimens examined dry pale grey). There are no fruits on the type specimen of *C. cuspidatus. Linociera cuspidata sensu* Merrill is therefore not the same as *C. cuspidatus* and so a new name is required for this taxon. 'Curvicarpus' is chosen as the curved fruit (which is also ridged longitudinally) is unique among Malesian *Chionanthus* species (Fig 2J in Kiew, 1980). Other species that have straight ridged fruits are larger (6.5 by 3.5 cm in *C. porcatus* from Borneo, 3-5 by 2-3 cm in *Linociera beccarii* from Sumatra and 3-7 by 1.5-3.5 cm in *C. sessiliflorus* (Hemsley) Kiew from New Guinea). The fruit of *C. curvicarpus* is 2.5 by 1.7 cm.

Chionanthus curvicarpus most closely resembles *C. oliganthus* (Merrill) Kiew of Borneo. Both species have white twigs, leaves which are thin, dry pale and have prominent veins below. However, it differs from *C. oliganthus* in the number of veins (8-15 as opposed to 6-9 in *C. curvicarpus),* longer inflorescence (0.5-1.5 cm versus 1.5-6 cm) and fruit shape (*C. curvicarpus* has globose fruits).

In Borneo *C. curvicarpus* is found in the lowlands, sometimes on hillsides up to 1000 m or near rivers. It is most common in Sabah. In Malaya it is known from a single flowering specimen, *Kiah 32325* (A, K, KEP, L, SING) from Sungai Kayu, E. Johore and four specimens have also been collected from Sumartra. This same distribution pattern, the Borneo element of Corner (1960), is also seen in *C. laxiflorus* Bl., which in Malaya is also rare (collected once from Fraser's Hill and from the Kuantan-Kluang-Mersing area), whereas it is more common in Borneo and Sumatra and in addition its distribution extends through Celebes to New Guinea.

Acknowledgements

The author thanks the Director of the Rijksherbarium, Leiden, The Netherlands for permission to work there and to Dr J. Dransfield for help with the latin diagnosis.

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A Revision of *Aniselytron* with Some New Combinations in *Deyeuxia* in SE. Asia (Gramineae)

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EFFECTIVE-PUBLICATION DATE: 7 MAR. 1985

Abstract

Aniselytron Merr. *(Gramineae),* better known as *Aulacolepis* Hack. (1934), *non* Ettingsh. (1893), has two species in SE. Asia and Malesia. A key and descriptions are given. *Anisachne* Keng is reduced to *Deyeuxia* Beauv. and some new combinations in that related genus are proposed. *Deyeuxia abnormis* Hook. f. is not identifical with *D. zenkeri* (Trin.) Veldk., which is an enigmatic species known only from the type from the Nilgiris, India.

Introduction

Aniselytron Merr. resembles *Deyeuxia* Beaux. best in the induration of the lemma but differs in that its lemma is distinctly longer than the lower glume. This feature is so aberrant in the *Aveneae* (including *Agrostideae)* in which, according to most descriptions, the glumes might be as long as or longer than the only or lowest lemma, that *Aniselytron* can not usually be identified with general keys. Its very short callus hairs, its minute, glabrous rachilla process and the usual absence of an arista are causes of the resemblance in the spikelets with those of uniflorous forms of *Poa* Linné. In fact, before it was realized that such species occur in *Poa,* one of its forms was included in *Aulacolepis* Hack. by which name the genus was known until recently. That *Aniselytron* obviously belongs to the alliance of *Agrostis* Linné can be noticed when callus hairs are seen; when present in *Poa,* they are abaxial and then usually somewhat arachnoid or woolly; in *Agrostis* and its related genera, they form a ring around the base of the lemma, often with the lateral hairs somewhat longer and giving the impression that there are two tufts. Moreover, in *Poa,* the lemmas are more or less keeled at the back while in the other genera, they are more rounded.

A similar reduction in glume size, though rarely as extreme as in *Aniselytron,* occurs sporadically in the *Aveneae* as in some species of *Deyeuxia* e.g., *D. abnormis* Hook. f. from India to S. China; *D. exilis* Veldk. and *D. pusilla* (Reeder) Jansen from New Guinea, the Australian *D. gunniana* (Nees) Benth., the circumarctic genus *Arctagrostis* Griseb., and the New Zealand *Simplicia* Kirk (1897). *Simplicia* especially is very similar to *Aniselytron* as was pointed out by Zotov (1971). Indeed, if its two species had been found in Asia, *Aniselytron* of 1910 would probably have been included in *Simplicia.* However, with the present great disjunction, we get the impression that we are dealing with the results of two convergent lines in the reduction of the spikelet, the cause of the apparent resemblance. The difficulty remains that there seem to be no clear differences whereby the two genera can be separated satisfactorily at the generic level. The most obvious distinctions are the width of the leaves: 1.5-3 mm in *Simplicia* and 3-17 mm in *Aniselytron;* the lemma: 3-nerved in *Simplicia* and 5-nerved in *Aniselytron* (although Zotov has remarked that in *S. laxa* Kirk there may be weak additional nerves...); the absence of callus hairs (at least in the single specimen seen by us of the same and neither mentioned nor depicted by Zotov); and the subterminal arista.

Zotov and the few other authors who have dwelt on *Aniselytron* repeated Hackel's remark (1907) that having the two proximate nerves of the palea would not make it distinct from *Aulacolepis* (means "fluted scale"). These nerves are indeed close to one another, with a more or less narrow depression in between, hardly a furrow. The minute rachilla process lies in this depression for which reason it is difficult to detect. It seems to us that Zotov had not actually seen material of *Aniselytron* for such a nervation is present also in at least the isotype of *S. laxa* in Kew. This proximity of the nerves seems to depend on the extent the palea is covered by the lemma; such close-set nerves are sometimes present in species of *Agrostis* and *Deyeuxia* as well.

It is therefore not surprising that Hitchcock (1934) was misled by the apparent similarity when he distinguished between *Aul. clemensae* Hitchc. from Sabah and *Aul. petelotii* Hitchc. from North Vietnam. Again, in 1936, he fell into the trap provided by the uniflorous *Poa* species when he proposed the combination *Aul. epileuca* for a taxon from New Guinea, one which was described by Stapf in *Deyeuxia*. However, it turned out that *Aul. epileuca* is not Stapf's species but another uniflorous *Poa* (see under "Excluded Names"). *Aul. petelotii* has had a rather chequered history: up to now the taxon has been included in *Agrostis, Anisachne* Keng and *Deyeuxia*. We regard the species as a member of the last genus.

The first mention of a representative of *Aniselytron* was based on material from Sikkim. Kuntze (1891) thought that it represented a *Milium* Linné. This was soon corrected by Stapf (1895), admitting that he included the species in *Deyeuxia*(!) for technically unsatisfactory reasons. He compared it with his *D. epileuca*, the *Poa* intended by Hitchcock (see above). Hooker f. (1896) also regarded it as a "very anomalous" species for *Deyeuxia*.

Hackel (1907) proposed a separate genus *Aulacolepis* for Kuntze's species and for some collections from Japan which he suspected might prove to be merely subspecies of one taxon. This suspicion was affirmed by Ohwi (1941), who regarded them as varieties while we think that they are merely two local races, not warranting any nomenclatural status.

In a number of instances, some authors have used *Index Nominum Genericorum* to achieve results by proposing all the new combinations under another generic name without any specialistic knowledge of the group concerned or without a laborious search for relevant material and/or literature. For them entries in the *Index Kewensis* apparently gave enough information. Thus three persons have made all the "necessary" combinations under *Aniselytron*, and a fourth, in the blissful ignorance of that name even proposed a new one, *Neoaulacolepis* (see also Wilson's comment, 1983).

As more collections from different places became available, more taxa were added to *Aulacolepis*. Ohwi (1935) included *Aul. milioides*(!) from Taiwan, which had previously been described as a *Poa*(!) by Honda (1927). As mentioned above, Hitchcock (1934; 1936) distinguished between *Aul. clemensae, Aul. petelotii* and *Aul. epileuca*. Ohwi (1956) included *Aul. pseudopoa*(!), a new combination of a species from North Sumatra, described previously by Jansen. The latter, as can be deduced from his correspondence in Leiden, had described it as a *Deyeuxia* on Ms. Vickery's suggestion, who had revised that genus for Australia where some species also have similar relatively short glumes.

The distribution of *Aniselytron* species is very scattered. The plants apparently prefer shaded, moist, rocky ravine floors, places out of reach except perhaps in Japan, and thus material is rare in herbaria. The form of Mt. Kinabalu, for instance, has been collected only by Ms. Clemens along the Masilau River and the Silau basin. The first locality seems close to the Paka Caves, a site frequently visited by botanists. The grass probably grows in the deep gorge below the Caves. Merrill (1910) remarked that *An. agrostoides* was uncommon on Mt. Pulog. As far as we know, it has been collected only twice again [BS *44989 (Ramos & Edano); Santos 7854*]. The scarcity could be attributed to its close resemblance with *Agrostis rigidula* Steud. as had been observed by Merrill. That is a rather common grass on Mt. Pulog.

From the present study we think that *Aniselytron* has only two species: one, *An. agrostoides,* occurring in Luzon and in Taiwan, the other, *An. treutleri,* ranging from Sikkim through Assam, north Burma, China, north Vietnam and Taiwan to Japan, Sabah and North Sumatra. The second species has a number of local races as is to be expected in disjunctive populations scattered over such a wide area. In Japan, only one form is rather widely spread but the situation in China is not clear because too few collections are available. The races can only be distinguished by a certain set of characters which occur in a different expression and/or combination in each individual race. Provenance is usually the best guide but is most unsatisfactory. We have therefore refrained from naming them officially. Although they are allopatric, the rank of subspecies automatically and uncritically bestowed on such taxa by some seems to be too honorific for the little-impressive differences.

Aniselytron

Aniselytron Merr.

In Merr. & Merritt, Philip. J. Sc. 5, Bot (1910) 329; Sojàk, Câs. Nár. Muz. 148 (1980) 202; Raizada & Bennett, Ind. For. 107 (1981) 433. — Type: *Aniselytron agrostoides* Merr.

Aulacolepis Hack. in Fedde, Repert. 3 (1907) 241; Hitchc., J. Washington Ac. Sc. 24 (1934) 290; Ohwi, Bot. Mag. Tokyo 55 (1941) 361; Bor, Grasses (1960) 394; Hsu, Fl. Taiwan 5 (1978) 433; *non* Ettingshausen (1893). — *Neoaulacolepis* Rauschert, Taxon 31 (1982) 561. — Lectotype: *Aulacolepis treutleri* (O. Ktze) Rauschert = *Aniselytron treutleri* (O. Ktze) Sojàk.

Tufted perennials, branching extra-vaginally at base. Culms simple, glabrous, smooth, but cataphylls and lowest sheaths finely puberulous. Ligules membranous, enlarging upward, the lower collar-shaped, usually rather thick, outside puberulous, the upper triangular, thinner, glabrous or not. Blades flat, flaccid, slightly unequal-sided, glabrous, smooth or scaberulous. Panicles of lax spikelets. Spikelets somewhat laterally compressed, 1-flowered, articulating above the glumes. Glumes membranous to slightly indurated in fruit, unequal to very unequal, at least the lower one (much) shorter than the lemma. Rachilla process minute, glabrous. Lemma ovate-lanceolate, indurated, scabrous. 5-nerved, muticous or (rarely) with an apical filiform arista, callus hairs very small, inconspicuous, around the base of the lemma, the laterals ± longest. Palea as the lemma, nearly completely clasped by it, nerves 2, rather close-set and slightly impressed in between. Lodicules glabrous, sometimes slightly fimbriate, thin, veinless, free. Anthers 3. Styles 2, free at base. Caryopsis ellipsoid, ± terete, not furrowed; hilum subbasal, punctiform; embryo 0.2-0.25 times the length of the caryopsis.

Distribution. Two species from Sikkim, N. Burma through China to Japan, Taiwan, Luzon, Sabah, N. Sumatra.

Ecology. High mountains, in shaded, moist forest.
Chromosome number. $x = 7$ (see under *A. treutleri*).

KEY

1. Lateral spikelets with rather uniform, short, up to 1-mm long pedicels. Lower glume virtually absent or a nerveless scale, up to 0.75 mm long, up to 0.2 times the length of the spikelet. Upper glume 1-nerved .... *1. An. agrostoides*

1. Lateral spikelets with filiform pedicels of variable length. Lower glume 0.5-2.5 mm long, 1-nerved, 0.25-0.71 times the length of the spikelet. Upper glume 3-nerved .... *2. An. treutleri*

1. Aniselytron agrostoides Merr.

In Merr. & Merritt, Philip. J. Sc. 5, Bot. (1910) 329; Enum. Philip. Fl. Pl. 1 (1923) 82. — *Aulacolepis agrostoides* Ohwi, Acta Phytotax. & Geobot. 4 (1935) 30; Bot Mag. Tokyo 55 (1941) 361, *comb. ill.* — Type: *Merrill 6483* (PNH, † holo; K, L, W Hb. J.V. Santos, *n.v.*), Philippines, Luzon, Mt. Pulog, 2400 m, May 1909.

Aulacolepis agrostoides (Merr.) Ohwi var. *formosana* Ohwi, Acta Phytotax. & Geobot. 4 (1935) 30; Hsu, Taiwan Gr. (1975) 303, t. 46; Fl. Taiwan 5 (1978) 434, t. 1389. *comb. ill.* — Type: *Ohwi 2363* (KYO, holo; K), Taiwan, Ilan Co., (Mt.) Taiheisan (Taipingshan), 26 May 1933.

Culms erect to geniculately ascending, up to 90 cm high, sometimes rooting in the lower notes. Ligule 0.3-1.5 mm high, margin erose to fimbriate. Blades 10-24 cm by 2.3-6 (-8.5) mm. Panicle erect to slightly nodding, usually ± contracted, to effuse with patent, sometimes slightly reflexed branches, 9-22 by 0.7-13.5 cm diam., axis glabrous, smooth, branches smooth to scaberulous, lowermost 2-5 together, the longest up to 7.5 cm long, naked in the lower 0.5-0.7th, spikelets 3-15 (-many), pedicels of lateral spikelets 0.3-1 mm long, of the terminal ones much longer. Spikelets 2.5-4 mm long. Lower glume virtually absent to a small, scabridulous, nerveless scale up to 0.75 (-1) mm long, up to 0.2 (-0.3) times as long as the spikelet; upper glume ovate-oblong to ovate-lanceolate, very variable, 1-2.75 mm long, (0.2-) 0.5-0.75 times the length of the spikelet, long-acuminate, 1-nerved, glabrous, smooth. Rachilla process 0.35-0.8 mm long. Lemma with the margins becoming scarious, attenuating upward into an acute to acuminate and then sometimes hook-like apex, muticous; callus hairs 0.05-0.2 mm long. Anthers (0.6-) 1.25-1.5 mm long, yellow. Caryopsis 1.25-1.5 mm long.

Distribution. Taiwan: Chiayi (Mt.) Arisan, ((Mt.) Morrison), Hsinchu ((Mt. Taihasensan), Hualien (Mt.) Chilaisan), Ilan ((Mt.) Daikansan, ((Mt.) Loyehweisan, (Mt.) Pahsiensan); Malesia; Philippines, Luzon (Mt. Pulog).

Ecology. Mixed montane forest, 2150-2850 m, or open grassland just below the summit of Mt. Pulog (but notes usually lacking on the labels).

Note. Merrill (1910) reported that this species was uncommon on Mt. Pulog. In fact it has been collected only twice again [BS *44989 (Ramos & Edano); Santos 7854*]. There seem to be no collections present in PNH (Dr. Santos, Manila, *in litt.).* A poor juvenile isotype (W) and some scraps of the second collection and Santos' specimen were all that were available but these fall well into the range of variability shown by the ample Taiwan material. When Ohwi proposed a distinct variety for Taiwan, as far as can be ascertained, he never saw any Philippine material but relied on descriptions only. His proposal cannot stand.

2. Aniselytron treutleri (O. Ktze) Sojàk

Câs. Nár. Muz. 148 (1980) 202; Bennett & Raizada, Ind. For. 107 (1981) 434. — *Milium treutleri* O. Ktze, Rev. Gen. Pl. 2 (1891) 780. -- *Deyeuxia treutleri* Stapf in Hook., Icon. Pl. 24 (1895) t. 2396; Hook. f. Fl. Br. Ind. 7 (1896) 269. — *Aulacolepis treutleri* Hack. in Fedde, Repert. 3 (1907) 242; Honda, J. Fac. Sc. Imp. Univ. Tokyo III, 3 (1930) 195; Schmid, l'Agron. Trop. 13 (1958) 484, f. 2; Bor, Grasses (1960) 394; Hsu, Taiwan Gr. (1975) 305, t. 47; Anon., Icon. Corm. Sin. 5 (1976) 104, t. 7037; Hsu, Fl. Taiwan 5 (1978) 434, t. 1390; *comb. ill.* — Lectotype: *Treutler 486* (K, holo; L, W; CAL, *n.v.*), Sikkim, Tanglo, 3050 m, 5 August 1874.

Aulacolepis japonica Hack. In Fedde, Repert. 3 (1907) 241; Honda, J. Fac. Sc. Imp. Univ. Tokyo III, 3 (1930) 195; Anon., Icon. Corm. Sin. 5 (1976) 104; *comb. ill.* — *Aulacolepis treutleri* (O. Ktze) Hack. var. *japonica* Ohwi, Bot. Mag. Tokyo 55 (1941) 361; Fl. Japan (1965) 158; *comb. ill.* — *Aniselytron japonicum* Bennett & Raizada, Ind. For. 107 (1981) 434. — *Neoaulacolepis japonica* Rauschert, Taxon 31 (1982) 561. — Lectotype: *Faurie 6394* (W, holo; P, *n.v.;* KYO, L), Japan, Honshu, Prov. Shinano, Mt. Komagetake, July 1905.

Poa milioides Honda, Bot. Mag. Tokyo 41 (1927) 641. — *Aulacolepis milioides* Ohwi, Acta Phytotax. & Geobot. 2 (1933) 161, 169; *comb. ill.* — *Aulacolepis treutleri* (O. Ktze) Hack. var. *milioides* Ohwi, Acta Phytotax. & Geobot. 6 (1937) 151; *comb. ill.* — *Aniselytron milioides* Bennett & Raizada, Ind. For. 107 (1981) 434. — Lectotype: *Faurie 205* (KYO, holo; L; P, *n.v.*), Taiwan, Chiayi Co., (Mt.) Arisan, 2500 m, December 1914.

Aulacolepis clemensae Hitchc., J. Washington Acad. Sc. 24 (1934) 290; *comb. ill.* — *Aniselytron clemensae* Sojàk, Cås. Nár. Muz. 148 (1980) 202; Bennett & Raizada, Ind. For. 107 (1981) 434. — *Neoaulacolepis clemensae* Rauschert, Taxon 31 (1982) 561. — Type: *Clemens 34448* (US, holo; BM, G, K, L), Sabah, Mt. Kinabalu, Masilau River, 26 December 1933.

Deyeuxia pseudopoa Jansen, Acta Bot. Neerl. 2 (1953) 363, f. 1. — *Aulacolepis pseudopoa* Ohwi, J. Jap. Bot. 31 (1956) 137; *comb. ill* — *Aniselytron pseudopoa* Sojàk, Cås. Nár. Muz. 148 (1980) 202; Bennett & Raizada, Ind. For. 107 (1981) 434. — Type: *Van Steenis 9135* (L, holo; BO, *n.v.*), Sumatra, Aceh, summit Goh Lembuh, 3000 m, 21/22 February 1937.

Culms erect, up to 1 m high, rarely somewhat geniculate or decumbent and rooting in the lower nodes. Ligules 0.5-7.5 mm long. Blades 10-26.5 cm by 3-17 (-21) mm. Panicle effuse, erect, 9-26 by 0.7-15.5 cm diam.; axis smooth; branches scabrid, the lowermost 2-7, usually 5 together, the longest up to 12.5 cm long, naked in the lower 0.45-0.7th, spikelets 7-many; pedicels of the lateral spikelets filiform and variable in length. Spikelets 2.35-4.6 mm long. Glumes usually distinctly unequal, ovate-lanceolate, acute, scabrous; lower glume 0.5-2.6 mm long, 0.25-0.85 times as long as the upper one, 0.2-0.7 times as long as the spikelet, 1-nerved; upper glume 1.6-3.8 mm long, 0.6-1 times as long as the spikelet, 3-nerved. Rachilla process 0.2-1.3 (-2) mm long. Lemma with an acute to acuminate apex, sometimes with a thinner tissue and then sometimes incurved, rarely with an apical, filiform arista up to 0.25 mm long, callus hairs up to 0.8 mm long. Anthers 0.75-1.5 (-2) mm long when chasmogamous, 0.75-1.35 mm long when cleistogamous. Caryopsis 1.25-2 mm long.

Distribution. (Most collections were summarily labeled with often just a rough indication of provenance. Many localities could not be traced, e.g. in Japan. Field notes were usually meager or absent). Sikkim (Jongri, Nanki, Shimong, Tonglo), Burma (Kachin: Uring Bum), China (Guizhou, Fan Ching Shan; Sichuan; north Guangxi), Taiwan (Chiayi, Ilan, Nantou, Taipei), north Vietnam (Fan Si Pan Mts., Chapu), Japan (Honshu: North to Shina; Prov. Kyushu: Bungo, Mt. Kuju), Malesia (Sabah: Mt. Kinabalu; Sumatra: Aceh, Mt. Leuser).

Ecology. Moist, shaded, often rocky places in midmontane to upper montane areas, often in ravines (see also under the entities).

Chromosome number. 2n = 42 (here published with the kind permission of Dr. T. Tateoka; vouchers: *Tateoka 9389, 9395,* KYO).

Notes. Although local forms seem to be present, the collections were usually so few that no clear idea of their variability could be formed. The differences between the entities, moreover, are expressions of a mixture of recurring characters each time with a slightly different value. We thought that it was therefore premature to describe different taxa for the various localities and have not accepted the varieties *japonica, milioides* and *treutleri* of previous authors. Short diagnoses should suffice here as an aid in future research.

Sikkim, Burma *('treutleri').* Lower glume 0.5-1.75 mm long, 0.25-0.8 time length of the upper, 0.2-0.65 time length of the lemma; upper glume 1.6-2.5 mm long, 0.7-0.9 time length of the lemma. Lemma 2.35-2.75 mm long. Rachilla process 0.2-0.4 mm long. Callus hairs up to 0.2 mm long. Anthers 0.75-1.25 mm long, often cleistogamous, if so, then of same size. Alt. 2275-3660 m.

China (Guizhou, Sichuan?, N. Guangxi). Lower glume (0.65-) 1-1.5 mm long, (0.3-) 0.45-0.7 time length of the upper, (0.2-) 0.3-0.5 time length of the lemma; upper glume 2.15-2.5 mm long, 0.67-0.8 time length of the lemma. Lemma 2.75-3.3 mm long. Rachilla process 0.35-0.75 mm long. Callus hairs 0.25-0.5 mm long. Anthers c. 1.1 mm long. No altitudes given.

Taiwan *(‘milioides’).* Lower glume 1-1.9 mm long, (0.33-) 0.45-0.8 time length of the upper, 0.35-0.55 time length of the lemma; upper glume 2.1-2.75 mm long, 0.7-0.85 time length of the lemma. Lemma 2.8-3.5 mm long. Rachilla process 1-1.35 mm long. Callus hairs 0.25-0.3 mm long. Anthers c. 1.25 mm long. An altitude of c. 2500 m was once mentioned, other ecological notes are lacking on the field labels and in the literature.

North Vietnam (and China, Sichuan?). Lower glume 2-2.1 mm long, 0.8-0.85 time length of the upper, 0.5-0.55 time length of the lemma; upper glume 2.35-2.55 mm long, 0.6-0.67 time length of the lemma. Lemma 3.8-4 mm long. Rachilla process 1-1.25 mm long. Callus hairs c. 0.3 mm long. Anthers 1-1.25 mm long. *N.B.* Only 1 collection seen (*Pételot 8025,* L, US), the duplicate in P, which could not be found, was presumably described by Schmid as *Au. treutleri.* His dimensions differ thus: ‘lower glume 1.7-2 mm long, upper glume 2.2-3 mm long, lemma 3-4 mm long’, measurements resembling those of ‘milioides’. The anonymous author(s) of the Icon. Corm. Sin. may have described this form as *Au. japonica;* if so, it would also occur in Sichuan Alt. c. 2900 m in Vietnam.

Japan *(‘japonica’).* Lower glume 0.9-1.6 mm long, 0.4-0.65 time length of the lemma; upper glume 2-3 mm long, (0.6-) 0.65-0.85 (-0.95) time length of the lemma. Lemma (2.65-) 3-3.55 mm long. Rachilla process (0.6-) 0.75-1.3 (-2) mm long. Anthers 1-1.35 (-2) mm long when chasmogamous, 0.75-1.35 mm long when cleistogamous. Alt. 1300-2500 m. 2n = 42. *N.B.* Some specimens have dorsally pilose lemmas.

Sabah *(‘clemensae’).* Lower glume 2-2.5 mm long, 0.7-0.8 time length of the upper, 0.55-0.7 time length of the lemma; upper glume 2.85-3.25 mm long, 0.8-1 time length of the lemma. Lemma 3.25-3.5 mm long. Rachilla process 0.4-1.15 mm long. Callus hairs 0.4-0.5 mm long. Anthers 1.25-1.5 mm long. Alt. c. 2100 m, with *Astilbe, Galium, Gunnera, Juncus.* Only found by Ms. Clemens!

Sumatra *(pseudopoa).* Lower glume 1.9-2.6 mm long, 0.55-0.75 time length of the upper one, 0.45-0.65 time length of the lemma; upper glume 3-3.8 mm long, 0.75-0.95 time length of the lemma. Lemma 3.75-4.6 mm long. Rachilla process 0.35-1.15 mm long. Callus hairs 0.25-0.35 mm long. Anthers 1-1.5 mm. Alt. 2500-3350 m. *N.B.* The lemmas in *Van Steenis 8660* and *De Wilde & De Wilde-Duyfjes 16816* are sparsely pilose on the midrib and the outer nerves, those in *Van Steenis 9135* and *De Wilde & De Wilde-Duyfjes 16371* are glabrous.

Excluded names and some new combinations in *Deyeuxia*

1. **Deyeuxia abnormis** Hook. f.

Fl. Br. Ind. 7 (1896) 268; Keng, J. Washington Acad. Sc. 48 (1958) 188, *in passim.* — Lectotype: *Hooker f. & T. Thomson s.n. (‘Agrostis 12’),* (K, holo, *n.v.;* L), India, Meghalaya, Mt. Khasia, 1525 — 1830 m. (Here designated).

Agrostis pleiophylla Mez In Fedde, Repert. 17 (1921) 301. — Syntypes: *C.B. Clarke s.n.* (B, †, holo; K, *n.v.*), Himalaya, Darjeeling; Khasia, Soynung (probably syntypes of *D. abnormis).*

Aulacolepis petelotti Hitchc. J. Washington Acad. Sc. 24 (1934) 291; Schmid, l’Agron. Trop. 13 (1958) 484, *comb. ill.* — *Aniselytron petelotii* Sojàk, Câs. Nár. Muz. 148 (1980) 202; Bennett & Raizada, Ind. For. 107 (1981) 434. — *Neoaulacolepis petelotii* Rauschert, Taxon 31 (1982) 561. — Type: *Pételot 4743* (US, holo; L; P, *n.v.*), north Vietnam, Fan Si Pan Mts, Chapu, 1900 m, August 1933.

Anisachne gracilis Keng, J. Washington Acad. Sc. 48 (1958) 117, f. 2; Anon., Icon. Corm. Sin. 5 (1976) t. 7036. — Type: *Hou Hsueh-Yuh 2143* (N, holo, *n.v.*), China, Kweichow, Pichieh Hsien, 1440 m, 1 June 1943.

That *Deyeuxia abnormis* is a rare but rather widely distributed species in SE. Asia was unknown until now as the species in each area went by a different name. When Keng described *Anisachne gracilis* he actually did think of *D. abnormis* but in the absence of material had to rely on Hooker f.'s description (1896) of it. Moreover, he remarked that he would have included his new species in *Deyeuxia* if the glumes had been longer. We now know (see also the Introduction) that glumes shorter than the lemma do occur sporadically in *Deyeuxia*. The additional presence of a relatively thickish, subterminal aristule, a hairy rachilla process, and fairly long callus hairs led us therefore to agree with Hooker f. that the species is better accommodated in *Deyeuxia*. Although we have not seen Keng's original material his description and plate are a good match for the material of *Au. petelotii* and *D. abnormis*.

Agrostis zenkeri Trin. was equated with *D. abnormis* Hook. f. by Bor (1954) in an extensive discussion on its provenance and identity. However, having seen the type specimens of both, we have to disagree with his conclusion and it would seem that the problem is even more complicated and enigmatic.

The description of *Ag. zenkeri* as given by Bor does not fit the actual type, but refers to the true *D. abnormis*, which is a different species. Both belong to *Deyeuxia* as accepted here and a new combination is necessary:

2. Deyeuxia zenkeri (Trin.) Veldk. *comb. nov.*

Agrostis zenkeri Trin., Mém. Acad. Sc. St. Pétersburg VI, 6 (1841) 363; Steud., Syn. 1 (1854) 170; Hook. f., Fl. Br. Ind. 7 (1896) 258, *sp. dub.*; Bor, *Kew Bull. (1954) 441;* Grasses (1960) 392. — Type: *Schmid, s.n.* (?) in Hb. Zenker (LE, holo; Kew neg. 2303), India, Tamil Nadu, Nilgiris.

The type of *D. zenkeri* consists of a single flowering culm, slightly geniculate, c. 35 cm long, with 5 leaves but without a base. Its life cycle can therefore not be determined. The internodes are glabrous, smooth, and also the sheaths, although the uppermost is slightly retrorsely scaberulous. Ligules truncate, erose, scaberulous outside, the lowermost longest, 2.25 mm long. Blades infolded, slightly expanded at the very base, the largest 4.5 cm long, 2.25 mm wide, smooth, glabrous. Panicle lax, spikelets few, 6.5 by 4.5 cm. Axis, branches, and pedicels smooth, axils swollen, glabrous. Branches short, filiform, wavy, the 2 lowermost together, the longest 3 cm long, spikelets 8, nearly perpendicularly forked several times, the pedicels subequal, 3-7 mm long, apex clavate, the spikelets apparently all terminal at the end of the branches. Spikelets 2.6-3.25 mm long. Lower glume as long as the spikelet, 0.1-0.3 mm the length of the upper, 1.05-1.15 times as long as the lemma. Lemma 2.25-2.95 mm long, 5-nerved, microscopically scaberulous, apex muticous, 5-dentate, callus hairs c. 1 mm long, process c. 0.5 mm long with c. 1-mm long hairs. Palea as long as the lemma to slightly longer. Anthers c. 1.2 mm long (1 seen).

The inflorescence of *D. zenkeri* is reminiscent of the plate of *Ag. tenuis* in Hubbard's well-known 'Grasses' (1968, f. 300), but with much fewer spikelets and is quite different from that of *D. abnormis*, as can be seen in Keng's plate of *Anisachne gracilis*, although that plate seems to have been based on a rather depauperate specimen. There the panicle is contracted with nearly erect, rather long, more or less straight, scaberulous branches with many appressed spikelets, usually with short, obconical (0.75-1 or more mm long) pedicels. The glumes and palea are distinctly shorter than the 5- but not the 3-nerved lemma, which often has an inconspicuous, subapical, straight arista hardly exceeding its apex. The anthers are 0.8-1 mm long.

The species was named after J. C. Zenker by Trinius and described from the Nilgiris. We agree with Bor that the type was probably collected by B. Schmid, who gave his material to Zenker to study (he never was in India) and that Zenker apparently passed on the grasses to Trinius. Now, no matching specimens have been collected ever since in the area, under this or another name and mention is not even made in the local floras of Fyson (Fl. Nilg. & Puln., 1915) and Fischer (in Gamble, Fl. Presid. Madras 3, 1928). So either this represents a very rare or overlooked species, or a mix-up has taken place and a non-Indian species was instead represented. We have been unable, however, to identify it with anything else. Because of the smooth, short, forked branches of the panicle, the long pedicels, the smooth glumes, the relatively short callus hairs (c. 1 mm long) and process (c. 0.5 mm long, overlooked by Trinius), and the glabrous, dentate, at least the unawned lemma here, it seems to differ from any American, Asian, Australian, European, or Indian species known to us.

3. Deyeuxia brachytricha (Steud.) Veldk., *comb. nov.*

Calamagrostis brachytricha Steud. Syn. 1 (1854) 189. – *Calamagrostis brevipila* Steud. ex Miq., Cat. Mus. Lugd. Bat. 1 (1870) 112, *nomen* (copied from label but the name had been changed by Steudel, 1854). – *Calamagrostis arundinacea* (Linne) Roth var. *brachytricha* Hack., Bull. Hb. Boiss. 7 (1899) 652. – *Deyeuxia silvatica* (Schrad.) Kunth var. *brachytricha* Hack. ex Rendle, J. Linn. Soc. London, Bot. 36 (1904) 396; Ohwi, Fl. Jap. (1965) 147. – Type: *Anon.*, *s.n.* (L, holo, *'Calamagrostis brevipila'* Steud. ms.), Japan, probably ex Hb. *Von Siebold* in view of the rice-paper label with Japanese handwriting (For further synonymy see Ohwi, 1965).

When regarded as a variety, the epithet should be taken from *Calamagrostis varia* (Schrad.) Host var. *longiaristata* Korsh., Acta Hort. Petrop. 12 (1892) 420 ('longearistata'), which is older than Hackel's use of *'brachytricha'.*

4. Deyeuxia debilis (Hook. f.) Veldk., *comb. nov.*

Calamagrostis debilis Hook. f., Fl. Br. Ind. 7 (1896) 262. — *Agrostis debilis* Bor, Grasses (1960) 387, *non* Poir, (1810). — *Agrostis neodebilis* Bennett & Raizada, Ind. For. 107 (1981) 433. — Type: *Hooker f., s.n. ("1 Calamagrostis"),* (K, holo; L), Sikkim, Chola, 3050 m.

Aniselytron agrostoides Marr. J. V. Santos no. 7854

	Reduced xerox copy of original illustration.	Actual size of specimen
	Magnification	
a. Habit of plant	X 1.43	49 cm. tall
b. Junction between sheath & blade	X 10.32	blade 2.3 mm wide ligule 1.4 mm long
Spikelet (3 views)	X 24.5	2.9 mm long
c. lateral view:		
Glume I		0.17 mm long
Glume II		1.2 mm long
d. dorsal view		
e. ventral view		
Lemma	X 24.5	2.8 mm long
f. lateral view: *hairs* of callus		0.05 – 0.2 mm long
g. spread out lemma		2.8 mm long 1.4 mm wide
Palea (3 views)	X 24.5	– 2.7 mm long
h. lateral view		
i. dorsal view: rachilla produced into an *awn*		0.5 mm long
j. ventral view		
k. Pistil and stamens	X 24.5	2.4 mm long ovary 1.23 mm long style 0.4 mm long stigma 0.8 mm long anther 0.86 mm long filament 1.75 mm long lodicules 0.3 mm long
l. *Caryopsis*	X 24.5	1.35 mm long 0.35 mm wide

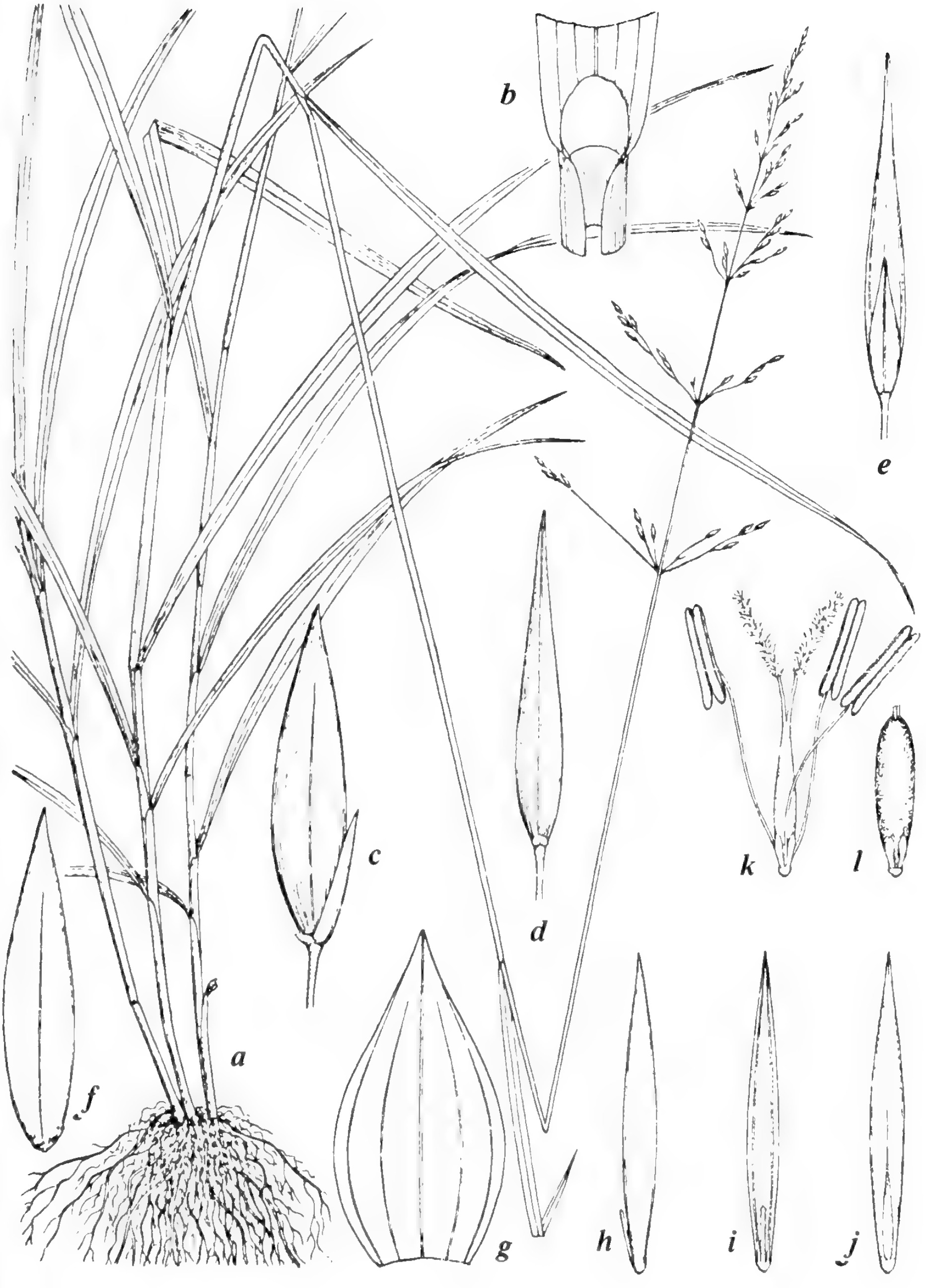

Fig. 1. *Aniselytron agrostoides (Santos 7854).*
a. Habit; *b;* ligule; *c.* spikelet lateral view; *d* id., dorsal view; *e.* id., ventral view; *f.* lemma, lateral view; *g.* id., flattened; *h.* palea lateral view *i.* id., dorsal view *j.* id., ventral view; *k.* pistil and stamens; *l.* caryopsis. (*a:* x 0.9; *b:* x 6.7; *c-l:* x 16.

5. Deyeuxia epileuca Stapf

Trans. Linn. Soc. London, Bot. II, 4 (1894) 247, t. 20c, 10-16. – *Aulacolepis epileuca* Hitchc., Brittonia 2 (1936) 177, *pro comb., comb. ill.* – *Aniselytron epileuca* Sojàk, Câs. Nár. Muz. 148 (1980) 202 *('epileucum');* Bennett & Raizada, Ind. For. 107 (1981) 434. – Type: *Haviland 1401* (K, holo), Sabah, Mt. Kinabalu, 3200 m.

= *Poa epileuca* (Stapf) Stapf in Hook., Icon. Pl. 27 (1899) t. 2607, *in obs.;* t. 2608.

This has long been a misunderstood taxon, partly because the spikelet is uniflorous, partly because it has generally been confused with *Poa papuana* Stapf (e.g., by Hitchcock, 1936), *Poa wisseiii* Jansen (cf. Chase, J. Arn. Arb. 24, 1943, 84) and other uniflorous *Poa* species (see also Veldk. in Van Royen, Alp. Fl. N. G. 2, 1980, 1100). For the differences with *Aniselytron* see the Introduction.

6. Deyeuxia mazettii Veldk., *nom. nov.*

Calamagrostis stenophylla Hand.-Maz., Symb. Sin. 7 (1936) 1298, t. 40, f. 1, *non D. stenophylla* Jansen (1952). – Type: *Handel-Mazetti 5173* (W, holo, *n.v.;* L), China, Sichuan, Lungchushan Mts., Huili, 3100-3400 m, 16 September 1914.

Index of collectors

Only numbered collections have been included. Specimens cited in literature but not seen are also included with their identifications (between brackets) when these seemed acceptable; otherwise they have been deleted.

BS 44989 (Ramos & Edano): 1.

Ching 6062: 2; Chuang 316: 1; Clarke 26044, 26046, 27482, 27438, Clemens 29692, 34448, 34448-A: 2.

Faurie 205, 6394, 6397: 2; Fukuyama 4778: 1.

Henry 4777, Hosomi 8970: 2; Hsu 437: 1; 5942: (2); 5942-A, Huang *et al.* 5766: (1).

Kao 5201: (2); 5868: (1); King 3101, Kingdon Ward 21568, Kunio 35886, Kuntze 2396: 2; Kuoh 1297, 7453: (1).

Matsuda Gram. 10, T-381: (2); Merrill 6483: 1.

Ohwi 2363, 2485, 3548, 3623: 1; Oka 35891: 2; Okamoto 32: 1.

Pètelot 8025: 2.

Santos 7854, Shimizu & Chuang 20182, Shimada 5103-B: 1; Van Steenis 8660, 9135, Steward *et al.* 514, Sun Yat Sen Univ. 51196: 2.

Tagawa 389, 3856: 2; Tamura & Koyama 23353: 1; Tanaka 15970, 25701, Tateoka 9389, 9395, Treutler 486: 2.

De Wilde & De Wilde-Duyfjes 16371, 16816:2.

Acknowledgements

This revision was started by Ms. H. M. Korthof during a course in advanced Angiosperm taxonomy at the Rijksherbarium, Leiden. It was finished by Dr. J. F. Veldkamp. The Keepers and Curators of BM, BO, G, K, KYO, L, MAK, NY, SING, TI, UC, US, and W are gratefully acknowledged for making available the necessary materials. From LE the type of *Ag. zenkeri* Trin. was received for inspection. No specimens could be found in P by JFV and in PNH by Dr. J. V. Santos (Manila), but

Dr. Santos did have one in his private collection (dupl. in L now), from which Mr. L. M. Gregorio prepared the drawing, which is reproduced here with their kind permission and we are most grateful. Dr. T. Tateoka, Tokyo, kindly allowed us to cite his unpublished chromosome count for the Japanese form of *An. treutleri.*

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Preliminary Pollen Study of the Oleaceae in Malesia

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Abstract

Preliminary work on pollen of the Oleaceae shows that it is of limited diagnostic value at the generic level. Small pollen grains (10-18μ diameter) are recorded for Malesian species of *Chionanthus, Myxopyrum* and *Olea.* The size of pollen grain is associated with style length.

1. Pollen morphology

The pollen morphology of the Oleaceae is reticulate and tricolporate (Wodehouse, 1965; Erdtman, 1971). A preliminary survey of Malesian species using JEOL 35 SEM, where the pollen grains were acetolysed before coating with gold, confirms this and also shows that there is variation between species for characters of the muri (whether beaded or smooth, high or low) and for the size of the lacunae (Table 1). The large lacunae are conspicuous under light microscopy in several species of *Jasminum* and in *Nyctanthes arbor-tristis* (personal observation e.g., and in *Ligustrum* (Wodehouse, *ibid).*

Some characters are constant for a genus e.g., all the species of *Olea* examined have large lacunae with spinules inside (Plate 1f); the muri of *Myxopyrum* are smooth (Plate 1d & e) and the muri of *Chionanthus* are high (Plate 1a & b). However, since only a single character is constant, a few species of different genera share the same characters, e.g. *Ligustrum confusum* and the pollen of male flowers of *Olea decussata* and the large grains of *Myxopyrum ovatum* all have large lacunae with high, smooth muri (Table 1). Pollen morphology cannot therefore be used infallibly to identify oleaceous pollen to genus. However, from this preliminary study certain character combinations do indicate generic identity e.g., small lacunae with low, smooth muri is characteristic only of *Myxopyrum.* A larger sample is needed to confirm this.

Variation of these characters may also occur within species, for example pollen from the male flower of *Olea decussata* has smooth, not beaded, muri, the large pollen grains of *Myxopyrum ovatum* have high muri instead of low (Plate 1e), and different samples of *Chionanthus ramiflorus* differ in the size of the lacunae and whether the muri are beaded or smooth (Table 1).

In addition, for the Oleaceae, pollen morphology also has limited value for identification at the family level as reported by Erdtman (1971): that several other families, such as Caprifoliaceae *(Viburnum)* and some species of the Celastraceae have very similar pollen to that of the Oleaceae. As such, pollen morphology is of limited taxonomic value above the species level in the Oleaceae.

Wodehouse (1965) suggested that the low muri of pollen grains of *Fraxinus,* compared with the other genera he examined, was related to its pollination by wind. *Myxopyrum* shows this same character but is very unlikely to be pollinated by wind as the anthers are almost sessile and are included within the corolla tube.

Table 1. Morphological characters of pollen of some Malesian Oleaceae

Species	Muri		Lacunae
	+ *beaded* – *smooth*	+ *high* – *low*	+ *large* – *small*
Olea brachiata	+	+	+
O. paniculata	+	+	+
O. decussata (male flowers)	–	+	+
(bisexual flowers)	–	–	+
Chionanthus enerve	+	+	+
C. ramiflorus	+ & –	+	+ & –
C. pluriflorus	–	+	–
Ligustrum confusum	–	+	+
Myxopyrum coriaceum	–	–	–
M. ovatum (small grain)	–	–	–
(large grain)	–	+	+

2. Size of Pollen

Wodehouse (1965) recorded the range of pollen grain diameter in the Oleaceae as between 19.5 and 30 μ and Erdtman (1971) gave the range of the longest axis as between 20 and 63 μ. These both fall within the medium-size class of pollen grains. Wodehouse *(ibid)* found that most angiosperm pollen grains fall within the 20 to 40 μ diameter range.

This study shows that while most of the genera of the Oleaceae do fall within this range, the pollen of *Chionanthus, Myxopyrum* and some species of *Olea* is much smaller, between 10 and 17 μ diameter (Table 2) i.e., fall within the small-size class of Wodehouse (1965) and Erdtman (1971).

Muller (1979) discussed possible causes for differences in size of pollen grains and reported cases where pollen size correlated with flower size, style length, anther length and latitude or altitude.

For the Oleaceae, the relationship is conspicuously between style length and pollen size (Table 2). Genera with sessile stigmas or styles up to 1 mm long produce pollen in the small-class size: *Chionanthus* (10-17.5 μ diameter), *Myxopyrum* (13-16 μ) and some *Olea* species (12-15 μ). Genera with styles 1 mm or more have in general pollen grains larger than 20 μ. The exception is *Osmanthus scortechinii* with style length between 1 and 4 mm but with pollen grains 17.5-22.5 μ diameter.

Baker & Baker (1979) also found that for 147 species with style lengths of 10 mm or longer they investigated, the mean pollen diameter was significantly larger than that of their shorter-styled counterparts.

The relation between pollen size and style length is also found in heterostylous species. Ganders (1979) recorded that in 50 out of 55 heterostylous genera, the thrum anthers produce larger pollen than the pin anthers. (It is the thrum pollen that has to grow down the longer pin style). It was first suggested by Darwin (1877, cited by Ganders, 1979) that pollen grains that need to produce long pollen tubes to grow down long styles would need greater food reserves and would therefore be larger.

The relation between flower size (corolla length) and pollen grain diameter is less obvious and flowers longer than 10 mm *(Jasminum, Forsythia, Nyctanthes* and *Syringa)* also have longer styles. For *Chionanthus,* where all species have sessile or short stigmas, there is a considerable difference in corolla length between the temperate species, *C. retusus* and *C. virginicus* with flowers more than 10 mm long, and the tropical species with small flowers less than 5 mm long, but the range in pollen size overlaps between these species with large and small flowers (Table 2). In addition,

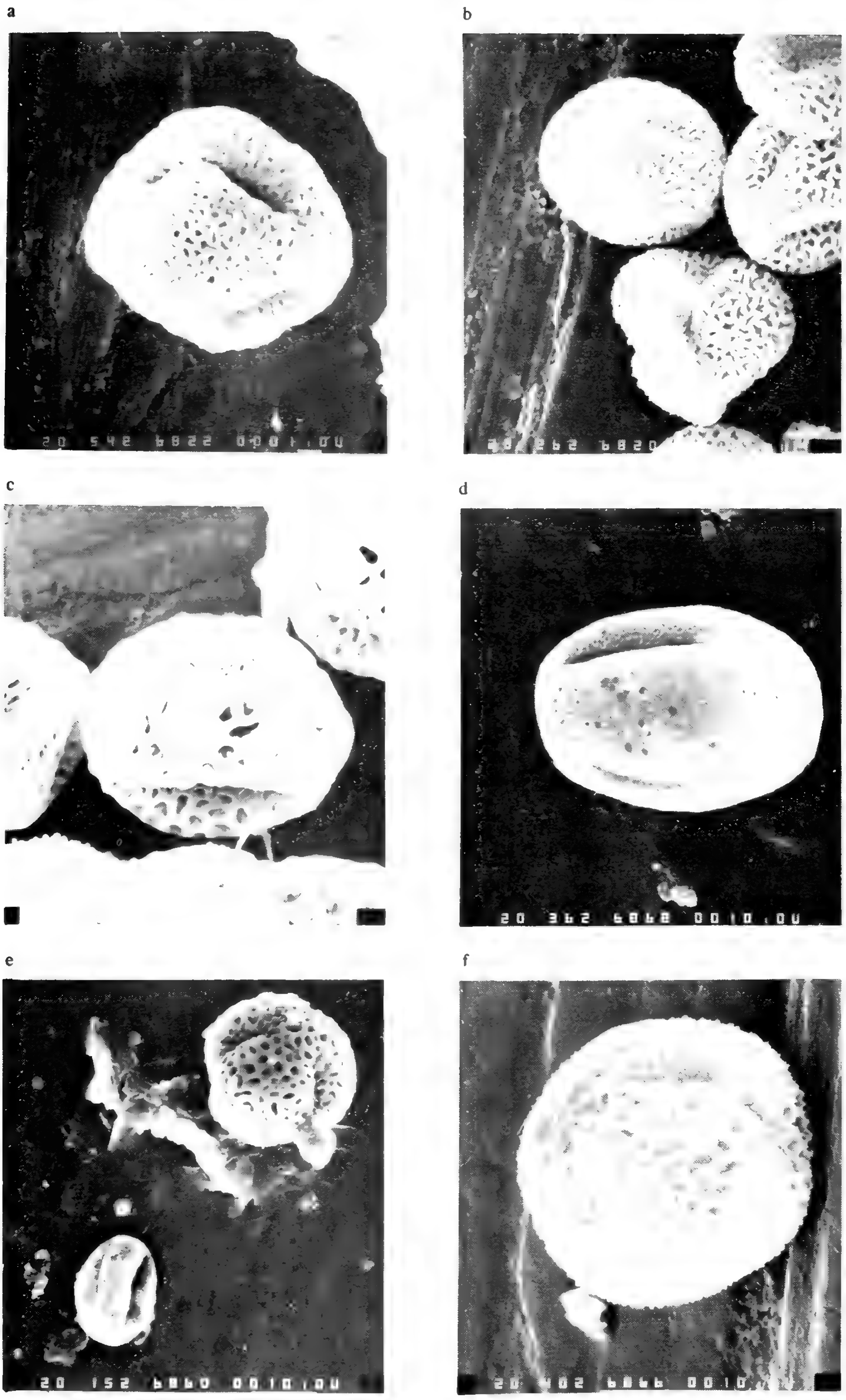

Plate 1. Pollen of Some Malesian Oleaceae
a: Chionanthus pluriflorus; b: C. ramiflorus; c. Ligustrum confusum; d: Myxopyrum coriaceum; e: M. ovatum (large and small grains); *f: Olea brachiata*

Table 2. Pollen Grain Size in the Oleaceae

SPECIES MEDIUM-SIZED POLLEN	DIAMETER (μ)	STYLE LENGTH (MM)	COROLLA LENGTH (MM)
Menodora integrifolia	63[3]	......	......
Jasminum crassifolium	(37.5) 43.5 (50)	10-20	35-55
J. humile	46[3]	......	......
J. multiflorum	(30) 34.5 (37.5)[1]	13[1]	33
J. sambac	(27.5) 29.5 (32.8)[2]	4[2]	33
	(33)-(90)[4]	......	......
Nyctanthes arbor-tristis	35-58	9	27-30
Schrebera holstii	35[3]	......	......
Syringa vulgaris	26.3[6]	......	8-15
Ligustrum confusum	(20) 22.5 (25)	1	3-4
L. glomeratum	(25) 28.3 (32.5)	1-2	2-3 (4)
L. ibota	(28) 30.5 (32)[6]	......	......
L. ovalifolium	28.5-31[6]	......	8
L. sinense	25	1	2-3
L. vulgare	28.5[6]	1	3
Fontanesia phillyraeoides	20[3]	......	......
Forsythia suspensa	(19.4) 28.5 (37.6)[6]	9[1]	19
Fraxinus americanus	24[6]	......	......
F. coriacea	20[6]	......	......
F. excelsior	22[3]	1	2-3
Osmanthus scortechinii	(17.5) 21 (22.5)	1-4	1.5-2.5
Phillyrea angustifolia	20.5[3]	......	......

SPECIES SMALL-SIZED POLLEN	Diameter (μ)	STYLE LENGTH (MM)	COROLLA LENGTH (MM)
Olea europaea	22[6]	0-1	5
O. brachiata	12.5 & 26	0-1	1.5-2.5
O. decussata (male flower)	7-9 & 13	0-1	2-4
(bisexual flower)	13	......	......
O. javanica	12.5	0-1	1-2 (3)
O. paniculata	12-15	0-1	2-3
Myxopyrum coriaceum	16	0-1	3-5
M. ovatum	13-15.5 & 21	0-1	2.5-4.5
Chionanthus retusus	(13) 14.1 (16)[5]	0	12-18
C. virginicus	(13) 14.3 (16)[5]	......	18-30
C. curvicarpus	12.5	0-1	2-3
C. enerve	17	0-1	1.5-2
C. laxiflorus	(10) 11.25 (12.5)	0-1	2-3
C. pluriflorus	(11.25) 13.5 (17.5)	0-1	3-3.5
C. porcatus	(11.25) 12.5 (13.75)	0-1	2
C. ramiflorus	10-25	0-1	3
C. rubrovenia	(10) 11 (12.5)	0-1	1.5-2.5
C. rupicolus	10	0-1	2-4

(1: long-styled; 2: short-styled; 3: Erdtman; 4: Raman *et al;* 5: Sohma; 6: Wodehouse)

Fraxinus, Ligustrum and *Osmanthus,* which have small flowers, have medium-sized pollen in the same range as the large-flowered genera (Table 2).

Specimens of some species have pollen grains of two sizes, the difference in size being almost double. This phenomenom I observed in *Olea brachiata* (with pollen grains 12.5 and 26 μ in diameter), *O. decussata* (with the majority being larger, 13 μ, than the other grains, 7-9 μ in diameter), and in *Myxopyrum ovatum* (the majority were 13-15.5 μ, with some larger, 21 μ Plate 1e).

Size differences have also been observed by Devi (1975) for *Jasminum callophyllum* where he found the size difference corresponded to the state in which the grain was shed — the smaller grains were 2- or 3-celled, the larger grains were multi-celled.

Differences in size can also be expected to be observed in the heterostylous genera of the Oleaceae: *Forsythia, Jasminum, Nyctanthes* and *Schrebera* (see above). Unfortunately, for pollen sizes given by other authors it is not recorded whether these are for the long- or short-styled flowers, so it is not possible to ascertain whether the range of size within species of these genera may be ascribed to flower type or difference between plants of the same flower type.

Polyploidy can affect the pollen size between individuals of a species. For example, Sohma (1972) noted that tetraploid plants of *C. retusus* from Taiwan are almost twice the size of normal diploid grains. Raman *et al.* (1970) reported a similar case for *Jasminum grandiflorum* where triploid plants produced some grains twice the size of those of diploid plants (Table 3). However, between species of *Jasminum* there is no correlation between size of grain and level of ploidy (Table 3), the tetraploid species falling within the range of other diploid species. The much larger grain of cv. 'Iruvatchi' of *J. sambac* suggests that it is also polyploid.

Table 3. Level of ploidy and diameter of pollen grains in some species of *Jasminum* (data from Raman *et al.* 1970)

Jasminum Species	Level of Ploidy	Diameter of grain (μ)
sambac	2n	33-52.8 (42-85.8 cv. 'Iruvatchi')
auriculatum	2n	29-52.8
grandiflorum	2n	33-46.2
	3n	29-102
communis	3n	33-52.8
rigidum	4n	39.6-49.5

Variation on a geographical basis is small (Table 4) for wild *Chionanthus* material, although it is larger for the cultivated *Nyctanthes arbor-tristis.* This latter species is also heterostylous and its range in size may be ascribed to heterostyly.

Table 4. Variation of pollen grain diameter on a geographical basis

Species	Locality	Pollen Grain Diameter (μ)
Chionanthus ramiflorus	Borneo	10-12.5
	New Guinea	10-15
C. retusus	China	13-15^{3}
	Japan	14-16^{3}
	Taiwan	13-15^{3}
Nyctanthes arbor-tristis	Java	42.5-52.5
	Malaya	35-55
	Singapore	39^{2}
	Thailand	58^{1}

(1: Erdtman, 2: Rao & Leong, 3: Sohma).

Within species, variation in size of the pollen grain in the Oleaceae can therefore be attributed either to heterostyly, polyploidy or the state of the development of the pollen grain when shed. Between species, variation in pollen size appears to be related to style length. The occurrence of small pollen grains in the Oleaceae is here reported for the first time and it is found in species of *Olea, Chionanthus* and *Myxopyrum,* all of which genera have sessile stigmas or styles less than 1 mm long.

Acknowledgements

The author is indebted to A-AUCS for a research visit to the University of New

England, Australia, where the SEM study was carried out and to the late Dr Jan Muller of the Rijksherbarium, Leiden, for stimulating and helpful discussions on the pollen of the Oleaceae.

APPENDIX

Material examined

1. *SEM. Chionanthus enerve* (Steenis) Kiew *S30433; C. pluriflorus* (Knobl.) Kiew *RK779; C. ramiflorus* Roxb. *NGF5969; Ligustrum confusum* Decn. *RK188; Myxopyrum coriaceum* Bl. *S30037; M. ovatum* Hill *NGF46864; Olea brachiata* (Lour.) Merrill *Ahmad s.n.* Kuala Lumpur; *O. decussata* (Heine) Kiew *S22516* (male flower), *Chew 939* (bisexual flower); *O. paniculata* R. Brown *NGF11948.*

2. *Light microscopy. Chionanthus curvicarpus* Kiew *SAN35826; C. laxiflorus* Bl. *SAN49386; C. pluriflorus* (Knobl.) Kiew *RK779; C. porcatus* Kiew *SAN43052; C. ramiflorus* Roxb. *SAN64322; C. rubrovenius* (Elmer) Kiew *Ramos & Edano 38584; C. rupicolus* (Lingels.) Kiew *Jacobs 9292; Jasminum crassifolium* Bl. *Elmer 20762; J. multiflorum* (Burm. f.) Andr. *RK1237; J. sambac* (L). Ait. *RK1238; Ligustrum confusum* Decn. *RK188; L. glomeratum* Bl. *SAN28544; L. sinense* Lour. *SA183; Myxopyrum ovatum* Hill *NGF46864; Nyctanthes arbor-tristis* L. *Junghuhn 33* (Java), *RK1001* (Malaysia); *Olea brachiata* (Lour). Merrill *T & P244; O. javanica* (Bl.) Knobl. *Kds10062; Osmanthus scortechinii* K. & G. *de*

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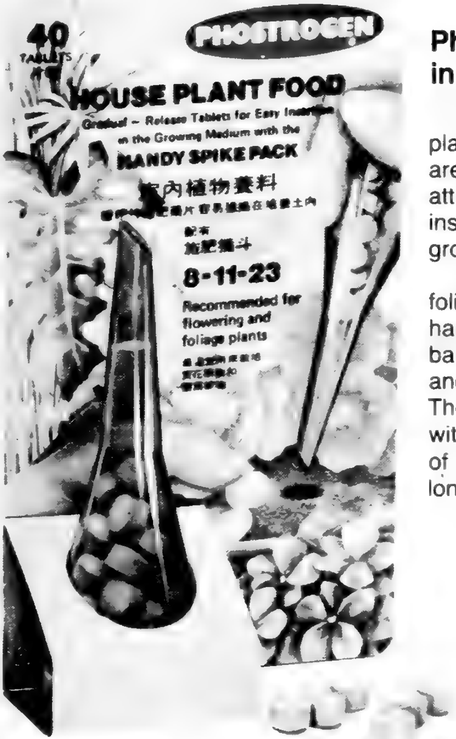
INDEX
Volume 37

Basionyms and synonyms appear in italics. Page numbers in italics indicate the presence of illustrations.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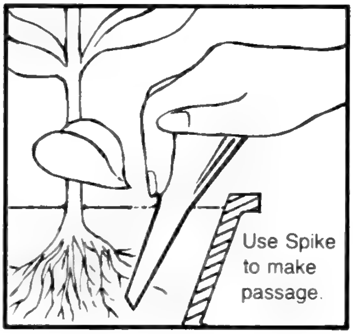
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