OBSERVATIONS ON STAMENS OF THE DIPTEROCARPACEAE

by

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CONTENTS

A. INTRODUCTION

The Dipterocarpaceae are a medium-sized family of approximately 15 genera and 580 species (Airy-Shaw, 1973). They are distributed over a large area of tropical Africa and the Indo-Malayan region from India, Ceylon, Indo-China, S.W. China to Malesia. In Malesia, according to Symington (1943) there are 14 genera and 168 species in the Malay Peninsula, 13 genera and 276 species in Borneo, 11 genera and 52 species in the Philippines, and 3 genera and 5 species in New Guinea.

The distribution of this family is interesting because it links the flora of tropical Asia with that of tropical Africa where 2 genera *Monotes* and *Marquesia* are present. Croizat (1952, p. 423) suggested that the dipterocarps are most certainly of Gondwanic origin, and they evolved and migrated from the continental mass that once occupied part of the Indian Ocean 100–500 million years ago. They later broke up into 2 major taxa, the Dipterocarpoideae, mostly confined to the continental Asia and Malesia, and the Monotoideae, restricted to Africa. They occur in areas which have had a relatively stable geology since the Cretaceous, probably the time of their origin (Meijer, 1974).

This family is especially noted for its many valuable timbers such as Meranti (*Shorea*), Keruing (*Dipterocarpus*) from Malaya, Serayas and Lauans (*Shorea* and *Parashorea*) from Borneo and the Philippines.

The existing schemes of classification of the Dipterocarpaceae are largely based on the gross morphology. It is hoped that the comparative studies of the stamens of various genera of dipterocarps, together with the information gathered from wood, pollens, cytology, embryogeny, phytochemistry and others, might eventually contribute towards a natural classification of the family.

This is an excerpt of the senior author's Honours' dissertation entitled "Comparative studies on the stamens and pollen grains of the Dipterocarpaceae", Department of Botany, University of Singapore, 1977–78. She wishes to thank Professor A.N. Rao of the Department for providing all the facilities, and to thank the Directors and Curators of the Herbarium of the Botanic Gardens, Singapore, the Forest Research Institute, Kepong, Malaya and the Forest department, Kuching, Sarawak, for having kindly supplied flowering materials for this study. Her thanks are also due to Mr. D. Teow for making photographs, and to Mr. J. Wee for advice on microtechniques.

B. MATERIALS AND METHODS

The study includes stamens of 42 species belonging to 13 genera of the Asiatic subfamily Dipterocarpoideae. The number of species investigated in each genus was as follows:

1. *Anisoptera* (2)
2. *Cotylelobium* (2)
3. *Dipterocarpus* (3)
4. *Doona* (2)

5. *Dryobalanops* (2)
6. *Hopea* (7)
7. *Neobalanocarpus* (1)
8. *Parashorea* (2)
9. *Pentacme* (1)
10. *Shorea* (15)
11. *Upuna* (1)
12. *Vateria* (1)
13. *Vatica* (3)

Dried flowers and flower buds were obtained from the herbarium specimens. A list of the voucher specimens are given at the end.

The dried flowers and buds were soaked and boiled in water till soft. The indehisced stamens were then removed from the flowers under a dissecting microscope, using fine needles and forceps. The method of clearing was by modification of Foster's clearing techniques (1949). Serial sections of the flower buds to show the transverse sections of *Neobalanocarpus heimii* and *Shorea parvifolia* were obtained by the paraffin method (Johansen, 1940). Sections were cut by means of the rotary microtome and these were stained with a combination of Safranin and Fast-green.

This study of the stamens is based on representative species of most of the genera of the family. Descriptions of the genera are presented in alphabetical order. Only in the genus *Shorea*, four sections (Symington, 1943) are further described separately. The general description for each genus presented is based on and confined to the representative species investigated. For *Shorea*, the general features for each section is also described based on the species studied.

C. DESCRIPTION OF STAMENS

Descriptions of the stamens include the general morphology, dimensions, and vasculature. Different parts of the stamen, such as the anthers, filaments and appendages to the connectives are also measured and described. The total lengths of the stamens include the appendages unless otherwise stated. The measurements were made in millimetres or in microns. Illustrations of the stamens of the species examined are prepared based on the revived herbarium materials, cleared in dilute sodium hydroxide and preserved in xylene. Details of the stamen (e.g. hairs and vasculature) are observed under the high magnification of a compound microscope.

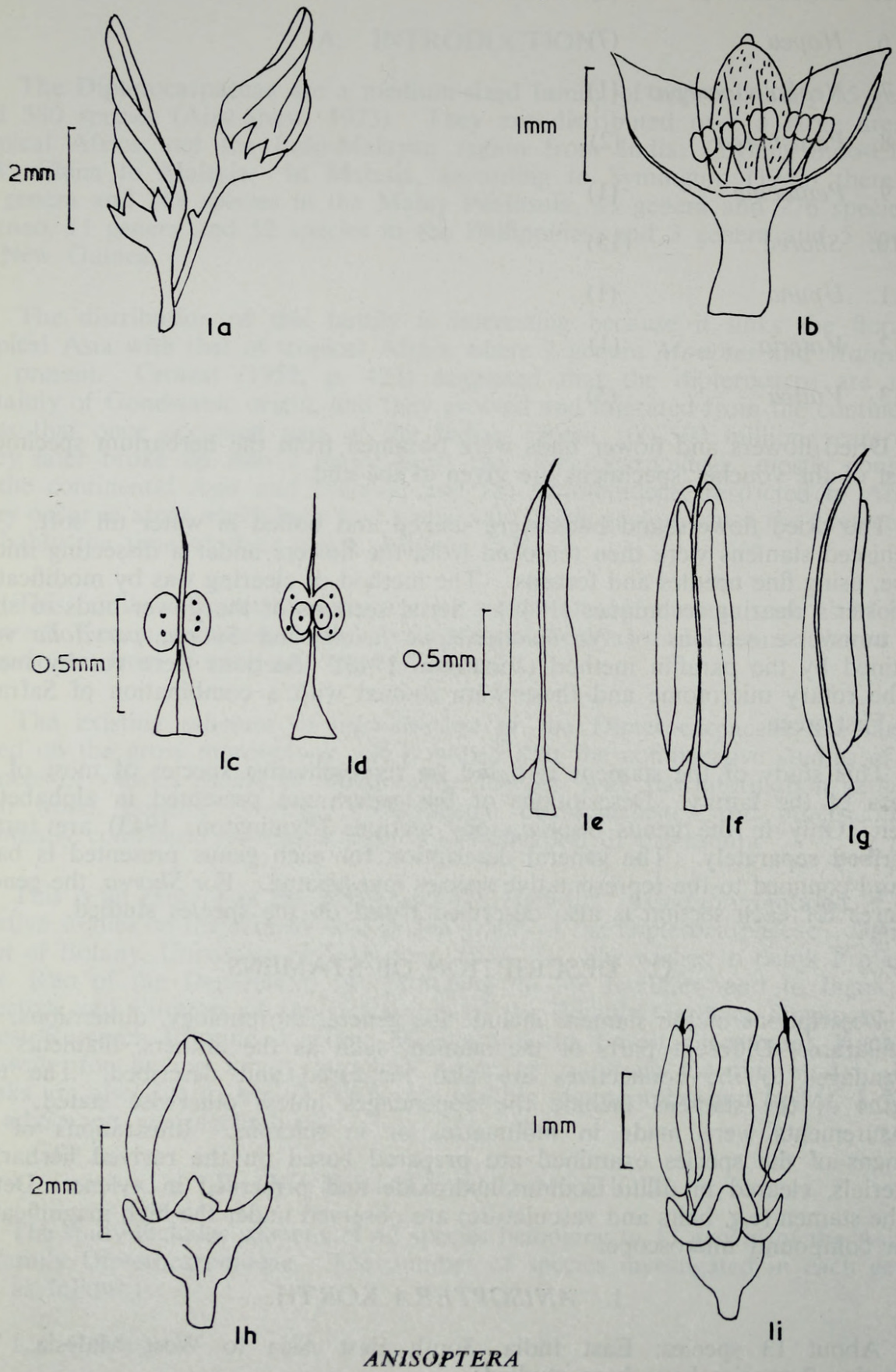
1. *ANISOPTERA* KORTH.

About 13 species; East India, South East Asia to West Malesia. The following 2 species have been studied:

(1) *Anisoptera curtisii* Dyer (Section *Pilosae*) (Fig. 1, a-d; Fig. 2, b-c);

(2) *Anisoptera laevis* Ridl. (Section *Glabrae*) (Fig. 1, e-i; Fig. 2, a).

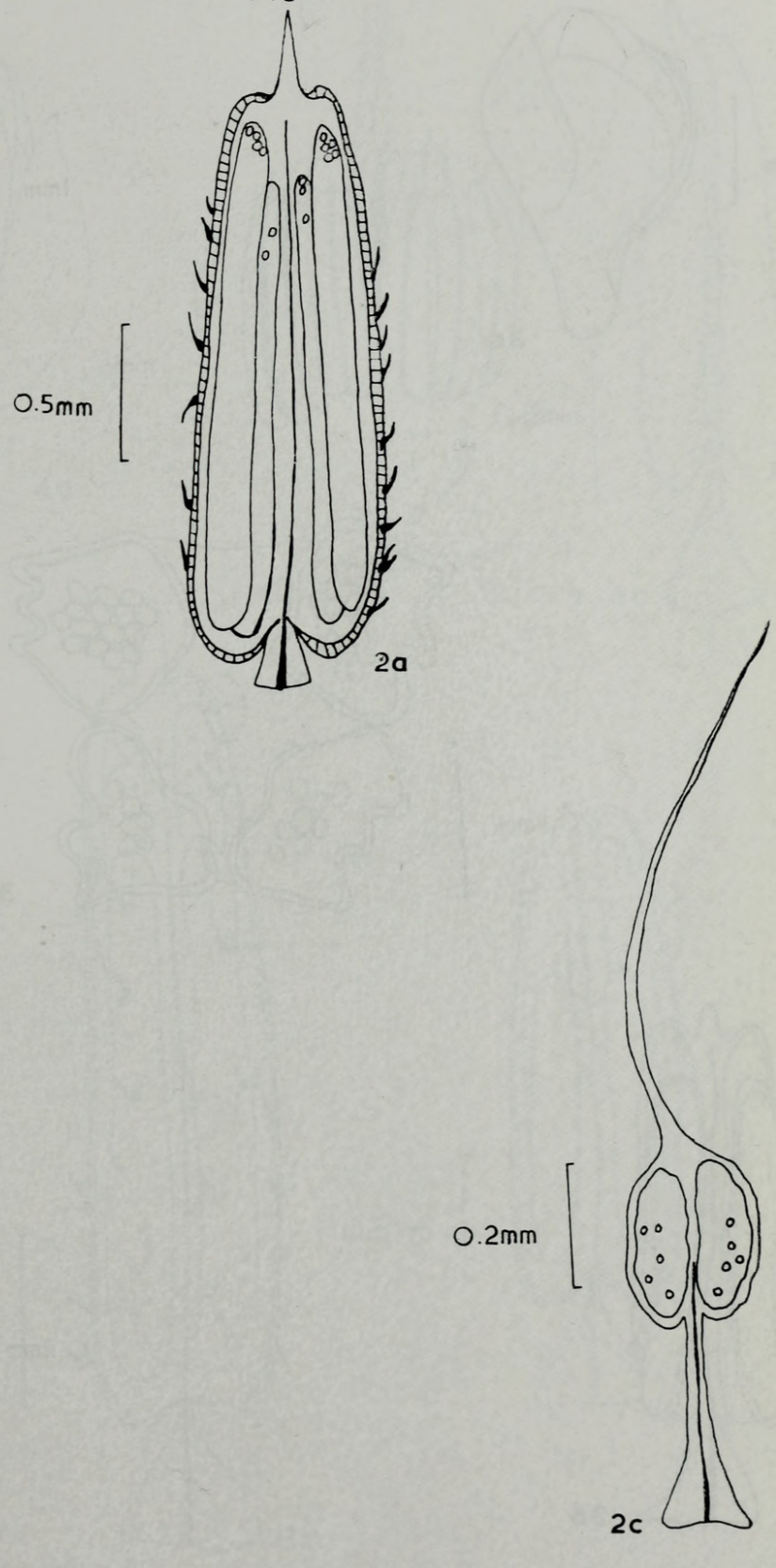
FIG 1



ANISOPTERA

A. curtisii a. flower bud. b. flower with parts of perianth removed to show arrangement of stamens. c. abaxial view of stamen. d. adaxial view of stamen. *A. laevis* e. abaxial view of stamen. f. adaxial view of stamen. g. oblique lateral view of stamen. h. flower bud. i. flower with perianth removed to show arrangement of stamens.

FIG 2

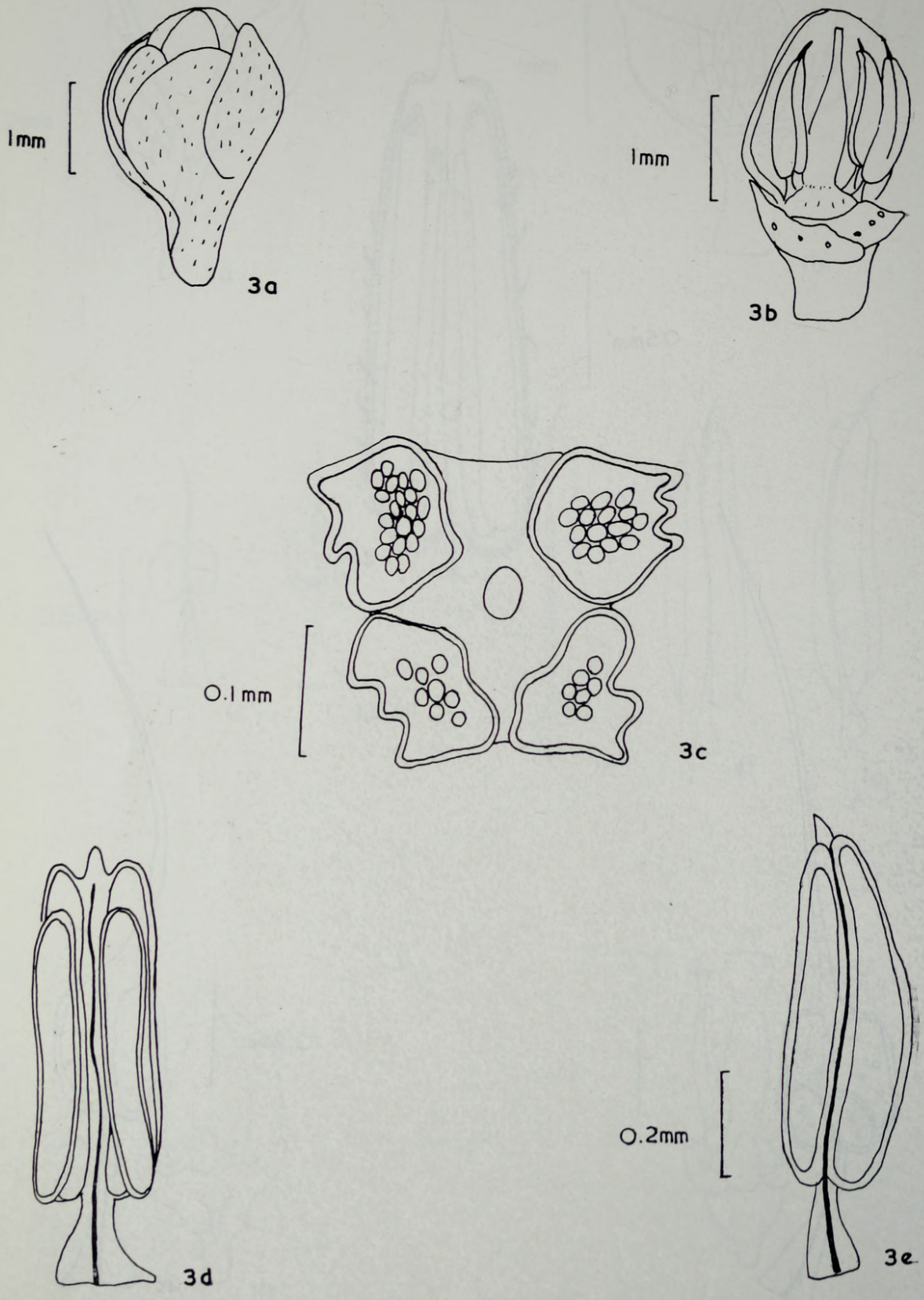


ANISOPTERA

Stamens. x 100

a. *A. laevis* : abaxial view. b. *A. curtisii* : adaxial view. c. *A. curtisii* : abaxial view.

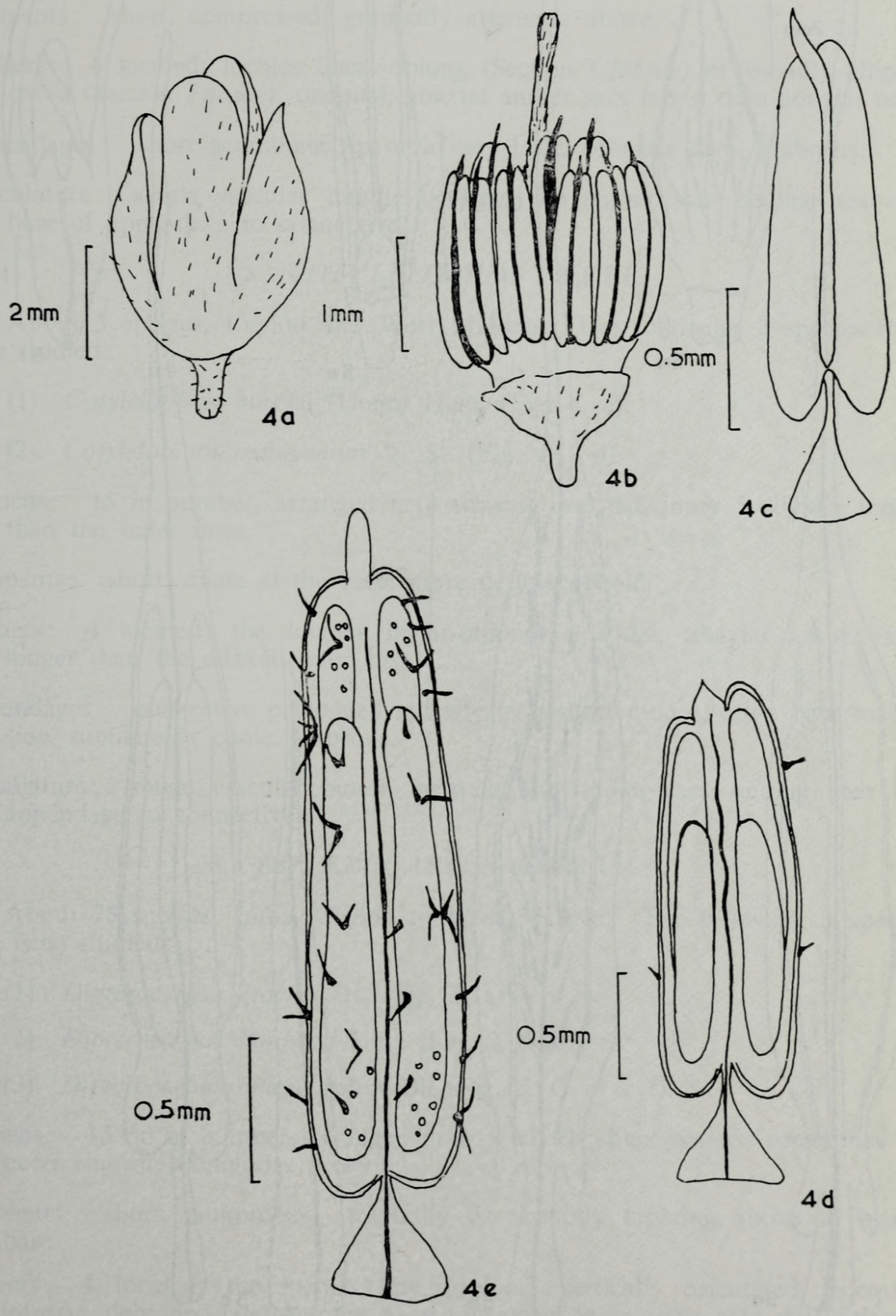
FIG 3



NEOBALANOCARPUS

N. heimii (= *Balanocarpus heimii*) a. flower bud. b. flower with perianth removed to show arrangement of stamens. c. transverse section of stamen. d. adaxial view of stamen. e. lateral view of stamen.

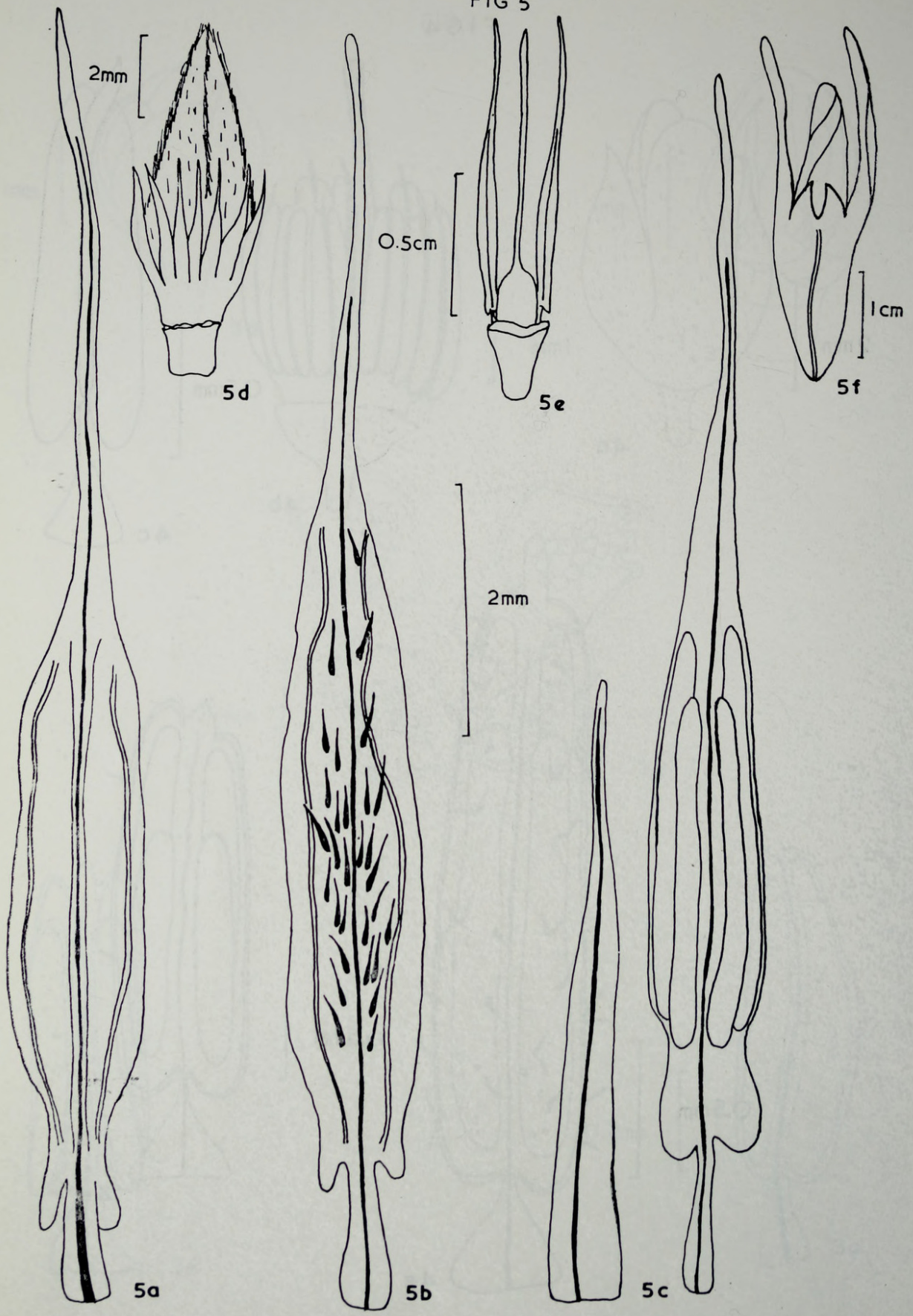
FIG 4



COTYLELOBIUM

C. malayanum a. flower bud. b. flower with perianth removed to show arrangement of stamens. c. abaxial view of stamen. d. stamen x 100.
C. burckii e. stamen x 100.

FIG 5



DIPTEROCARPUS

D. gracilis a. stamen : adaxial view.
D. kunstleri b. stamen : abaxial view. e. flower with perianth removed to show position of stamens.
D. oblongifolius c. staminode and adaxial view of stamen. d. flower with perianth and stamens removed to show ring of staminodes. f. flower bud.

Stamens: 15–30 in number, arranged in 2 or 3 whorls; glabrous; unequal, outer stamens shorter than the inner ones.

Filaments: short, compressed; gradually attenuate above.

Anthers: 4 loculed; locules linear-oblong (Section *Glabrae*) or broadly elliptic-ovoid (Section *Pilosae*); unequal, abaxial anther sacs larger than adaxial ones.

Appendages: short acuminate tip or a very long, subulate awn; glabrous.

Vasculature: single vascular bundle between the anther sacs ending near the base of appendage to connective.

2. *COTYLELOBIUM* PIERRE

About 5 species; Ceylon and West Malesia. The following 2 species have been studied:

(1) *Cotylelobium burckii* (Heim) Heim (Fig. 4, e);

(2) *Cotylelobium malayanum* V. Sl. (Fig. 4, a-d).

Stamens: 15 in number, arranged in 2 whorls; unequal, inner 5 slightly longer than the outer ones.

Filaments: short, dilate at the base, more or less deltoid.

Anthers: 4 loculed; the locules linear-oblong; unequal, abaxial anther sacs longer than the adaxial pair; hispid.

Appendages: connective prolonged apically to a short mucro, often bent to one side, subulate or conic, glabrous.

Vasculature: single vascular bundle between the anther sacs, ending near the appendage to connective.

3. *DIPTEROCARPUS* GAERTN. f.

About 76 species; India, Ceylon to West Malesia. The following 3 species have been studied:

(1) *Dipterocarpus gracilis* Bl. (Fig. 5, a);

(2) *Dipterocarpus kunstleri* King (Fig. 5, b & e);

(3) *Dipterocarpus oblongifolius* Bl. (Fig. 5, c, d & f).

Stamens: 15–36 in number, arranged in 2–3 whorls; hypogynous; sometimes an outer ring of staminodes present.

Filaments: short, compressed, gradually or abruptly tapering above to broad base.

Anthers: 4 loculed; the locules linear-oblong, vertically orientated, unequal, introrse, dehiscing laterally; the basal portion of the anthers with sterile tissue, fleshy, usually auriculate.

Appendages: appendage erect, long and tapering, produced from apical sterile tissues of anthers; glabrous.

Vasculature: single vascular bundle between the anther sacs, usually ending within the appendage. Staminodes also supplied by a single vascular trace.

4. *DOONA* THW.

Over 10 species; endemic to Ceylon. The following 2 species have been studied:

(1) *Doona gardneri* Thw. (Fig. 6, a, b, e, f, g; Fig. 7, a-c);

(2) *Doona macrophylla* Thw. (Fig. 6, c, d, h, i; Fig. 7, d).

Stamens: 15 in number; arranged in 2 whorls around the ovary, all exceeding the style.

Filaments: compressed, loricate, tapering gradually above.

Anthers: 4 loculed, the locules fusiform or elongated; unequal, abaxial anther sacs slightly longer than adaxial pair; latrorse; dehiscing longitudinally.

Appendages: appendage stout, fleshy, clavate.

Vasculature: single vascular bundle between the anther sacs, branching out within the appendage.

5. *DRYOBALANOPS* GAERTN. f.

About 9 species, confined to Sumatra, Malaya and Borneo. The following 2 species have been studied:

(1) *Dryobalanops aromatica* Gaertn. f. (Fig. 8, a-f; Fig. 9, a);

(2) *Dryobalanops oblongifolia* Dyer. (Fig. 8, g-i; Fig. 9, b).

Stamens: 30 in number, arranged compactly in 3 whorls; unequal, the innermost whorl longest; hypogynous.

Filaments: long, compressed, applanate; tapering abruptly above, connate at the base.

Anthers: 4 loculed; the locules linear-oblong, apiculate at both ends; unequal, the abaxial anther sacs much longer than the adaxial pair; introrse; dehiscing longitudinally.

Appendages: acumen short, erect, stout, cuspidate; exceeding the anther apex.

Vasculature: staminal bundle in *D. oblongifolia* branches out to give rise to 3 vascular traces. Each stamen is served by single vascular trace which ends near the appendage to connective.

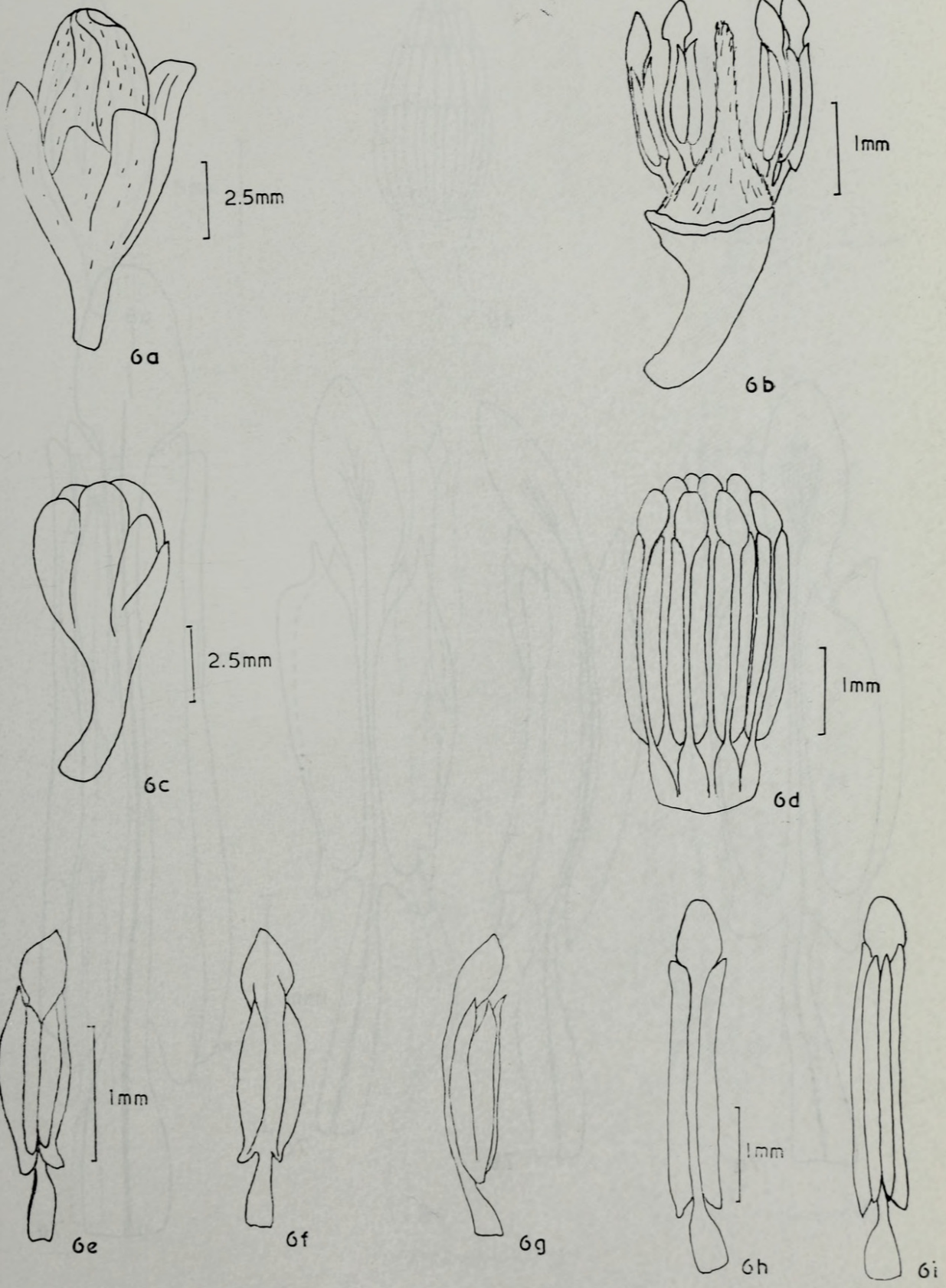
6. *HOPEA* ROXB.

Over 90 species, South India to South China and the Malay Islands. The following 6 species have been studied:

(1) *Hopea apiculata* Sym. (Fig. 10, a, b, c; Fig. 12, e);

(2) *Hopea beccariana* Burck. (Fig. 10, d, e, f; Fig. 12, b);

FIG 6

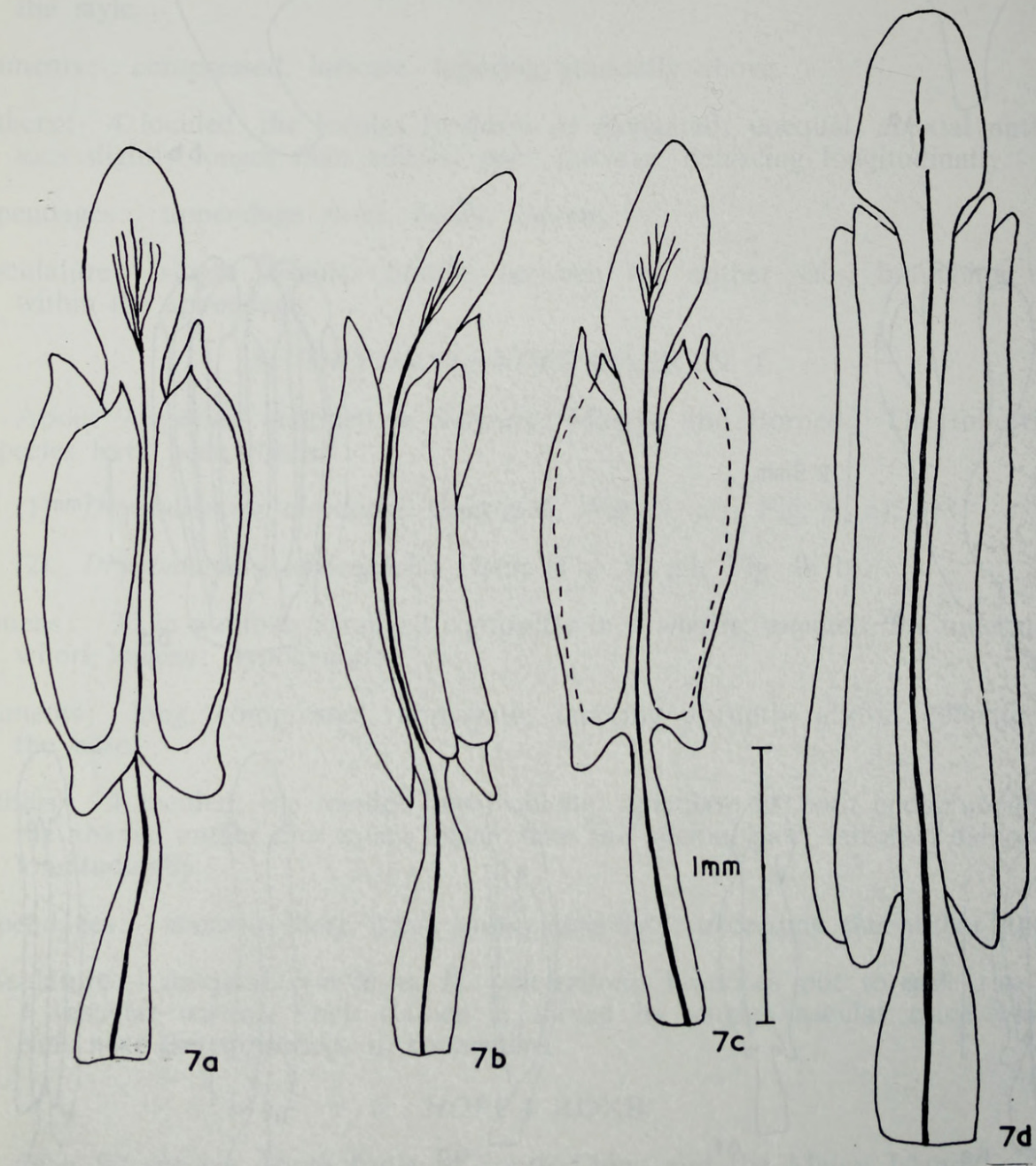


DOONA

D. gardneri a. flower bud. b. flower with perianth removed to show position of stamens. e. adaxial view of stamen. f. abaxial view of stamen. g. lateral view of stamen.

D. macrophylla c. flower bud. d. flower with perianth removed to show arrangement of stamens. h. abaxial view of stamen. i. adaxial view of stamen.

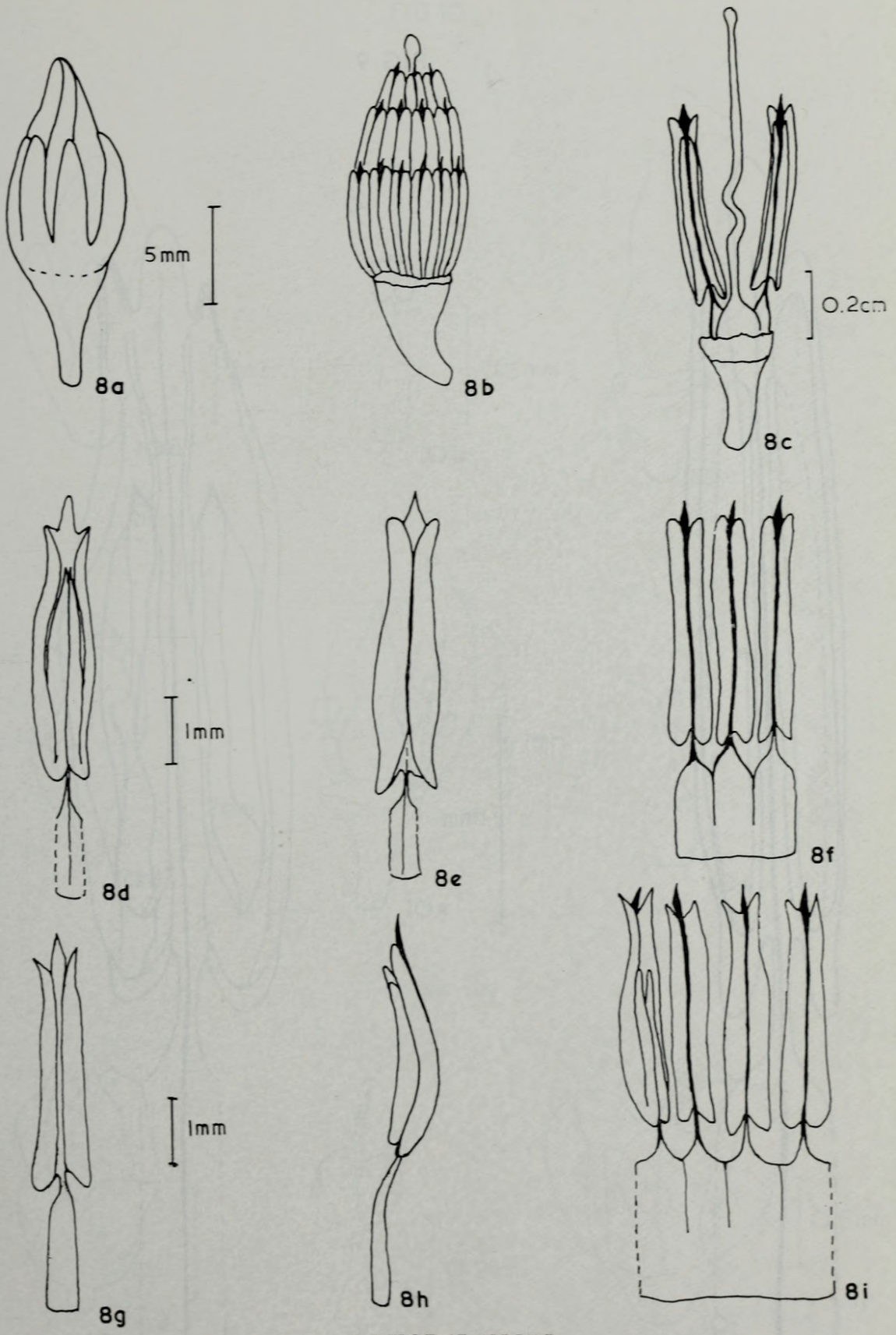
FIG 7



DOONA

D. gardneri a. adaxial view of stamen. b. lateral view of stamen. c. abaxial view of stamen.
D. macrophylla d. abaxial view of stamen.

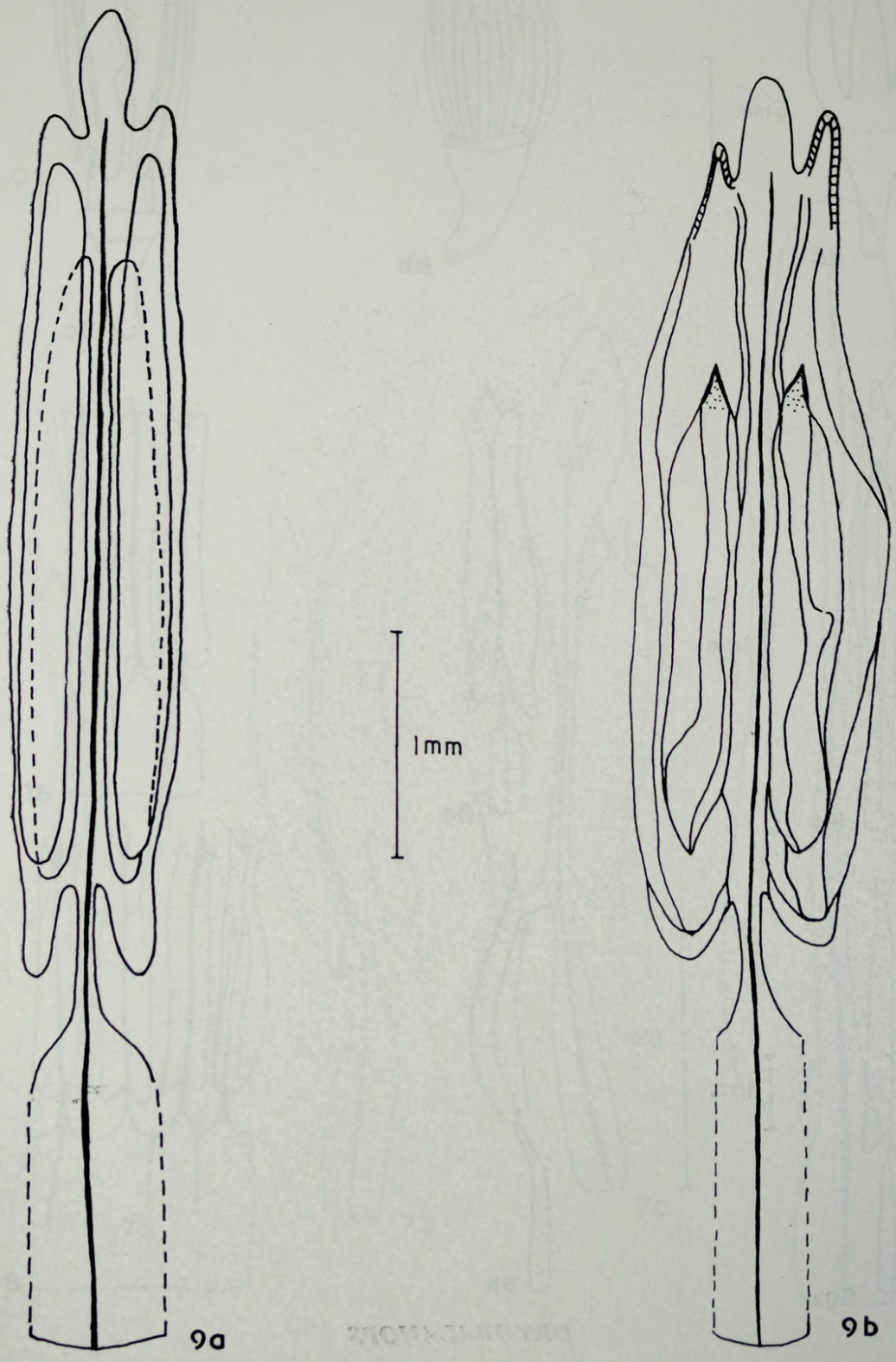
FIG 8



DRYOBALANOPS

D. aromatica a. flower bud. b., c. flower with perianth removed to show position of stamens. d. stamen : adaxial view. e. stamen : abaxial view f. partial whorl of stamens with connate filaments.
D. oblongifolia g. abaxial view of stamen. h. lateral view of stamen. i. partial whorl of stamens with connate filaments.

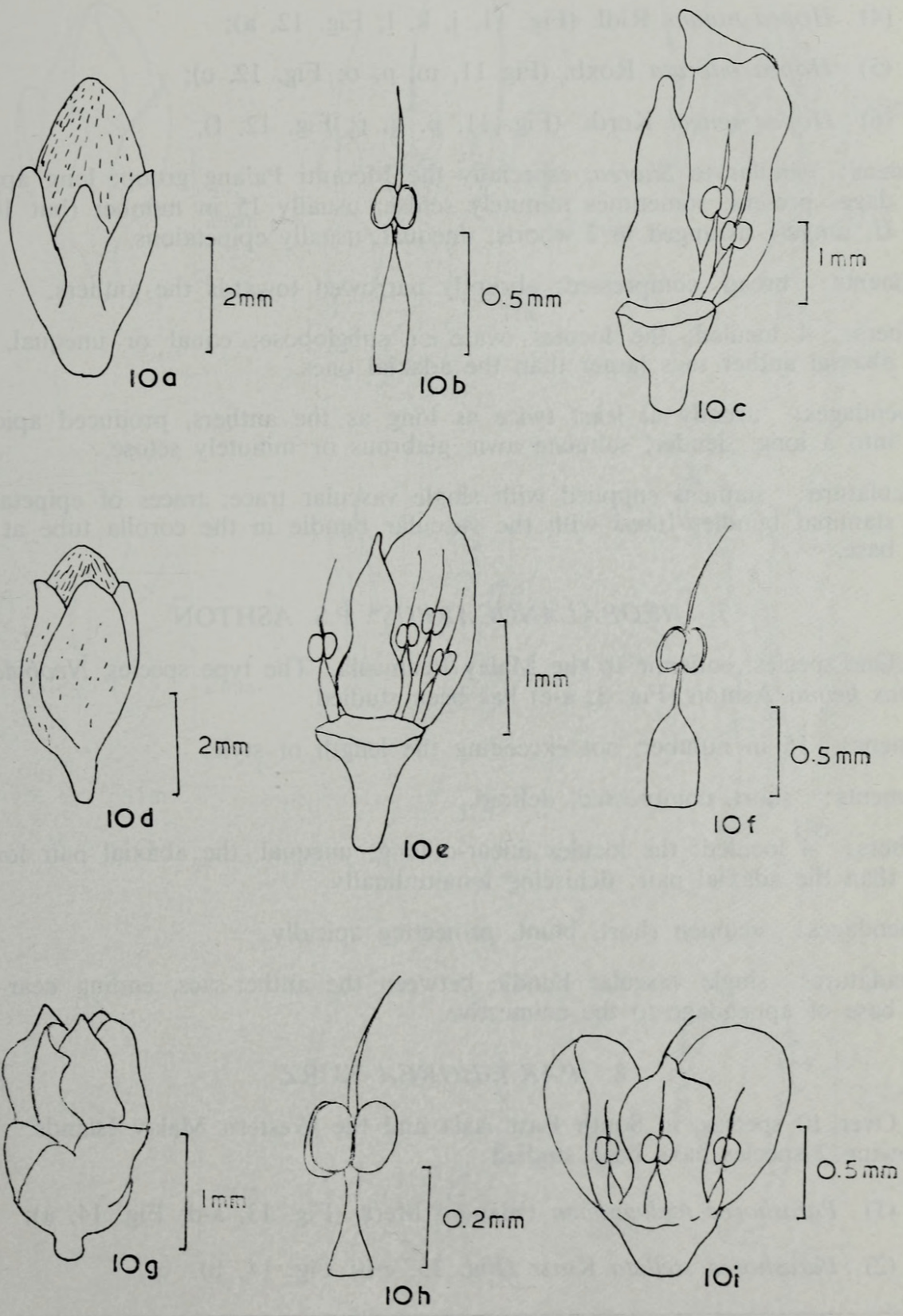
FIG 9



DRYOBALANOPS

Stamens. x 100
a. *D. aromatica* : adaxial view. b. *D. oblongifolia* : adaxial view.

FIG 10



HOPEA

H. apiculata a. flower bud. b. stamen — abaxial view. c. flower with parts of perianth removed to show arrangement of stamens.
H. beccariana d. flower bud. e. flower with parts of perianth removed to show arrangement of stamens. f. stamen — adaxial view.
H. minima g. flower bud. h. stamen — abaxial view. i. flower with parts of perianth removed to show arrangement of stamens.

(3) *Hopea minima* Sym. (= *Balanocarpus curtisii* King) (Fig. 10, g, h, i; Fig. 12, d);

(4) *Hopea nutans* Ridl. (Fig. 11, j, k, l; Fig. 12, a);

(5) *Hopea odorata* Roxb. (Fig 11, m, n, o; Fig. 12, c);

(6) *Hopea sangal* Korth. (Fig. 11, p, q, r; Fig. 12, f).

Stamens: similar to *Shorea*, especially the Meranti Pa'ang group; long appendages present, sometimes minutely setose; usually 15 in number (but 10 in *H. sangal*), arranged in 2 whorls; unequal, usually epipetalous.

Filaments: broad, compressed; abruptly narrowed towards the anthers.

Anthers: 4 loculed; the locules ovate or subglobose; equal or unequal, the abaxial anther sacs larger than the adaxial ones.

Appendages: usually at least twice as long as the anthers, produced apically into a long, slender, subulate awn, glabrous or minutely setose.

Vasculature: stamens supplied with single vascular trace; traces of epipetalous staminal bundles fused with the vascular bundle in the corolla tube at the base.

7. *NEOBALANOCARPUS** P.S. ASHTON

One species; endemic to the Malay Peninsula. The type species, *Neobalanocarpus heimii* Ashton (Fig. 3, a-e) has been studied.

Stamens: 15 in number, not exceeding the length of style.

Filaments: short, compressed, deltoid.

Anthers: 4 loculed; the locules linear-oblong; unequal, the abaxial pair longer than the adaxial pair; dehiscing longitudinally.

Appendages: acumen short, blunt, projecting apically.

Vasculature: single vascular bundle between the anther-sacs, ending near the base of appendage to the connective.

8. *PARASHOREA* KURZ

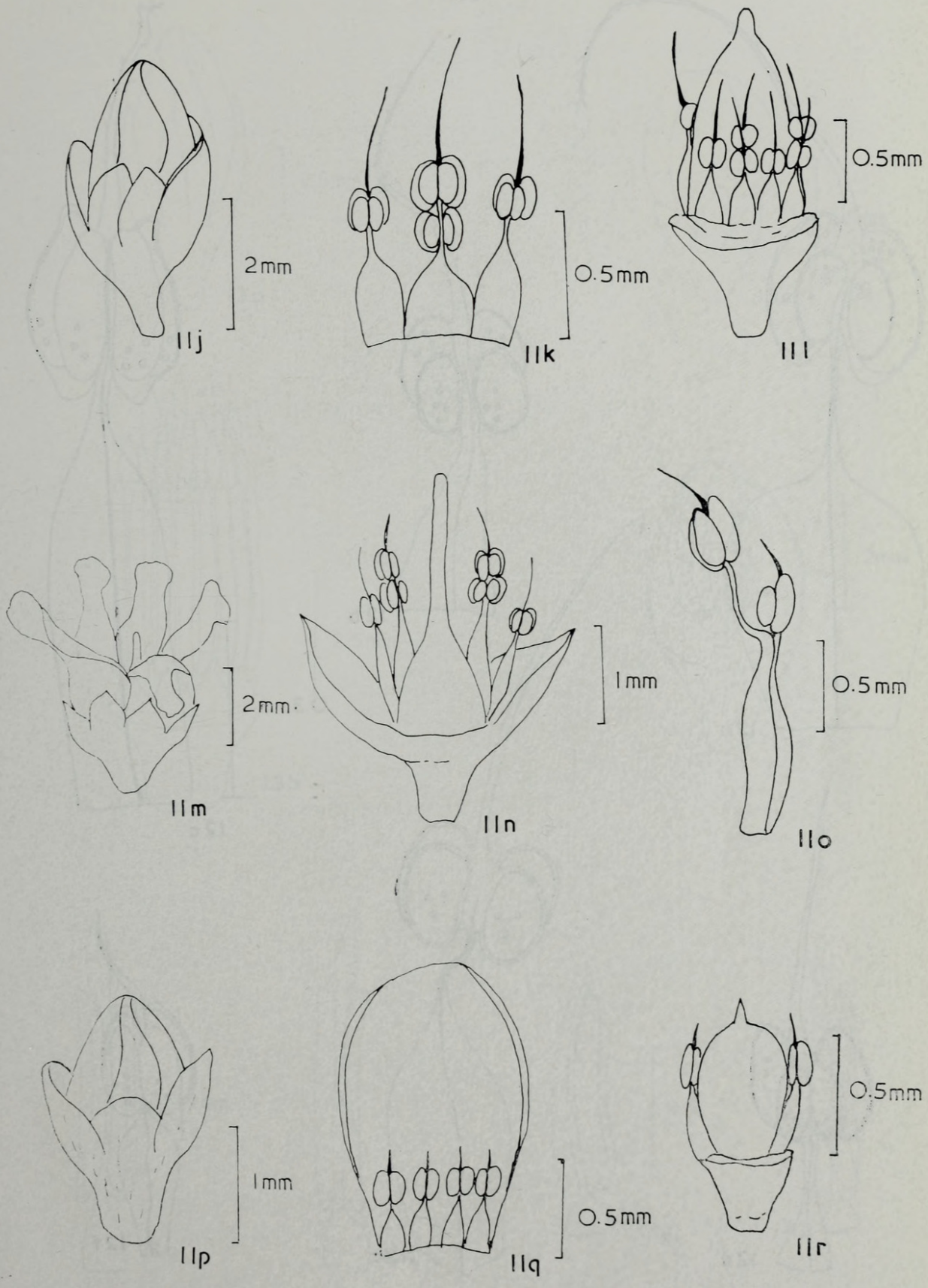
Over 10 species, in South East Asia and the Western Malay Islands. The following 2 species have been studied:

(1) *Parashorea malaanonan* (Blanco) Merr. (Fig. 13, a-d; Fig. 14, a);

(2) *Parashorea stellata* Kurtz (Fig. 13, e-h; Fig. 14, b).

**Neobalanocarpus* is a new genus recently established by Dr P. S. Ashton (in Gard. Bull. Singapore 31: 27, 1978). It contains only one species, *N. heimii* (King) Ashton, formerly known as *Balanocarpus heimii* King. The genus *Balanocarpus* (excluding this Malayan species) with about 15 species, occurring from India to West Malesia, has been reduced to *Hopea* by Bole (in Kew Bull. 1951, p. 146).

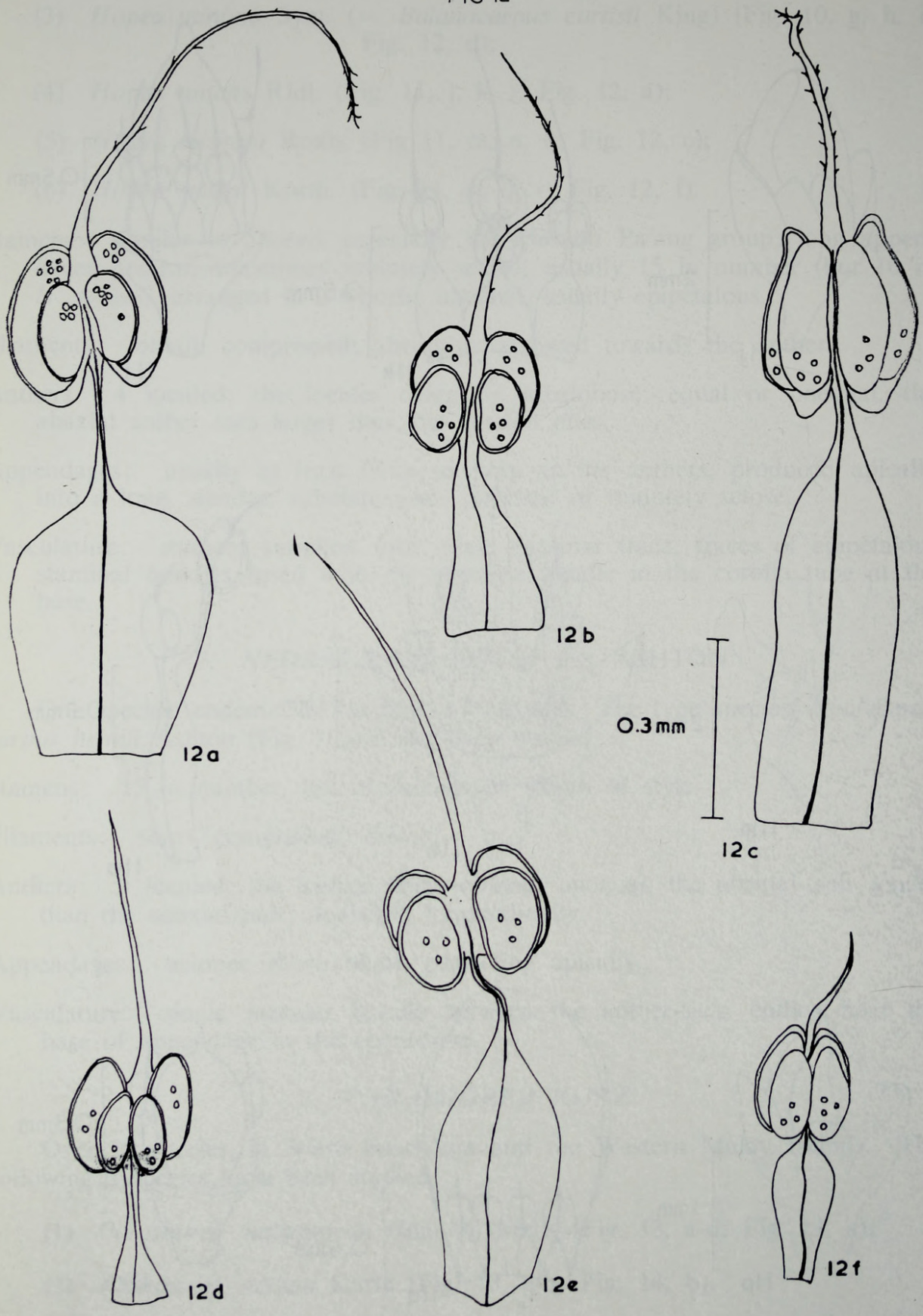
FIG 11



HOPEA

H. nutans j. flower bud. k. single and double stamens alternating. l. flower with perianth removed to show arrangement of stamens.
H. odorata m. flower. n. flower with perianth removed to show arrangement of stamens. o. lateral view of stamens.
H. sangal p. flower bud. q. petal with epipetalous stamens. r. flower with perianth removed to show position of stamens.

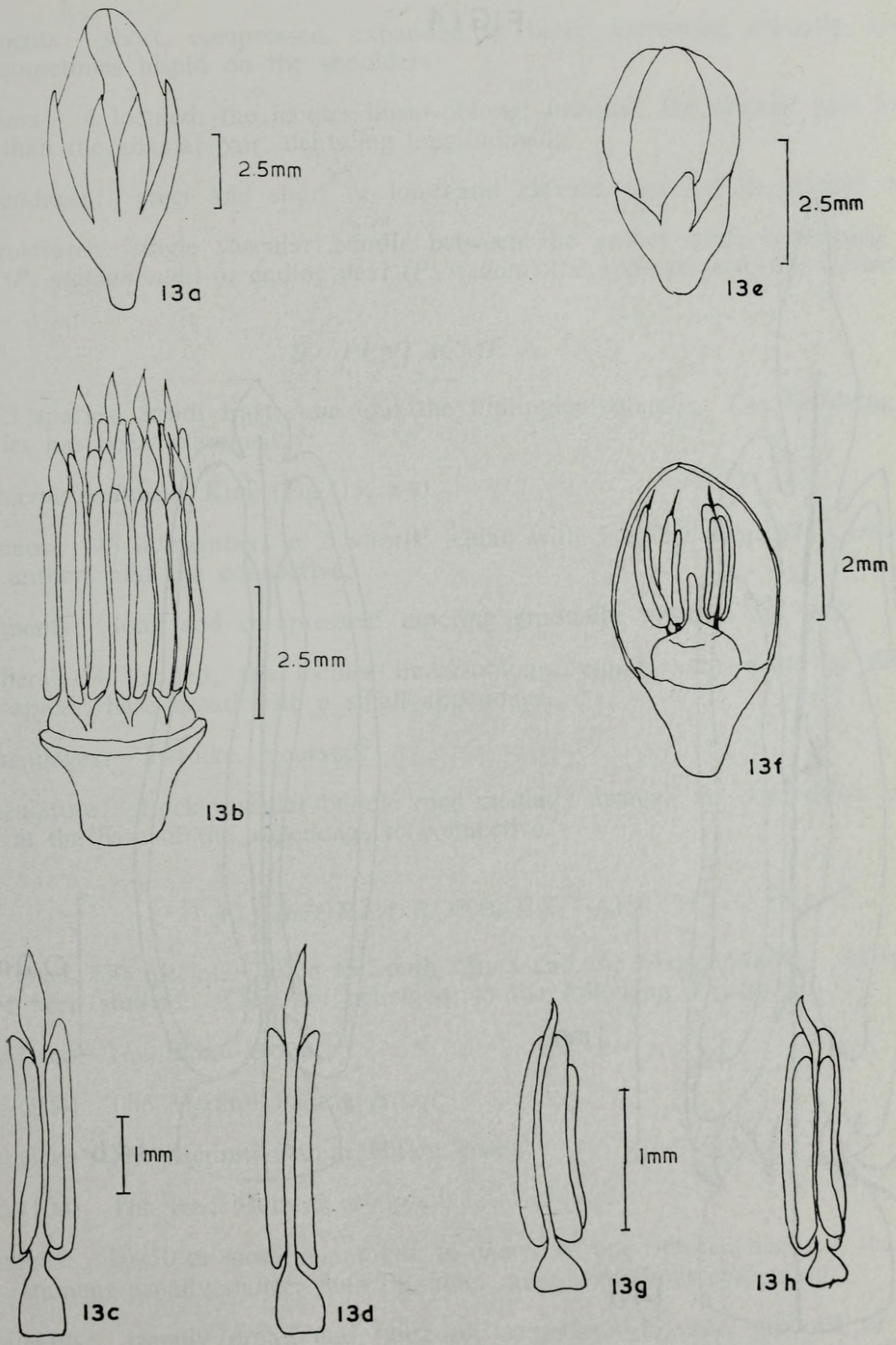
FIG 12



HOPEA

Stamens. x 100 : adaxial views.
a. *H. nutans* b. *H. beccariana* c. *H. odorata* d. *H. minima* e. *H. apiculata* f *H. sangal*

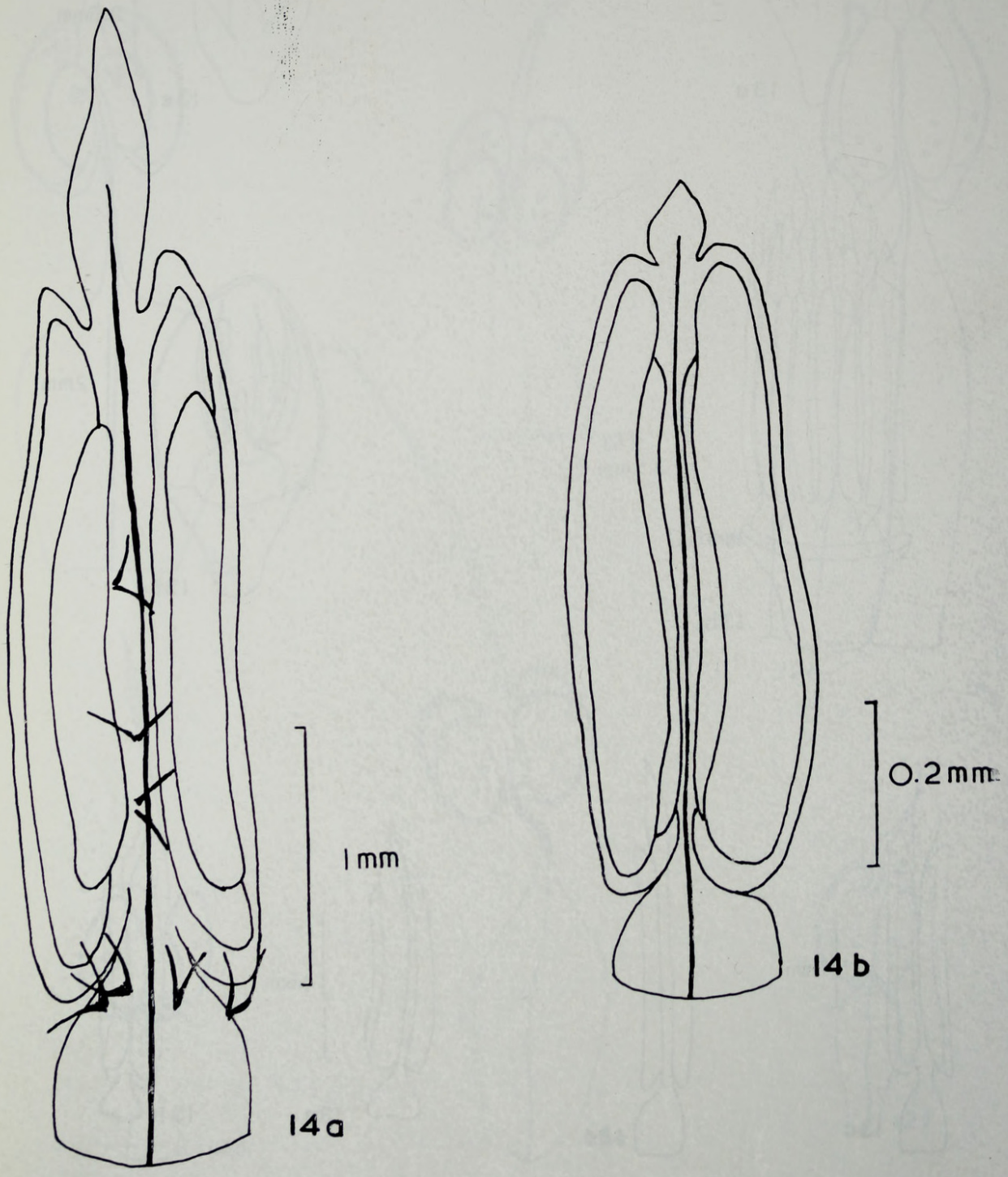
FIG 13.



PARASHOREA

P. malaanonan a. flower bud. b. flower with perianth removed to show arrangement of stamens. c. adaxial view of stamen. d. abaxial view of stamen.
P stellata e. flower bud. f. flower with parts of perianth removed to show position of stamens. g. oblique abaxial view of stamen. h. adaxial view of stamen.

FIG 14



PARASHOREA

Stamens. x 100
a. *P. malaanonan* b. *P. stellata*

Stamens: 15, in 2 whorls (10 + 5); unequal.

Filaments: short, compressed, expanded at base; narrowing abruptly above; sometimes hispid on the shoulders.

Anthers: 4 loculed; the locules linear-oblong; unequal, the abaxial pair longer than the adaxial pair; dehiscing longitudinally.

Appendages: erect and short or long and clavate, tapering to pointed apex.

Vasculature: single vascular bundle between the anther sacs; continuing into (*P. malaanonan*) or ending near (*P. stellata*) the appendage to the connective.

9. *PENTACME* A. DC.

3 species, South East Asia and the Philippine Islands. The following one species has been examined;

Pentacme malayana King (Fig. 15, a-e).

Stamens: 15 in number, in 2 whorls; equal; with 5 apical projections from the anthers and the connective.

Filaments: long and compressed; tapering gradually towards the top.

Anthers: 4 loculed; the locules linear-oblong; equal; with acute to filiform apices; base broad with a small appendage.

Appendages: awl-like, recurved.

Vasculature: thick vascular bundle runs medially through the connective, ending at the base of the appendage to connective.

10. *SHOREA* ROXB. EX GAERTN.

Over 200 species, Ceylon to South China and the Malay Islands. 15 species have been studied. They are belonging to the following 4 groups:

(10a) The Balau group;

(10b) The Meranti Pa'ang group;

(10c) The Meranti Damar Hitam group;

(10d) The Red Meranti group.

Stamens: 10–50 or more in number, in one to several whorls; unequal, the outer stamens usually shorter than the inner ones; sometimes epipetalous.

Filaments: usually broad and flattened, sometimes ligulate, gibbous or fused at the base, gradually or abruptly tapering above to form connective of anthers; sometimes barbate on the shoulders.

Anthers: mostly 4 loculed but 2 loculed in the *Meranti Damar Hitam group;* the locules elliptic-ovate or oblong; abaxial locules larger than the adaxial locules.

Appendages: connective usually produced into a long, filiform acumen of various lengths; erect or reflexed and projecting abaxially, sometimes apically; setose, pubescent or glabrous.

Vasculature: a single vascular trace usually runs medially through the filament ending near the base of appendage to connective or in some species of the Red Meranti group, the single vascular trace branches, thus there are 3 short traces in the connective. In the case of stamens whose filaments are fused at the base, the staminal bundle originates from the central stele of the flower, branching out to give rise to 3 or several vascular strands, each strand entering a single stamen.

(10a) *The Balau group of Shorea*

For this group, the following 3 species have been examined:

(1) *Shorea exelliptica* Meijer (Fig. 16, a-g; Fig. 18, c);

(2) *Shorea foxworthyi* Sym (Fig. 17, j-m; Fig. 18, a);

(3) *Shorea seminis* (de Vriese) V. Sl. (Fig. 17, h, i; Fig. 18, b).

Stamens: 30–45 in number, arranged in 3 whorls; of 3 different lengths, the innermost whorl the longest.

Filaments: compressed; the base broad or narrow; filaments of different whorls radially fused at the base into bundles; shoulders of the filaments are barbate.

Anthers: 4 loculed; the locules elliptic to oblong; unequal, the abaxial anther sacs larger than the adaxial ones; basifixed, adnate to the filament; dehiscing longitudinally; sometimes barbate.

Appendages: short and blunt, less than the length of anthers, projecting abaxially; setose or barbate, bristles long.

Vasculature: staminal bundles are present, each branching out to give rise to 3 vascular strands, each trace entering a single filament.

(10b) *The Meranti Pa'ang group of Shorea*

For this group, the following species have been examined:

(1) *Shorea gratissima* Dyer (Fig. 19, h; Fig. 21, a);

(2) *Shorea resinosa* Foxw. (Fig. 19, a-g; Fig. 21, b);

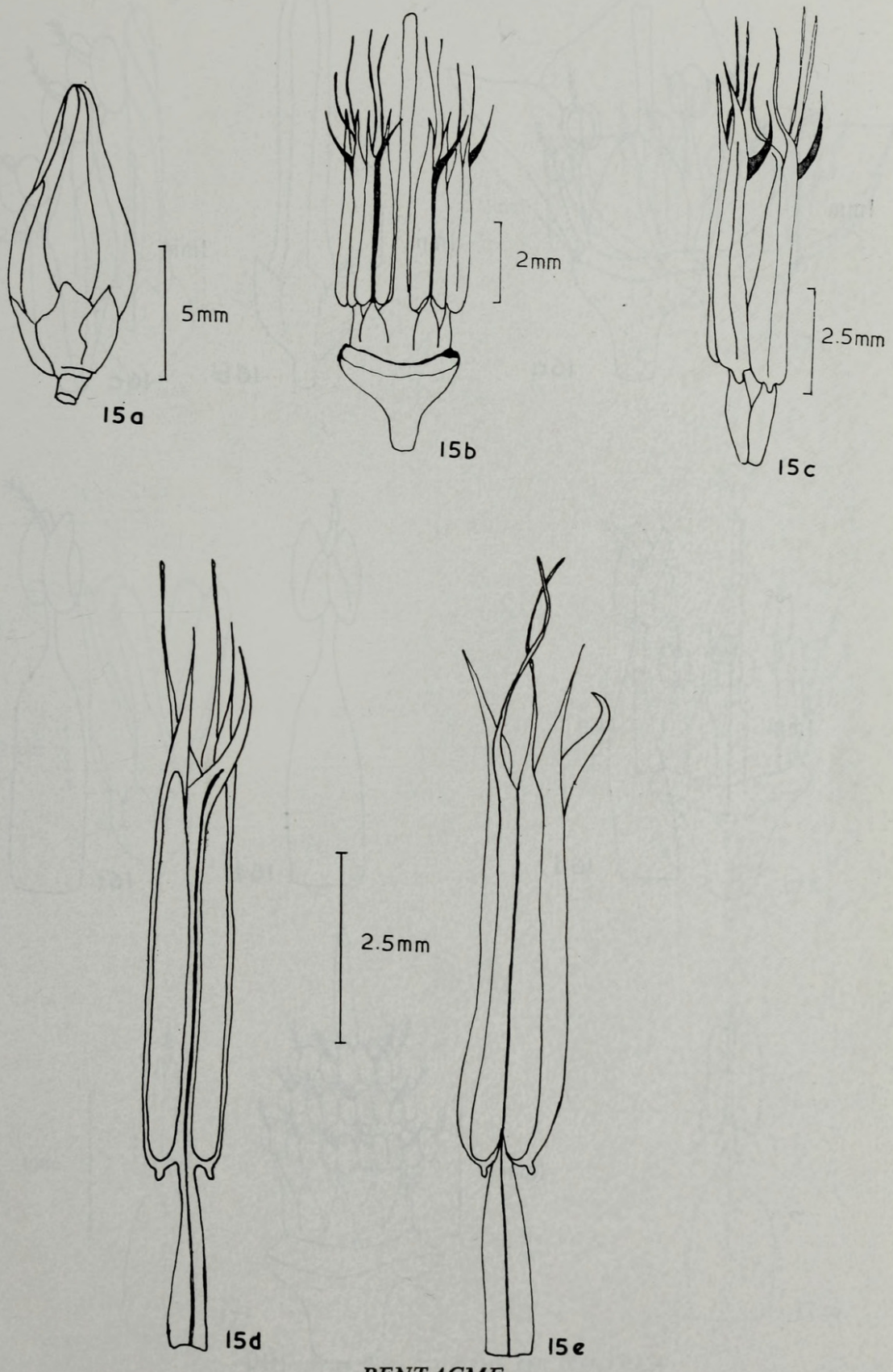
(3) *Shorea talura* Roxb. (Fig. 20, i-n; Fig. 21, c).

Stamens: 15 to 30 in number, usually 15 in 2 whorls; dimorphic, longer and shorter stamens arranged alternately, sometimes epipetalous.

Filaments: compressed and flattened; gradually or abruptly narrowed towards the anthers; the base narrow or broad.

Anthers: 4 loculed; the locules oblong; unequal, abaxial anther sacs usually larger than adaxial ones; basifixed, adnate to filament; dehiscing longitudinally.

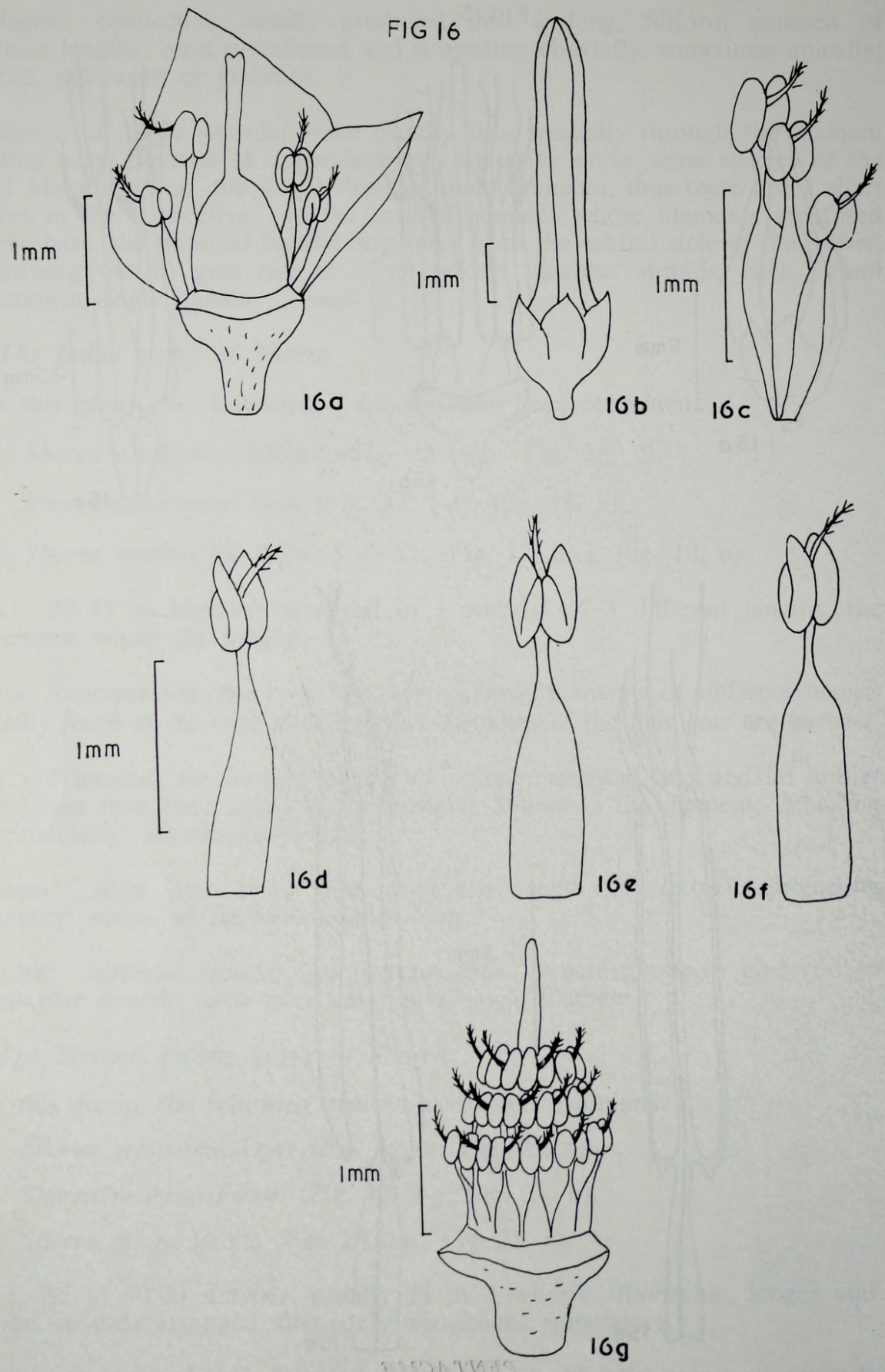
FIG 15



PENTACME

P. malayana a. flower bud. b. flower with perianth removed showing position of stamens. c. lateral view of stamens.
Stamens. x 100
d. abaxial view of stamen. e. adaxial view of stamen.

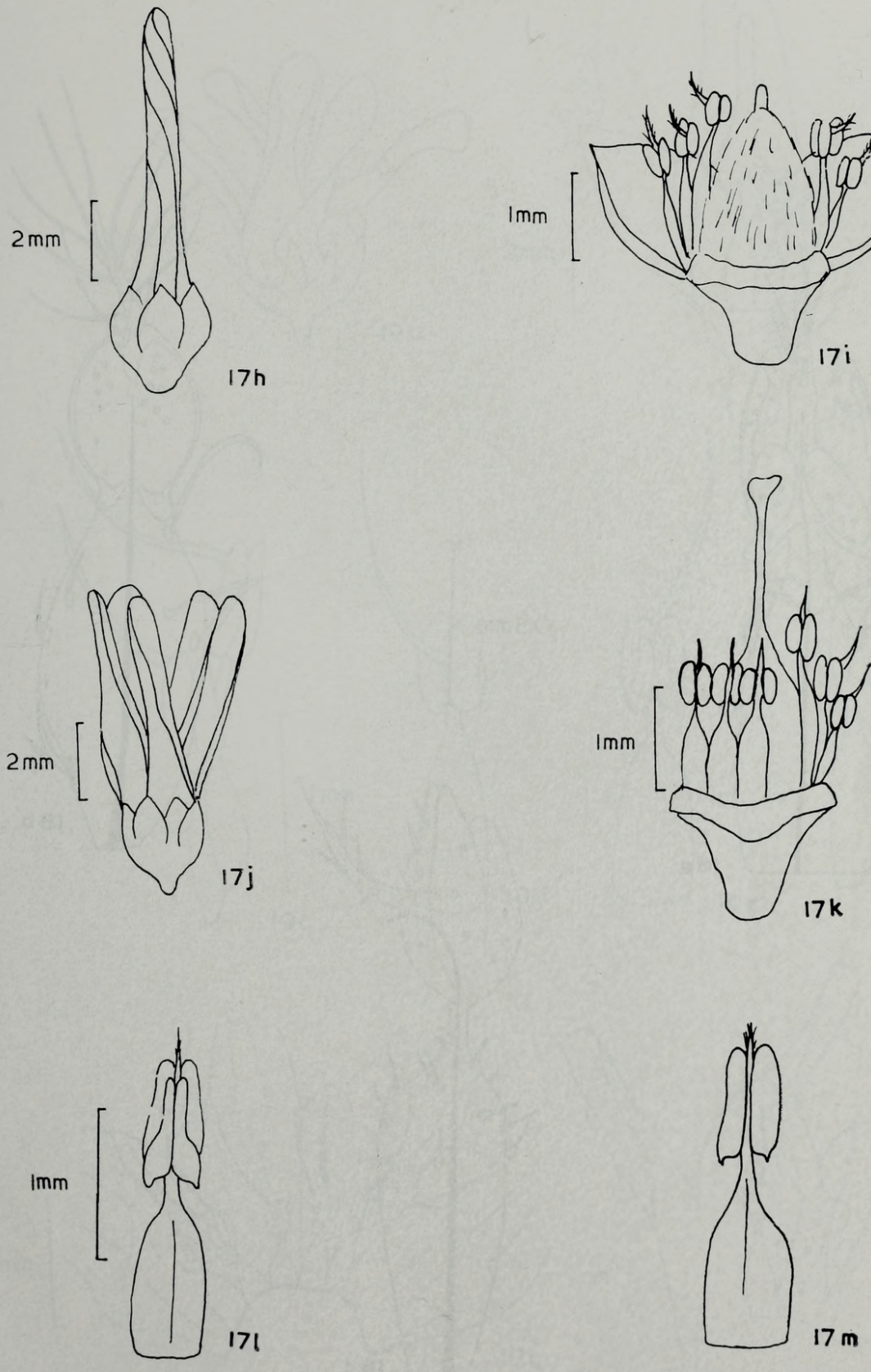
FIG 16



THE BALAU GROUP OF SHOREA

S. exelliptica a. flower with parts of perianth removed showing arrangement of stamens. b. flower bud. c. stamens of different whorls with filaments connate at base. d. lateral view of stamen. e. adaxial view of stamen. f. abaxial view of stamen g. flower with perianth removed showing complete arrangement of stamens.

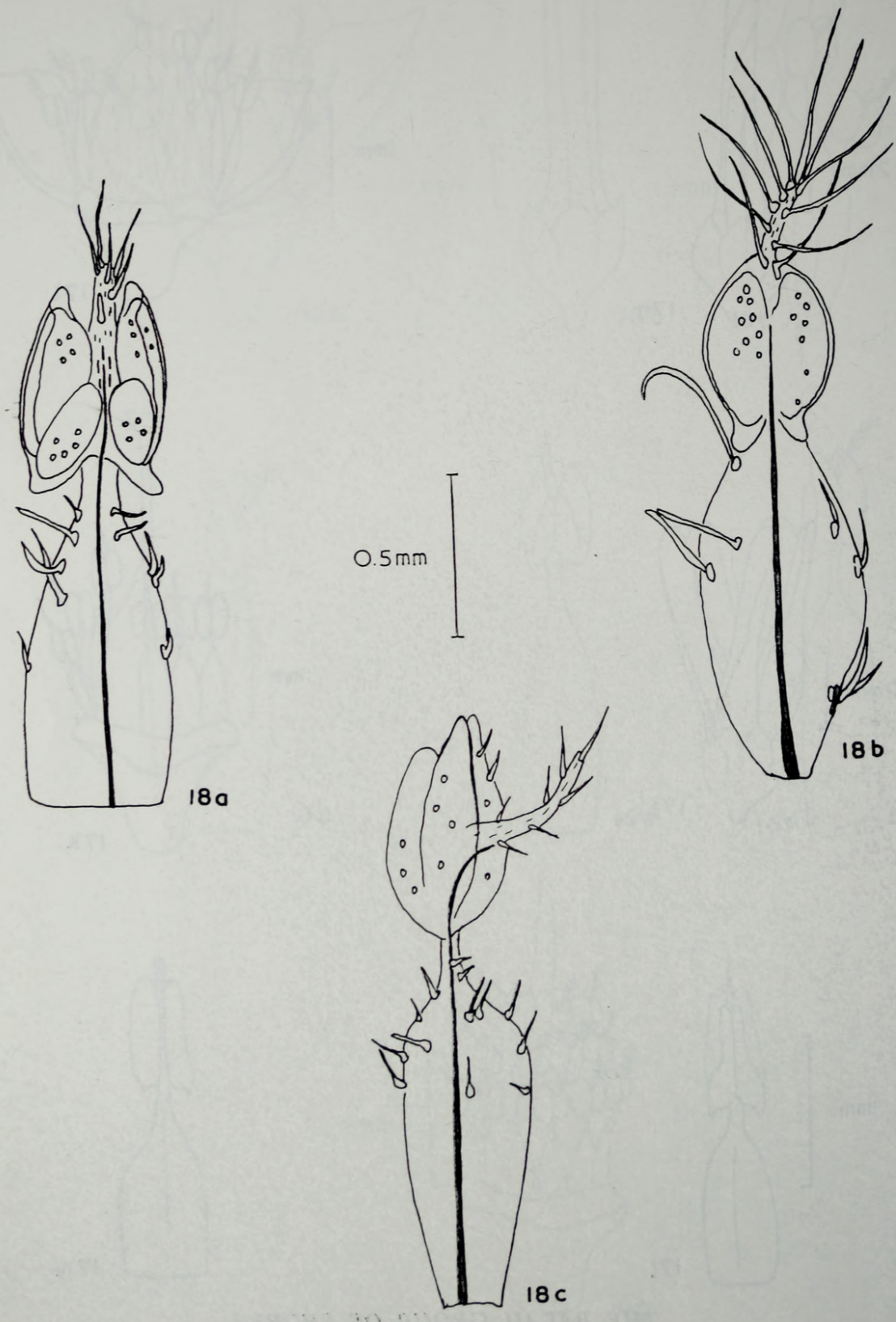
FIG 17



THE BALAU GROUP OF SHOREA

S. seminis h. flower bud. i. flower with parts of perianth removed showing position of stamens.
S. foxworthyi j. flower bud. k. flower with perianth removed showing position of stamens. l. adaxial view of stamen. m. abaxial view of stamen.

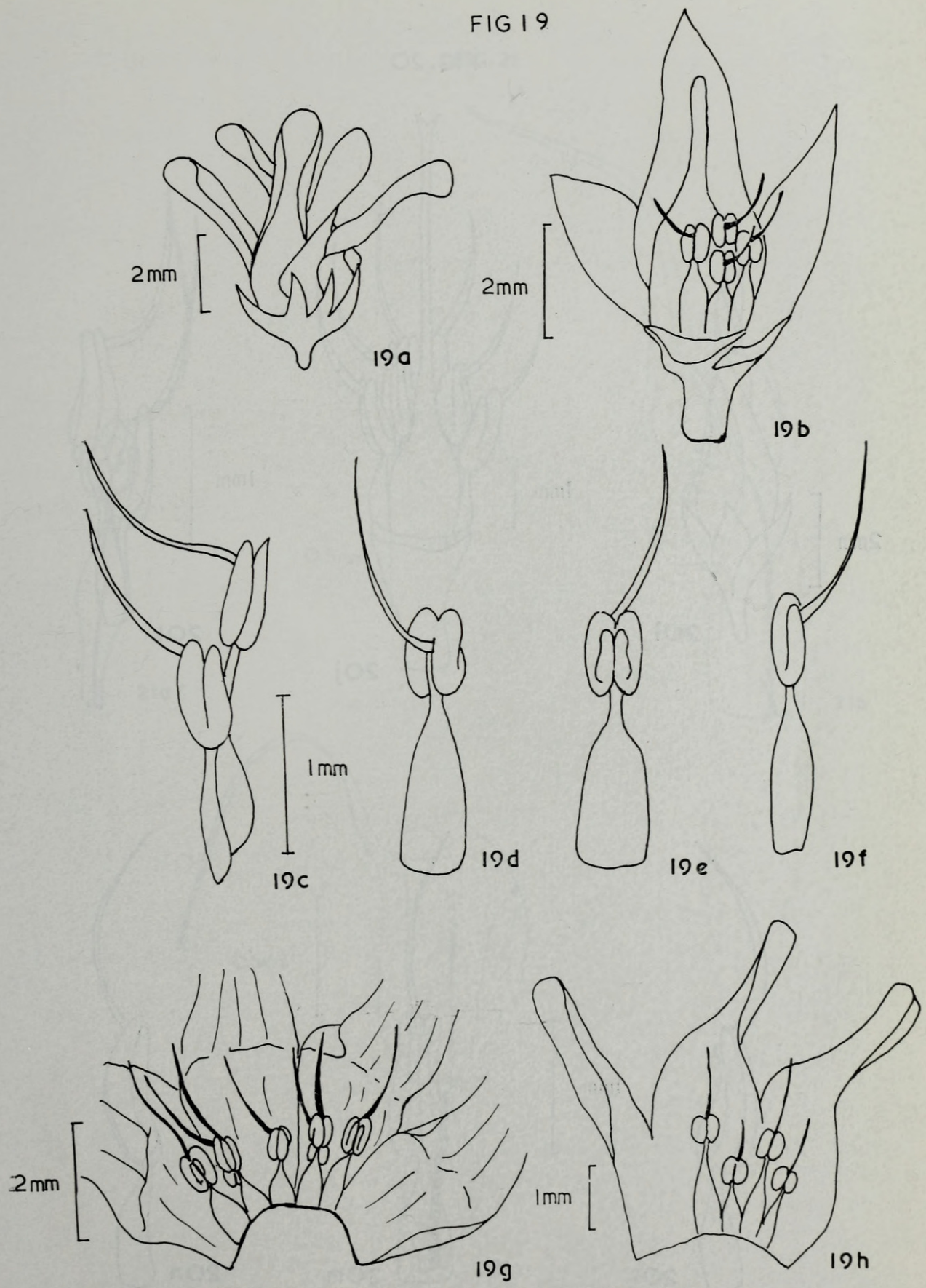
FIG 18



THE BALAU GROUP OF SHOREA

Stamens. x 100
a. *S. foxworthyi* b. *S. seminis* c. *S. exelliptica*

FIG 19

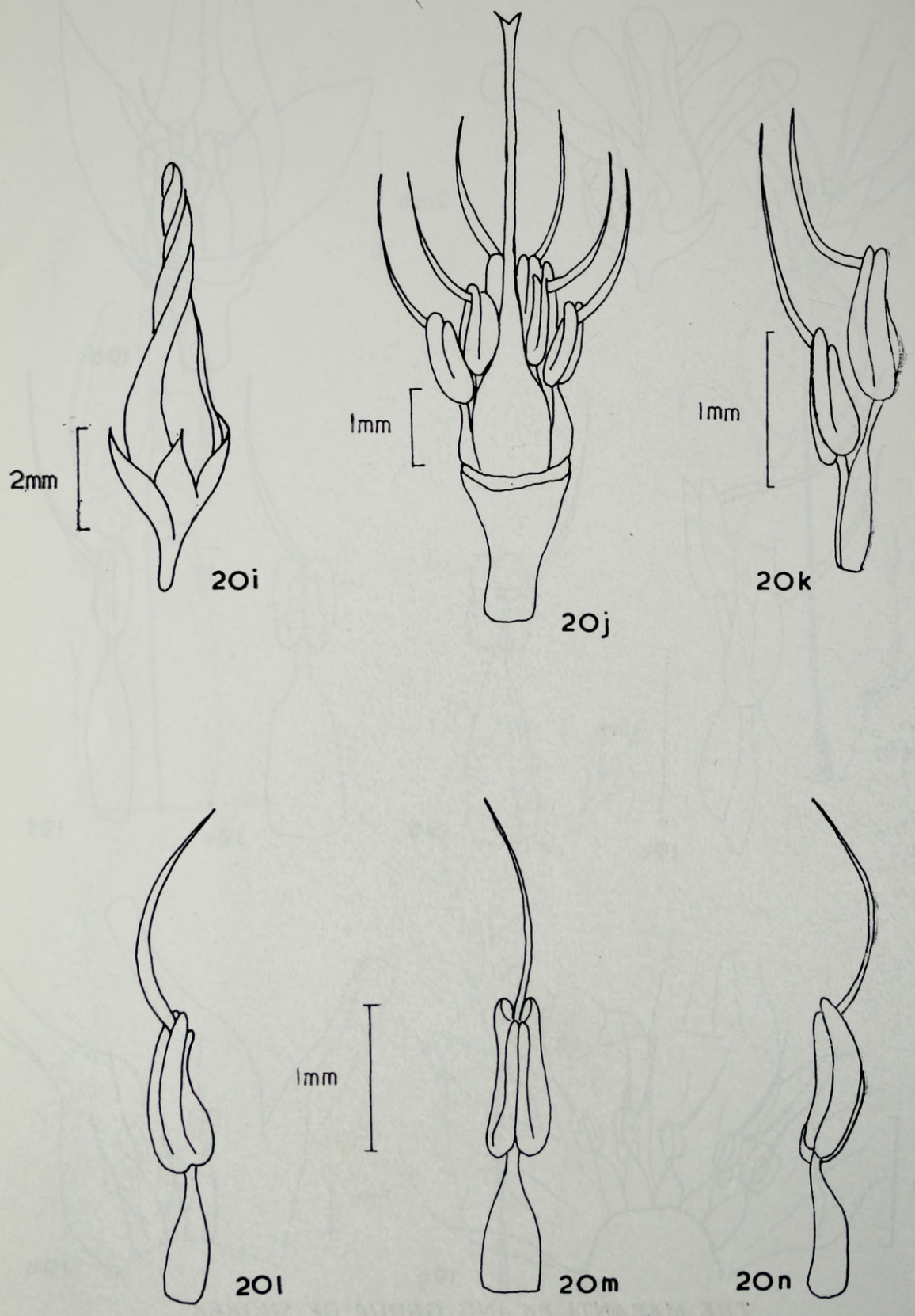


THE MERANTI PA'ANG GROUP OF SHOREA

S. resinosa a. flower bud. b. flower with parts of perianth removed showing stamens. c. lateral view of stamens of 2 different whorls. d. abaxial view of stamens. e. adaxial view of stamens. f. lateral view of stamens. g. part of corolla with epipetalous stamens.

S. gratissima h. part of corolla with epipetalous stamens.

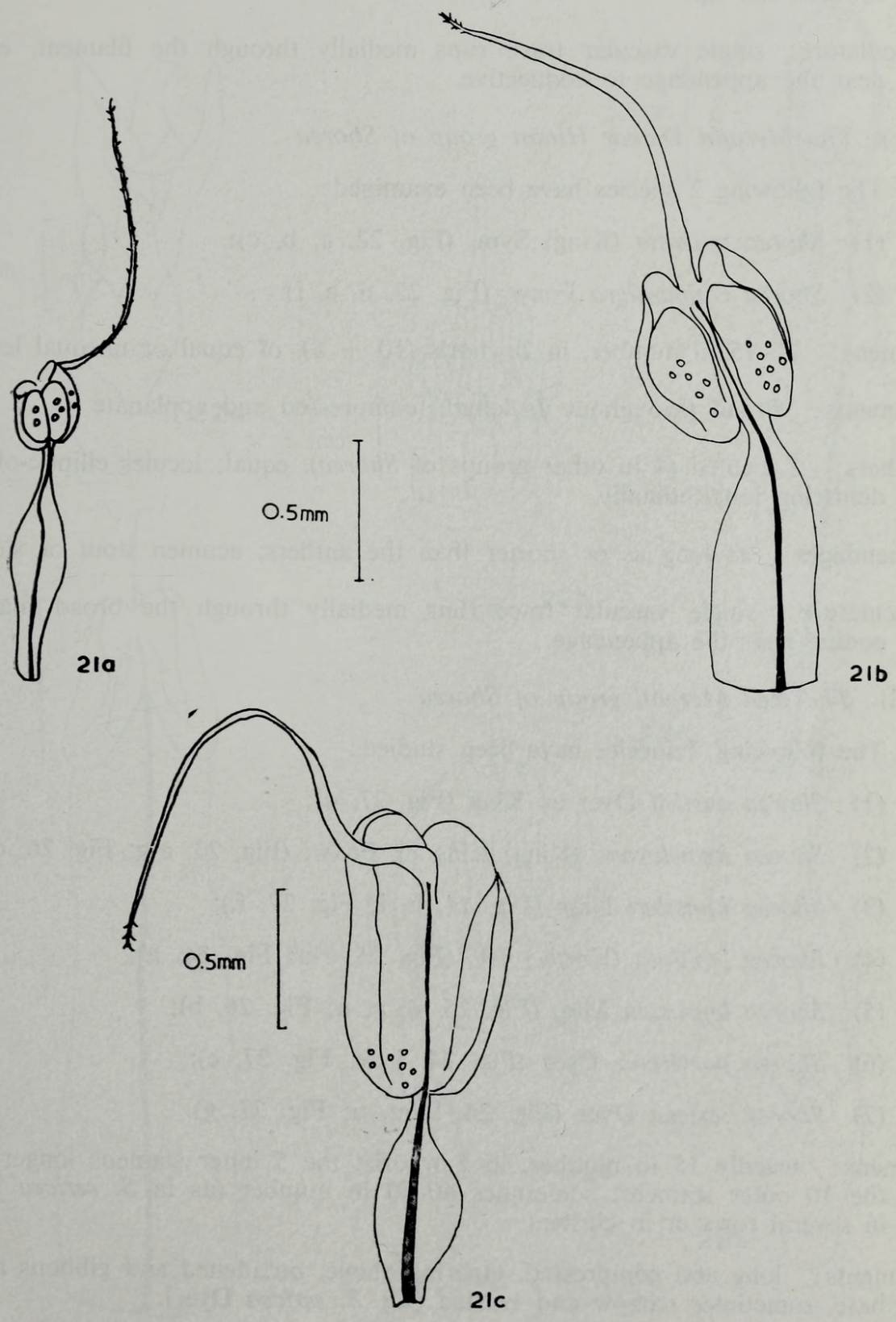
FIG 20



THE MERANTI PA'ANG GROUP OF SHOREA

S. talura i. flower bud. j. flower with perianth removed showing arrangement of stamens. k. lateral view of stamen of 2 different whorls. l. oblique abaxial view of stamen. m. adaxial view of stamen. n. lateral view of stamen.

FIG 21



THE MERANTI PA'ANG GROUP OF SHOREA

Stamens. x 100
a. *S. gratissima* b. *S. resinosa* c. *S. talura*

Appendages: awn-like, nearly 2 to 3 times longer than the anthers; projecting abaxially; usually reflexed, long, curving, filiform; sometimes sparsely setose towards the tip.

Vasculature: single vascular trace runs medially through the filament, ending near the appendage to connective.

(10c) *The Meranti Damar Hitam group of Shorea*

The following 2 species have been examined:

(1) *Shorea maxima* (King) Sym. (Fig. 22, a, b, c);

(2) *Shorea resina-nigra* Foxw. (Fig. 22, d, e, f).

Stamens: 10–15 in number, in 2 whorls (10 + 5), of equal or unequal lengths.

Filaments: broad throughout its length, compressed and applanate.

Anthers: 2 loculed (4 in other groups of *Shorea*), equal; locules elliptic-oblong, dehiscing longitudinally.

Appendages: as long as or shorter than the anthers; acumen stout or slender.

Vasculature: single vascular trace runs medially through the broad filament, ending near the appendage.

(10d) *The Red Meranti group of Shorea*

The following 7 species have been studied:

(1) *Shorea curtisii* Dyer ex King (Fig. 27, d);

(2) *Shorea hemsleyana* (King) King ex Foxw. (Fig. 23, a-g; Fig. 26, c);

(3) *Shorea kunstleri* King (Fig. 24, h, i; Fig. 27, f.);

(4) *Shorea lepidota* (Korth.) Bl. (Fig. 25, r-u; Fig. 26, a);

(5) *Shorea leprosula* Miq. (Fig. 25, o, p, q; Fig. 26, b);

(6) *Shorea parvifolia* Dyer (Fig. 24, j, k; Fig. 27, e);

(7) *Shorea sericea* Dyer (Fig. 24, l, m, n; Fig. 27, g).

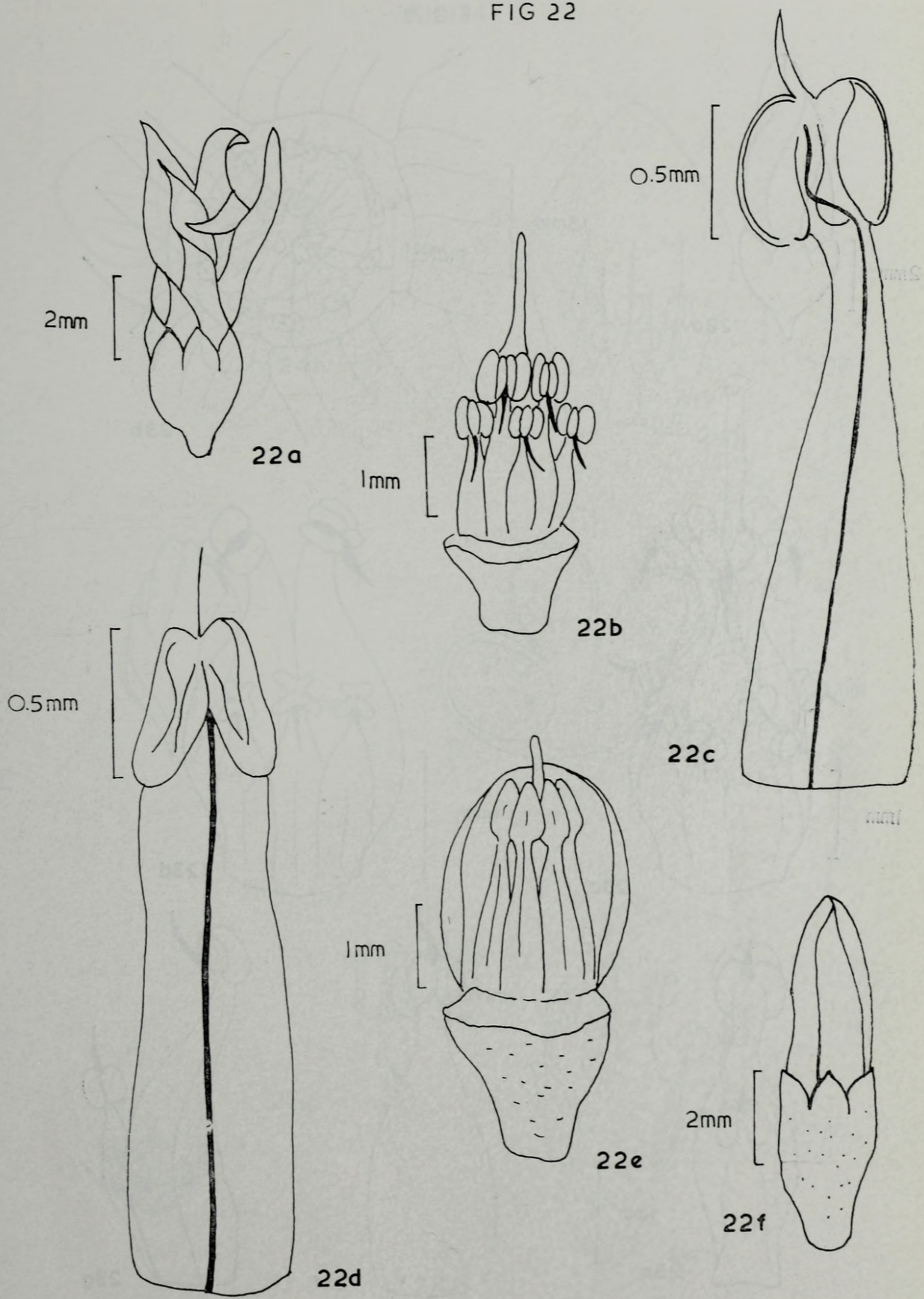
Stamens: usually 15 in number, in 2 whorls; the 5 inner stamens longer than the 10 outer stamens; sometimes 40–50 in number (as in *S. sericea* Dyer) in several rows or in clusters.

Filaments: long and compressed, tapering above, broadened and gibbous at the base, sometimes narrow and twisted (e.g. *S. sericea* Dyer).

Anthers: 4 loculed, the locules elliptic, subglobose or ovoid; unequal, abaxial anther sacs slightly larger than the adaxial pair.

Appendages: of various lengths, either shorter or longer than the anthers, apex pointed or blunt, slender, glabrous.

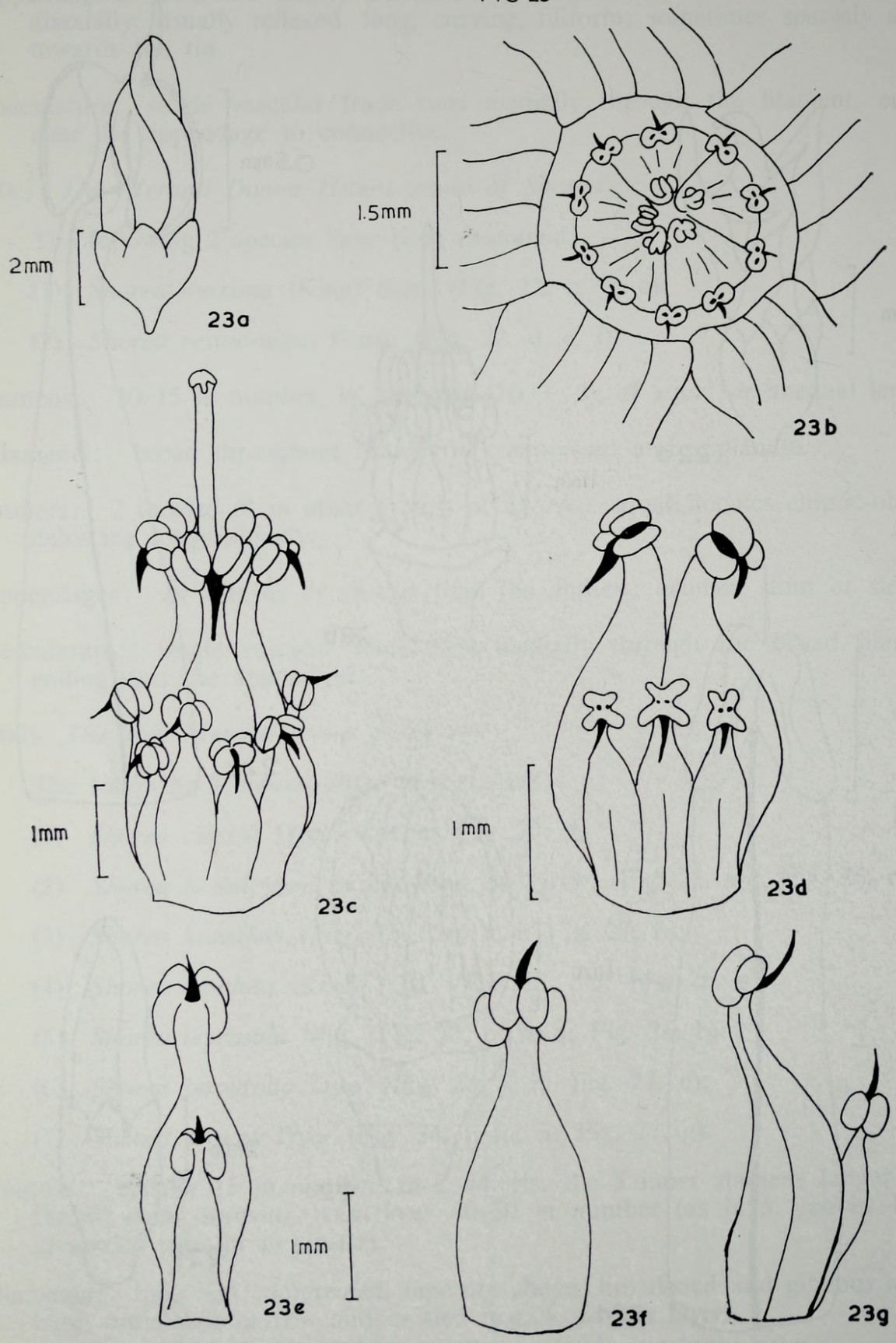
FIG 22



THE MERANTI DAMAR HITAM GROUP OF SHOREA

S. maxima a. flower bud. b. flower with perianth removed showing arrangement of stamens. c. stamen. x 100 : adaxial view.
S. resina-nigra d. stamen. x 100 : adaxial view. e. flower with parts of perianth removed showing arrangement of stamens. f. flower bud.

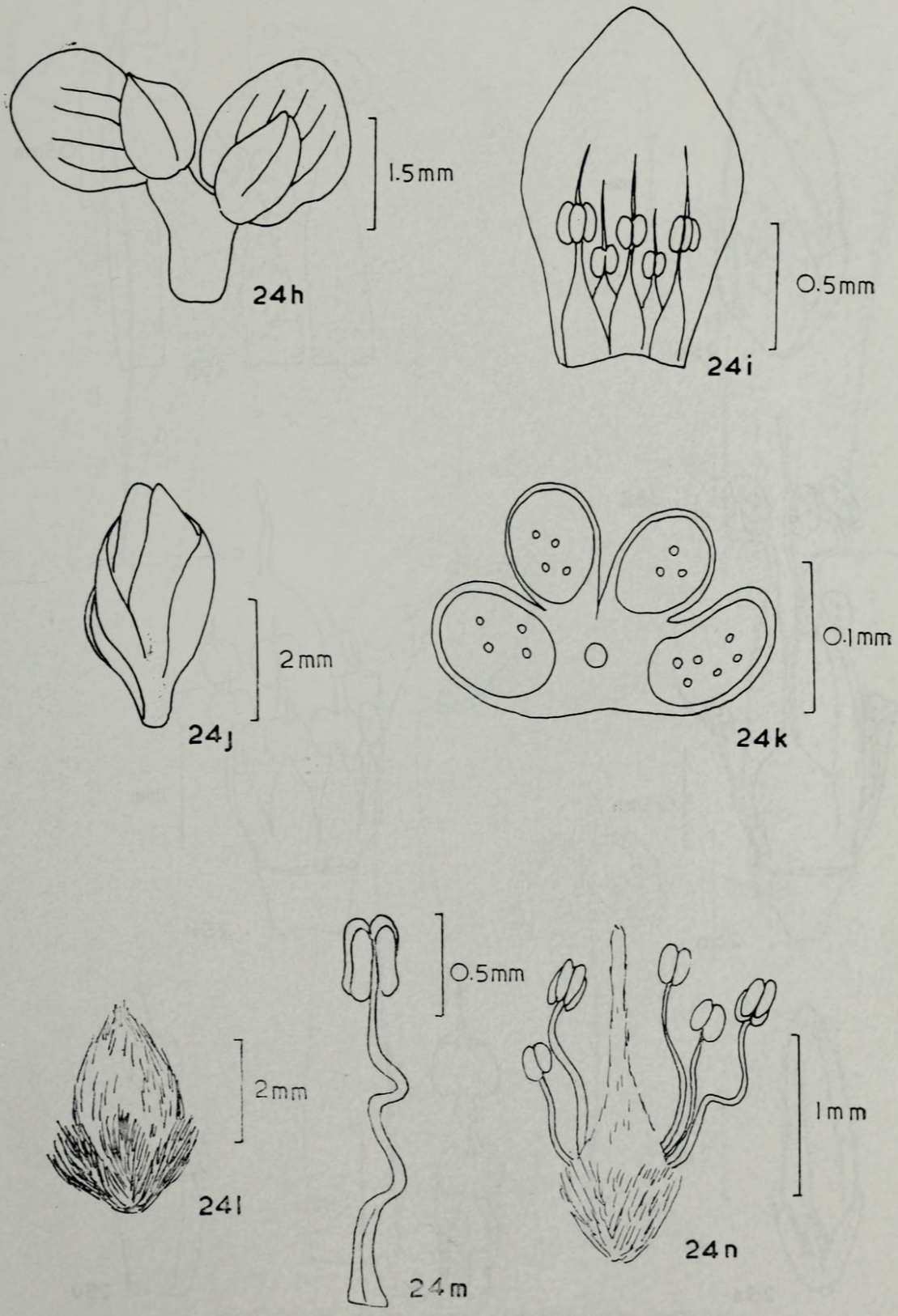
FIG 23



THE RED MERANTI GROUP OF SHOREA

S. hemsleyana a. flower bud. b. top view of flower showing arrangement of stamens. c. flower with perianth removed showing stamen whorls. d. stamens of 2 different whorls of different lengths. e. abaxial view of stamens. f. adaxial view of stamens. g. lateral view of stamens of different whorls with filaments fused at base.

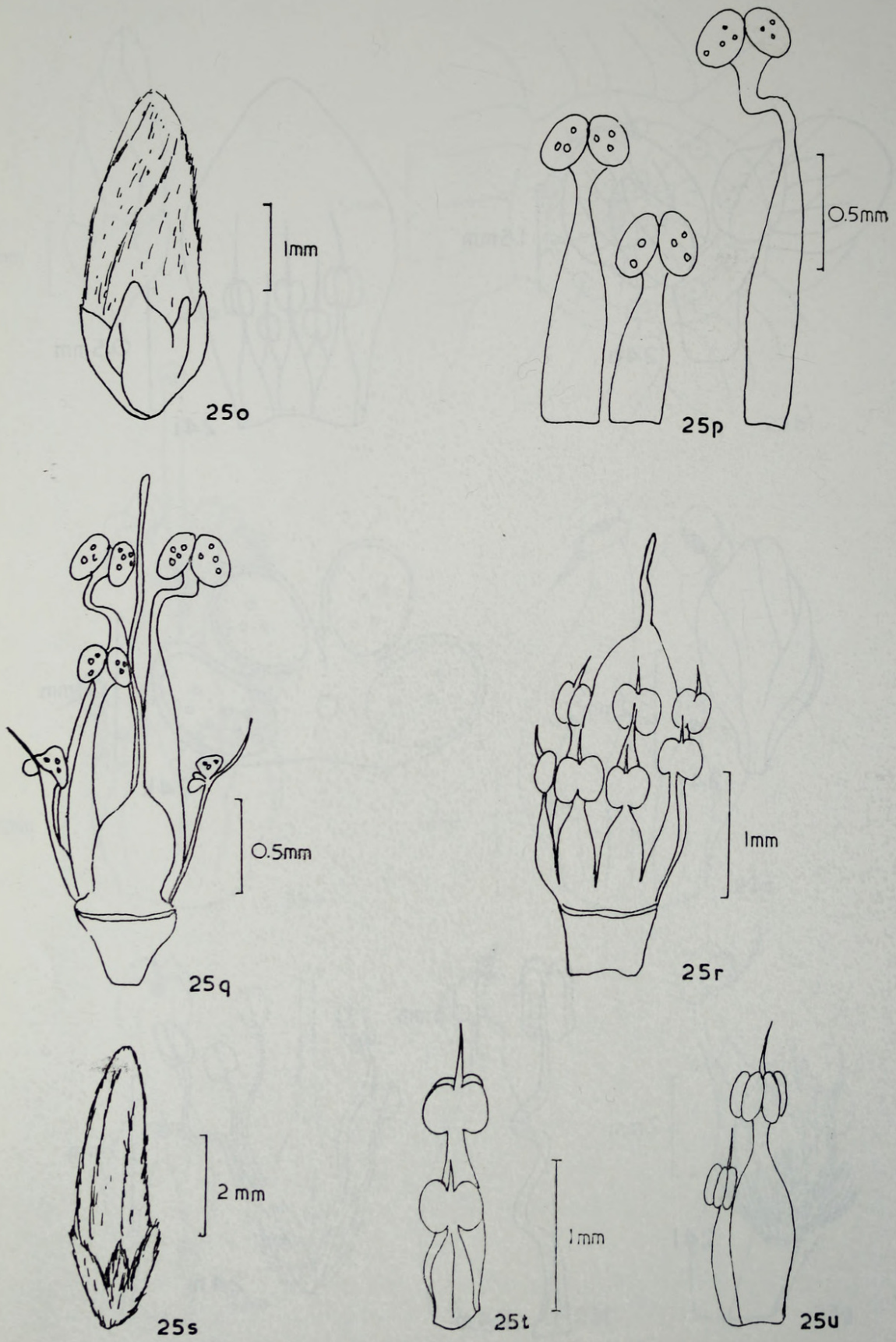
FIG 24



THE RED MERANTI GROUP OF SHOREA

S. kunstleri h. flower bud. i. single petal showing epipetalous stamens.
S. parvifolia j. flower bud. k. transverse section of anthers.
S. sericea l. flower bud. m. stamen with twisted filament. n. flower with perianth removed showing arrangement of stamens.

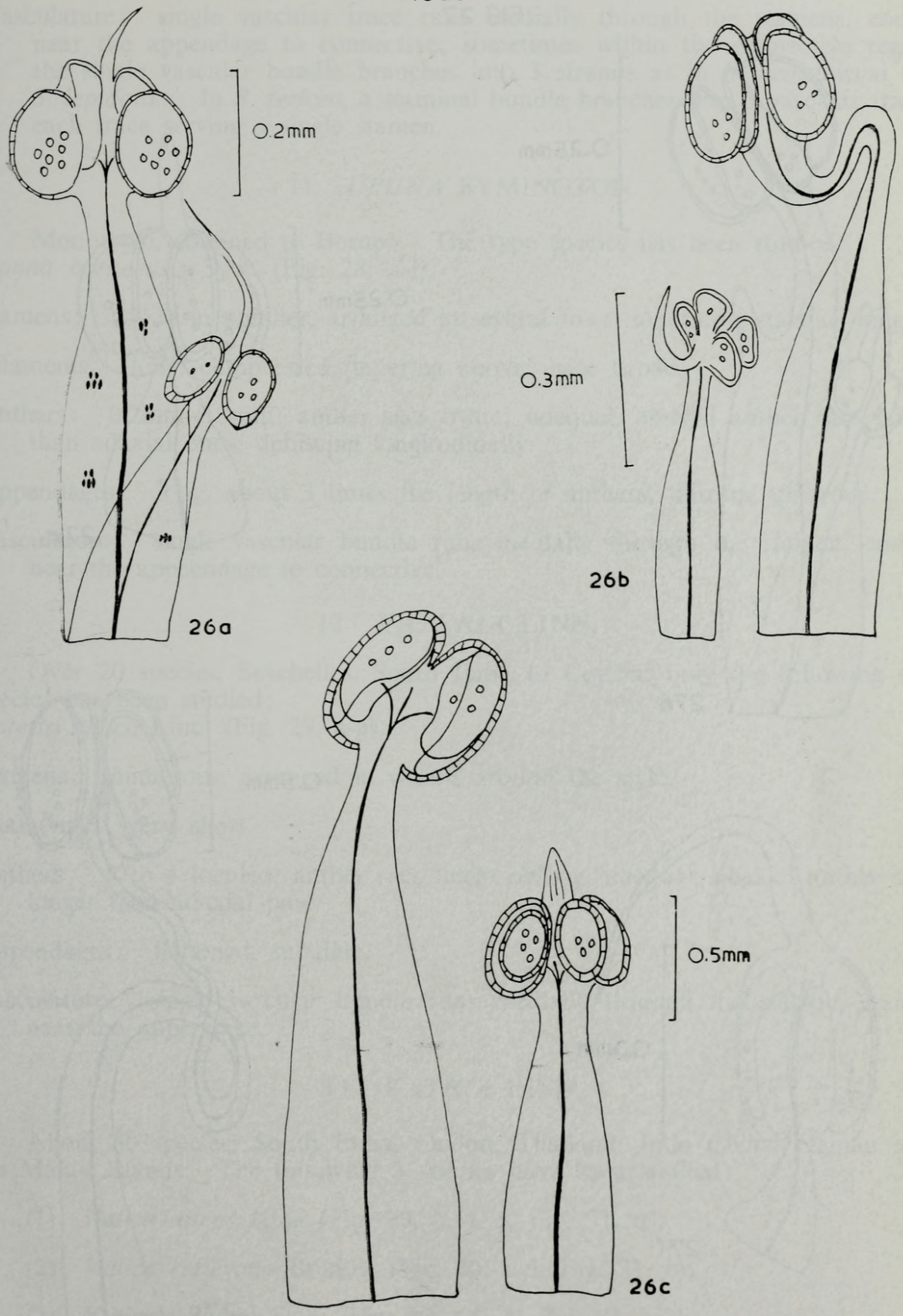
FIG 25



THE RED MERANTI GROUP OF SHOREA

S. leprosula o. flower bud. p. stamens of 3 unequal verticils. q. flower with perianth removed showing arrangement of stamens.
S. lepidota r. flower with perianth removed showing arrangement of stamens. s. flower bud. t. abaxial view of stamens. u. adaxial view of stamens.

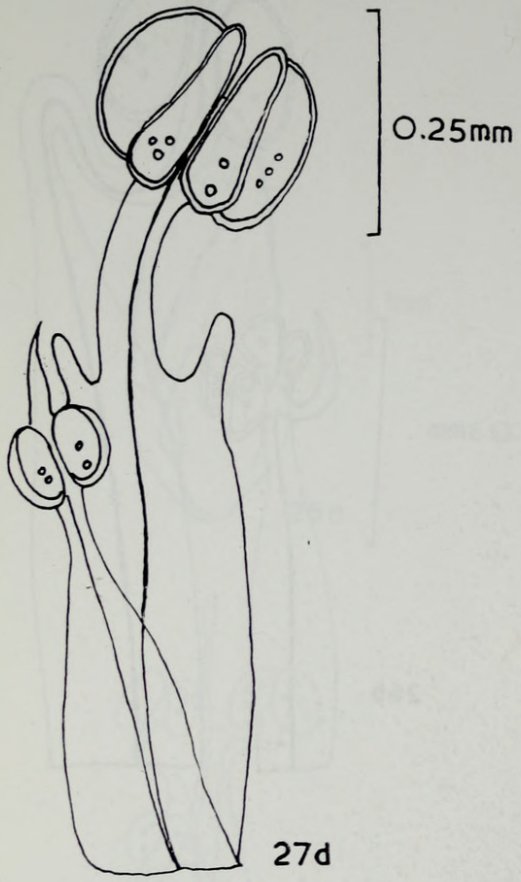
FIG 26

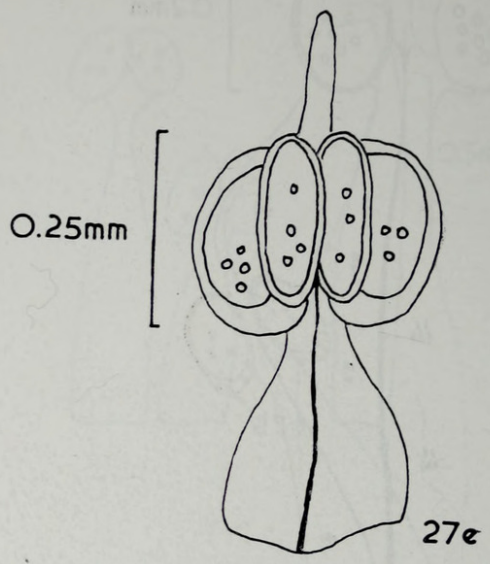


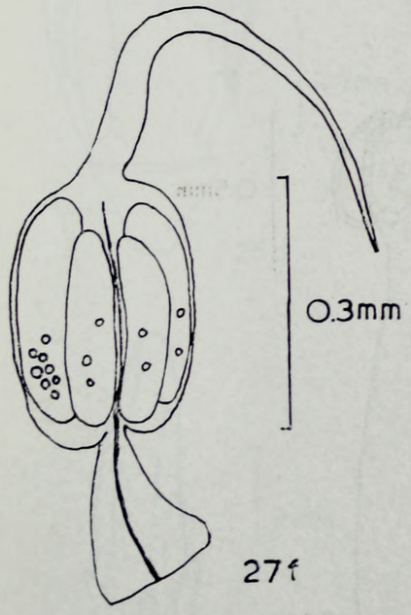
THE RED MERANTI GROUP OF SHOREA

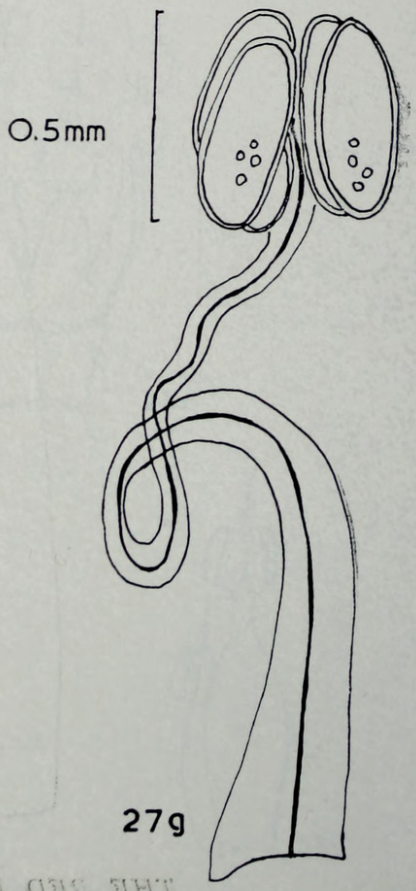
Stamens. x 100
a. *S. lepidota* : abaxial view. b. *S. leprosula* : abaxial view. c. *S. hemsleyana* : adaxial view.

FIG 27









THE RED MERANTI GROUP OF SHOREA

d. *S. curtisii* : adaxial view. e. *S. parvifolia* : adaxial view. f. *S. kunstleri* : adaxial view. g. *S sericea* : adaxial view.

Vasculature: single vascular trace runs medially through the stamens, ending near the appendage to connective; sometimes within the connective region, the single vascular bundle branches into 3 strands as in *S. hemsleyana* and *S. lepidota.* In *S. sericea,* a staminal bundle branches into 5 vascular traces, each trace serving a single stamen.

11. *UPUNA* SYMINGTON

Monotypic, confined to Borneo. The type species has been studied:
Upuna borneensis Sym. (Fig. 28, a-f).

Stamens: 25–30 in number, arranged in several rows; innermost stamens longest.

Filaments: long, compressed, tapering above; base broad.

Anthers: 0.2mm–0.3mm; anther sacs ovate; unequal, abaxial anther sacs larger than adaxial ones; dehiscing longitudinally.

Appendages: long, about 3 times the length of anthers; filiform, glabrous.

Vasculature: single vascular bundle runs medially through the stamen, ending near the appeendage to connective.

12. *VATERIA* LINN.

Over 20 species, Seychelles, South India to Ceylon; only the following one species has been studied:
Vateria indica Linn. (Fig. 29, a-g).

Stamens: numerous, arranged in whorls around the style.

Filaments: very short.

Anthers: 2 to 4 loculed; anther sacs linear-oblong, unequal, abaxial anther sacs longer than adaxial pair.

Appendages: flattened, subulate.

Vasculature: single vascular bundle runs medially through the stamen, ending near the appendage.

13. *VATICA* LINN.

About 80 species; South India, Ceylon, Thailand, Indo China, Hainan and the Malay Islands. The following 3 species have been studied:

(1) *Vatica nitens* King (Fig. 30, h, i, j; Fig. 31, d);

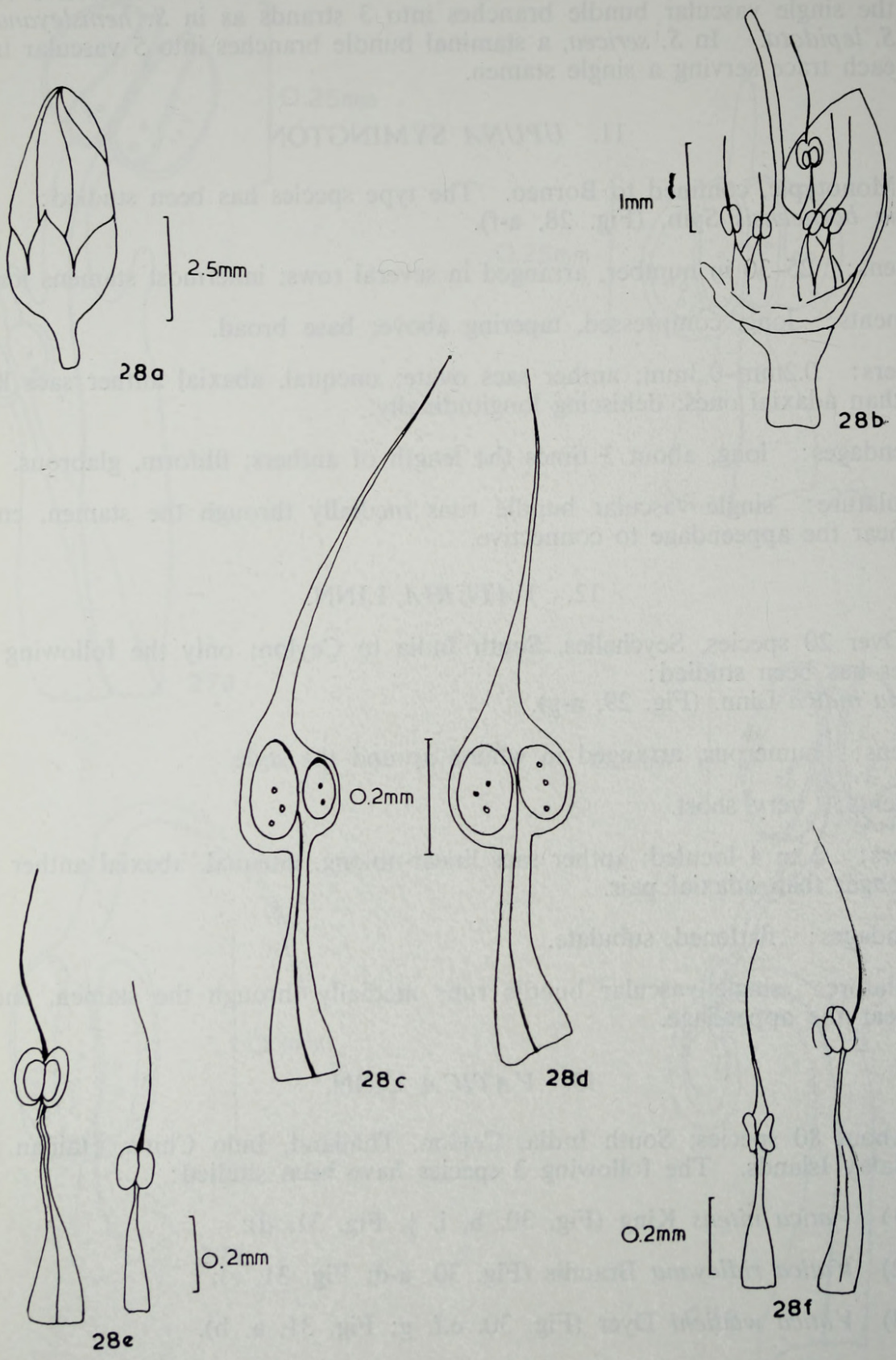
(2) *Vatica ridleyana* Brandis (Fig. 30, a-d; Fig. 31, c);

(3) *Vatica wallichi* Dyer (Fig. 30, e,f, g; Fig. 31, a, b).

Stamens: 15 in number; short, glabrous, arranged in 2 whorls; inner stamens longer than outer stamens.

Filaments: short in outer stamens, long in inner stamens, upper portion broad, constricted in the middle, broadened at the base.

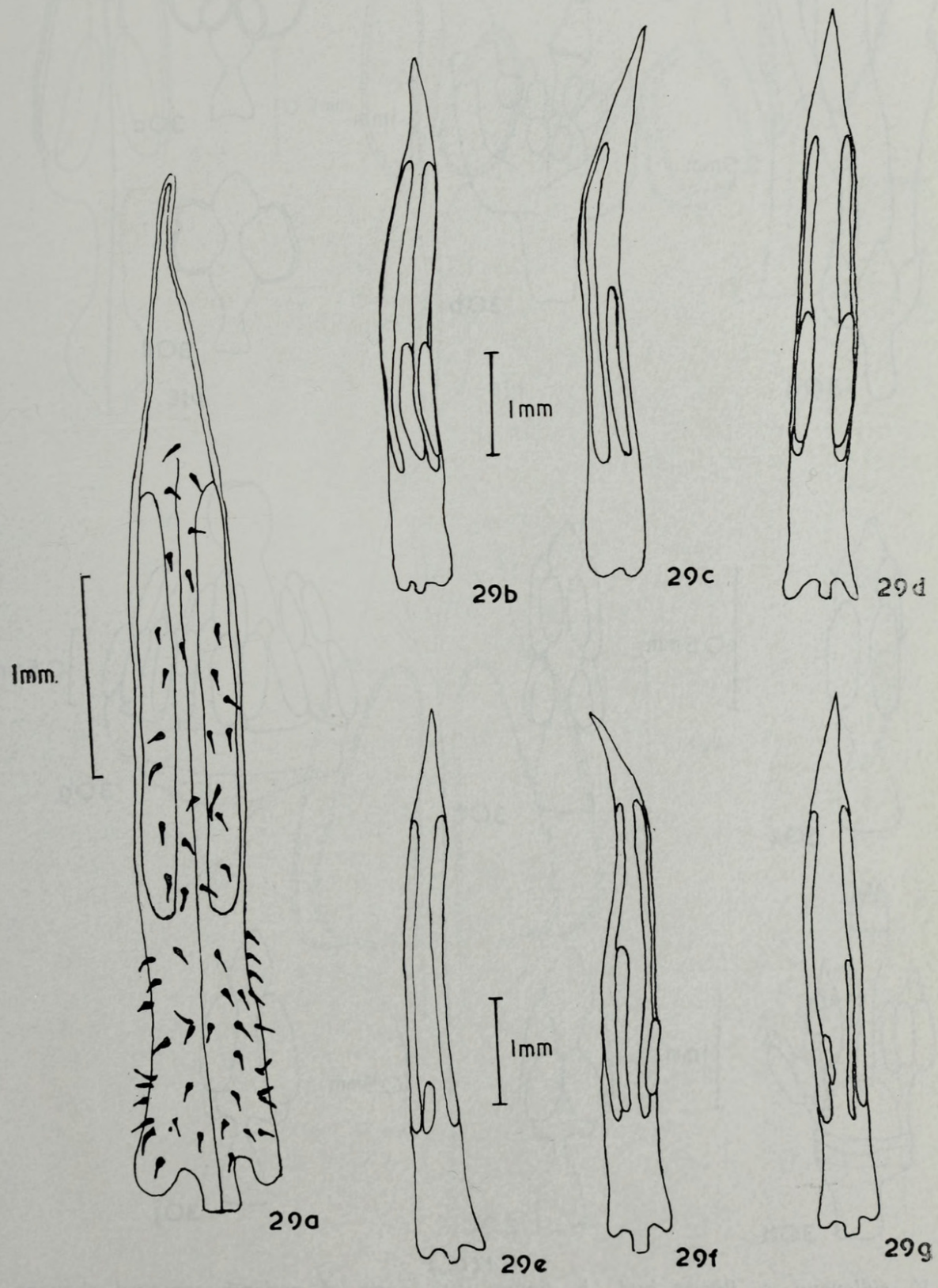
FIG 28



UPUNA

U. borneensis a. flower bud. b. flower with perianth removed showing arrangement of stamens. c. lateral view of stamens. d. abaxial view of stamens. e-f. stamens of different lengths.

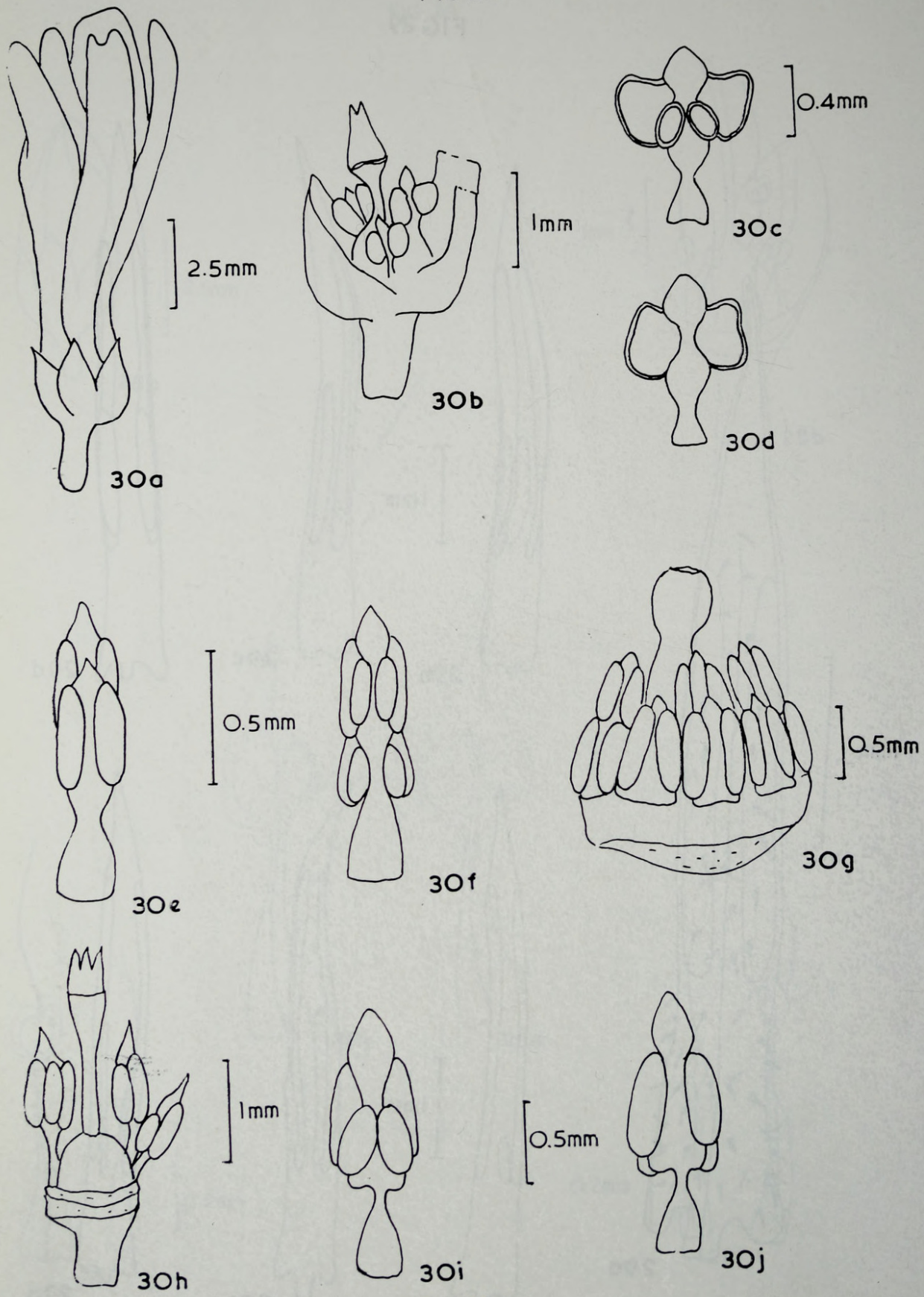
FIG 29



VATERIA

V. indica a. adaxial view of stamen with 2 locules. x 100. b. oblique lateral view of stamens with 4 locules. c. lateral view. d. adaxial view. e-g. stamens with adaxial locules of different sizes.

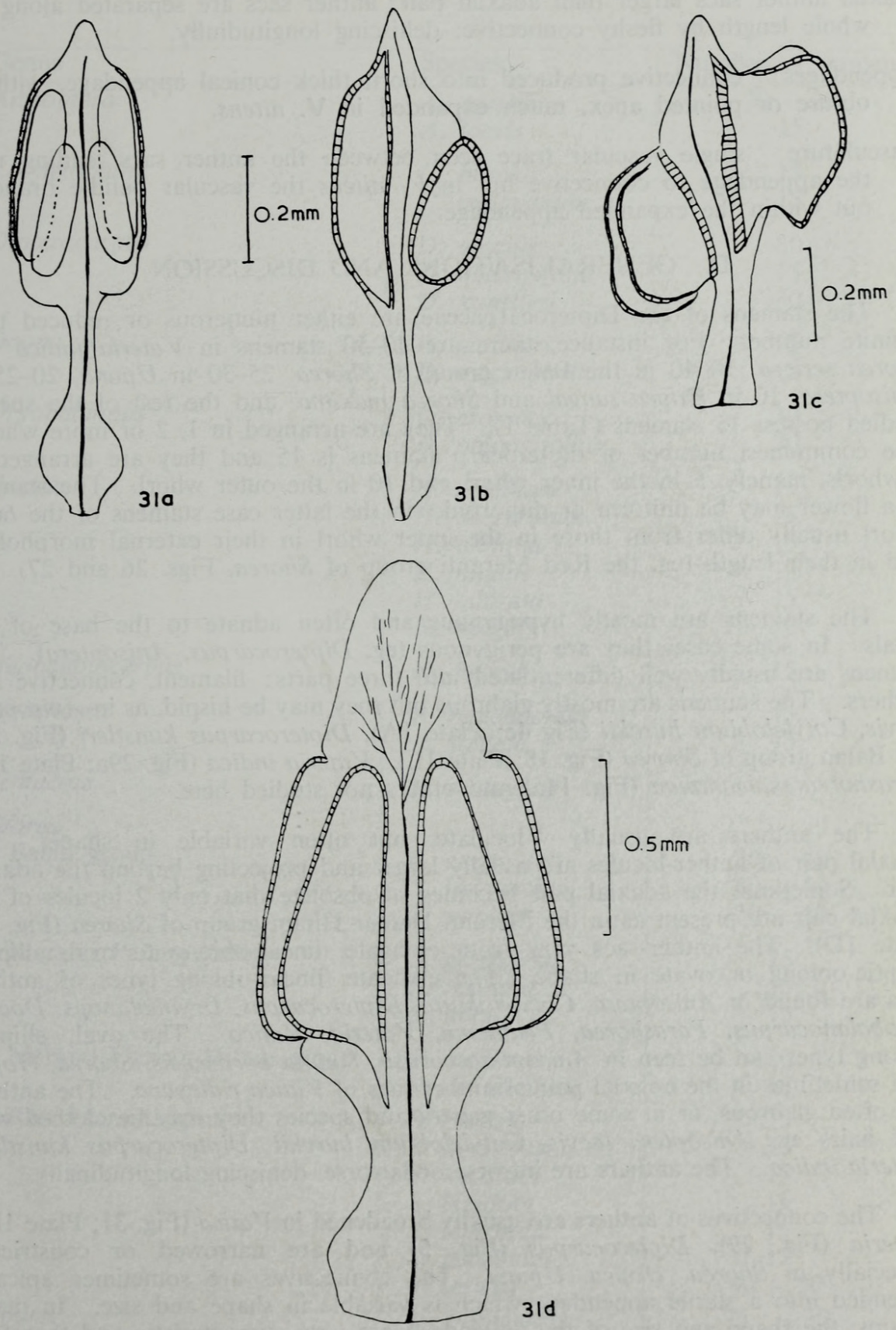
FIG 30



VATICA

V. ridleyana a. flower bud. b. flower with parts of perianth removed showing arrangement of stamens. c. adaxial view of stamen. d. abaxial view of stamen.
V. wallichi e. abaxial view of stamens. f. adaxial view of stamens. g. flower with perianth removed showing arrangement of stamens.
V. nitens h. flower with perianth removed showing arrangement of stamens. i. adaxial view of stamens. j. abaxial view of stamens.

FIG 31



VATICA

Stamens. x 100

a. & b. *V. wallichi* : adaxial and lateral view of stamen. c. *V. ridleyana* : lateral view. d. *V. nitens* : adaxial view.

Anthers: 4 loculed; the locules ovate-elliptic; short and broad, introrse; unequal, abaxial anther sacs larger than adaxial pair; anther sacs are separated along the whole length by fleshy connective; dehiscing longitudinlly.

Appendages: connective produced into short, thick conical appendage, with an obtuse or pointed apex, much expanded in **V.** *nitens.*

Vasculature: single vascular trace seen between the anther sacs, ending near the appendage to connective but in *V. nitens* the vascular bundle branches out within the expanded appendage.

D. GENERALISATIONS AND DISCUSSION

The stamens of the Dipterocarpaceae are either numerous or reduced to a definite number. For instance, there are 40–50 stamens in *Vateria indica* and *Shorea sericea*, 30–40 in the Balau group of *Shorea*, 25–30 in *Upuna*, 20–25 in *Anisoptera*, 10 in *Hopea sangal* and *Shorea maxima;* and the rest of the species studied possess 15 stamens (Table 1). They are arranged in 1, 2 or more whorls. The commonest number of dipterocarp stamens is 15 and they are arranged in 2 whorls, namely 5 in the inner whorl and 10 in the outer whorl. The stamens in a flower may be uniform or dimorphic, in the latter case stamens of the outer whorl usually differ from those in the inner whorl in their external morphology and in their length (eg. the Red Meranti group of *Shorea*, Figs. 26 and 27).

The stamens are mostly hypogynous and often adnate to the base of the petals. In some cases they are perigynous (eg. *Dipterocarpus, Anisoptera*). The stamens are usually well differentiated into three parts: filament, connective and anthers. The stamens are mostly glabrous but they may be hispid, as in *Anisoptera laevis, Cotylelobium burckii* (Fig 4e; Plate 1A), *Dipterocarpus kunstleri* (Fig. 5b), the Balau group of *Shorea* (Fig. 18; Plate 1E), *Vateria indica* (Fig. 29a; Plate 1G), *Parashorea malaanonan* (Fig. 14a) and others not studied here.

The anthers are usually 4-loculate, but often variable in shape. The abaxial pair of anther-locules are usually larger and projecting beyond the adaxial pair. Sometimes the adaxial pair becomes so obsolete that only 2 locules of the abaxial pair are present as in the Meranti Damar Hitam group of *Shorea* (Fig. 22; Plate 1D). The anther-sacs vary from elongate, linear-oblong to oval, elliptic, elliptic-oblong or ovate in shape. The elongate, linear-oblong types of anther-sacs are found in *Anisoptera, Cotylelobium, Dipterocarpus, Dryobalanops, Doona, Neobalanocarpus, Parashorea, Pentacme, Vateria, Vatica.* The oval, elliptic-oblong types can be seen in *Anisoptera curtisii, Upuna borneensis, Shorea, Hopea* and sometimes in the adaxial pair of anther-sacs of *Vatica ridleyana.* The anthers are often glabrous, or in some other genera and species they may be clothed with stiff hairs eg. *Anisoptera laevis, Cotylelobium burckii, Dipterocarpus kunstleri, Vateria indica.* The anthers are introrse or latrorse, dehiscing longitudinally.

The connectives of anthers are usually broadened in *Vatica* (Fig. 31; Plate 1H), *Vateria* (Fig. 29), *Dipterocarpus* (Fig. 5) and are narrowed or constricted especially in *Shorea, Hopea, Upuna.* The connectives are sometimes apically extended into a sterile appendage which is variable in shape and size. In many groups, the shape and size of the appendage are very characteristic and therefore of diagnostic value. In *Anisoptera laevis* (Fig. 2a), *Neobalanocarpus heimii* (Fig. 3d, e), *Dryobalanops* (Fig. 9a), *Cotylelobium* (Plate 1A), *Parashorea malaanonan* (Fig. 14a), the appendages are in the form of a short, erect, apiculate mucro. The length of appendages varies from 1/20 to 1/5 the length of the

TABLE 1

Genus	Species	Number of stamens
Anisoptera	*A. curtisii*	20 – 25
	A. laevis	15
Cotylelobium	*C. burckii*	15
	C. malayanum	15
Dipterocarpus	*D. gracilis*	30
	D. oblongifolia	15
	D. kunstleri	30
Doona	*D. gardneri*	15
	D. macrophylla	15
Dryobalanops	*D. aromatica*	30
	D. oblongifolius	30
Hopea	*H. apiculata*	15
	H. beccariana	15
	H. minima	15
	H. nutans	15
	H. odorata	15
	H. sangal	10
Neobalanocarpus	*N. heimii*	15
Parashorea	*P. malaanonan*	15
	P. stellata	15
Pentacme	*P. malayana*	15
Shorea		
Balau group	*S. exelliptica*	30 – 40
	S. foxworthyi	30 – 40
	S. seminis	30 – 40
Meranti Pa'ang group	*S. gratissima*	25
	S. resinosa	15
	S. talura	15
Meranti Damar Hitam group	*S. maxima*	10
	S. resina-nigra	15
Red Meranti group	*S. curtisii*	15
	S. hemsleyana	15
	S. kunstleri	15
	S. lepidota	15
	S. leprosula	15
	S. parvifolia	15
	S. sericea	40 – 50
Upuna	*U. borneensis*	25 – 30
Vateria	*V. indica*	40 – 50
Vatica	*V. nitens*	15
	V. ridleyana	15
	V. wallichi	15

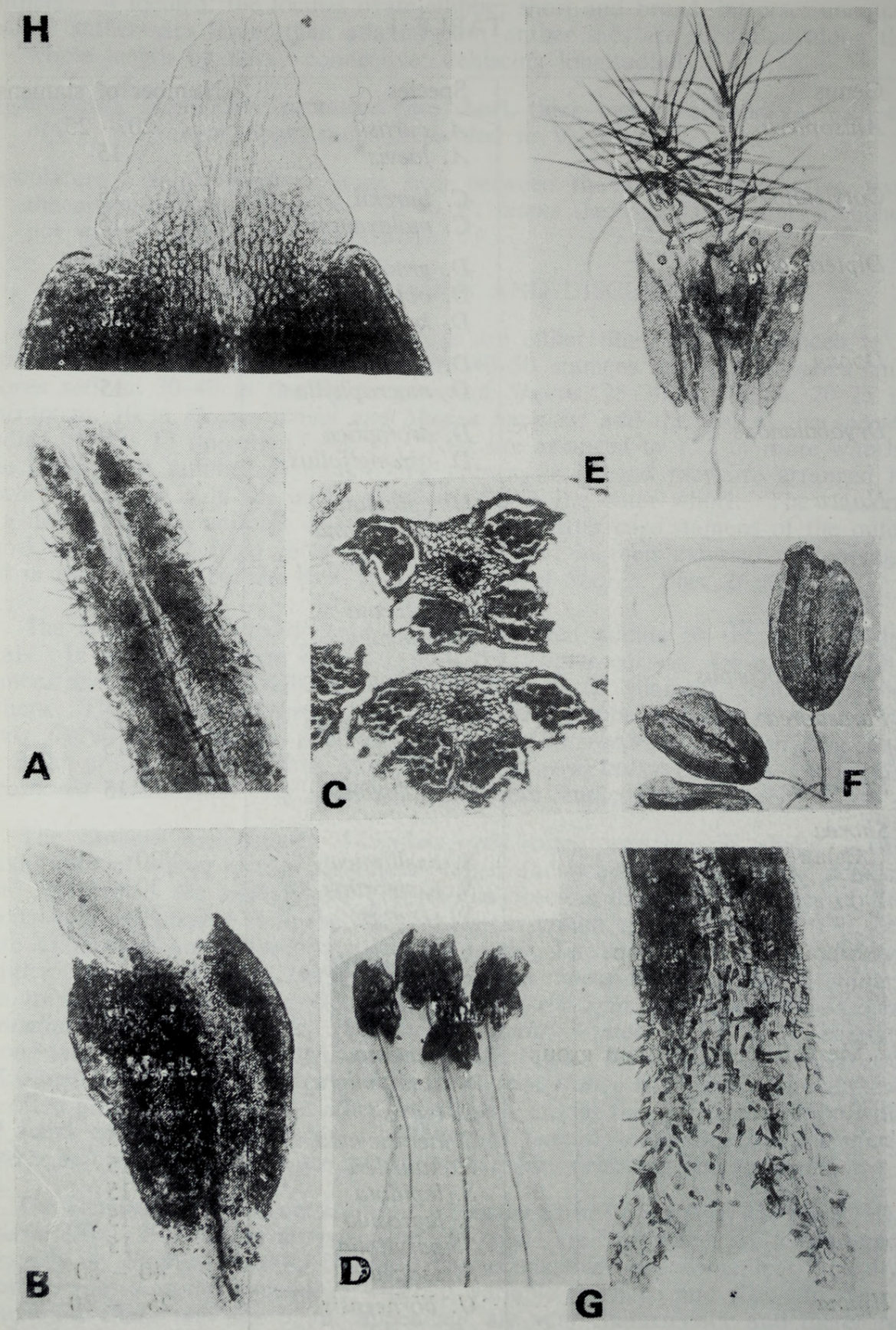


Plate I *STAMENS OF THE DIPTEROCARPACEAE*

A. *Cotylelobium burckii,* showing hispid anther (in part); B. *Doona gardneri,* showing a stamen with clavate appendage; C. *Neobalanocarpus heimii,* transverse section of flower bud showing anthers; D. *Shorea resina-nigra,* showing stamens with an inconspicuous, needle-like appendage; E. *Shorea siminis,* showing stamens with a densely barbate appendage; F. *Shorea talura,* showing stamens with a linear appendage; G. *Vateria indica,* showing part of hispid anther with auriculate base; H. *Vatica nitens,* showing tip of anther with stout, conical appendage.

stamens. Short, slender, subulate forms (length varying from 1/20 to 1/4 the length of the stamen) are seen in most *Shorea* except the Meranti Pa'ang group (Fig. 21; Plate 1F) in which the long appendages are filamentous, whip-like with a setaceous tip (length varies from 1/2 to 3/4 the length of the stamen). Long, filamentous, whip-like setose or glabrous appendages are found in *Hopea* (setose) (Fig. 12), *Anisoptera curtisii* (glabrous) (Fig. 2b, c), Meranti Pa'ang group of *Shorea* (setose) (Fig. 21; Plate 1F) and it is especially long in *Upuna* (glabrous (Fig. 28) which may be as long as or even longer than the whole length of the stamen. Appendages of the Balau group of *Shorea* (Fig. 18; Plate 1E) are densely pubescent.

In *Dipterocarpus* (Fig. 5) and *Vateria indica* (Fig. 29), the sterile tissues of the anthers extends out apically as an erect, flattened, long and pointed appendage. The appendage is very long in *Dipterocarpus* (as long as the stamen) and shorter in *Vateria indica* (1/6 to 2/5 the length of the stamen). Clavate, fleshy appendages are found in *Doona* (Fig. 7; Plate 1B), *Parashorea* (Fig. 14a), *Pentacme* (Fig. 15) and *Vatica* (Fig. 31d; Plate 1H), they vary from 1/8 to 1/3 the length of the stamens. The clavate appendage with an obtuse or truncate apex is found in *Doona*, or with cuspidate apex as in *Parashorea malaanonan*. In *Pentacme malayana*, the appendage is falciform. The stamens of *Vatica* have a conical stout, tapering appendage, continuous with the sterile tissues of the anthers. The apical appendages are usually erect or sometimes bent abaxially egs. *Shorea exelliptica* (Fig. 18c), Meranti Pa'ang group of *Shorea* (Fig. 21; Plate 1F) and *Pentacme malayana* (Fig. 15); or it may be reflexed at anthesis eg. *Shorea hemsleyana* (Fig. 23.) Inappendiculate stamens are seen in *Shorea sericea* (Fig. 27g).

The filaments are mostly free or sometimes connate at the base eg. *Dryobalanops* (Fig. 8f, i). They are sometimes adnate to the petals eg. *Hopea* (Fig. 11q), Meranti Pa'ang group of *Shorea* (Fig. 19g, h) or united into bundles eg. *Shorea sericea*. The filaments in general are uniform in shape throughout the genera, compressed and applanate, narrowed at the top, and tapering gradually or abruptly towards the base. In *Shorea sericea* the filament is elongated, slender, twisted and thread-like.

Each stamen receives a single vascular bundle usually ending at the base of the appendage to the connective, sometimes extending into the appendages as in *Dipterocarpus* (Fig. 5), *Doona macrophylla* (Fig. 7d), *Parashorea malaanonan* (Fig. 14a), and branching out within the fleshy appendages of *Doona gardneri* (Fig. 7a, b, c) and *Vatica nitens* (Fig. 31d; Plate 1H). In *Hopea nutans* and *Hopea sangal*, the traces of epipetalous staminal bundles are fused with the vascular bundle in the corolla tube at the base. In the Red Meranti group of *Shorea*, egs. *S. hemsleyana* and *S. lepidota* the single vascular trace branches, thus there are 3 short traces in the connective. In the case of stamens whose filaments are fused at the base, a staminal bundle originates from the central stele of the flower, branching out to give rise to 2, 3 or more vascular strands, each strand entering a single stamen. Examples of the staminal bundle giving rise to 3 branches have been observed in *Dryobalanops oblongifolia*, in the Balau group of *Shorea* (Plate 1E) (egs. *S. exelliptica*, *S. foxworthyi*, and *S. seminis*) and in *Hopea nutans*. In *Shorea sericea*, the staminal bundle seems to branch out to 5 vascular traces, each supplying a single stamen.

Following the classical theory, the primitive stamen is a broad three-veined microsporophyll possessing two pairs of linear, non-marginal sporangia, deeply embedded in its surface (Canright 1952, Eames 1961). Such relatively unmodified stamens are found in the woody ranalean families, eg. Degeneriaceae, Himantandraceae (Bailey and Smith 1942; Bailey et al 1943), *Austrobaileya* and certain genera of the Magnoliaceae. The connective thus constitutes a major part of the anther in primitive families and the sporangia are relatively minor structures. In advanced families, the connective is a slender, median axis, sometimes hardly more than a thread or point of attachment for the anther lobes. The distal appendage of the connective, which is a typical feature of the anther in more or less primitive families like Magnoliaceae, Nymphaeaceae, is largely lost in advanced families, though it may persist there and even be elaborated for pollination, rather than the persistence of a primitive character. Filaments vary in shape from broad and dilated to terete and threadlike and from short to long. The shorter and broader types of filaments are in general more primitive. In vasculature, there is reduction in number of veins from three traces to one trace in the advanced stamens. The sporangium is primitively slender and elongate in less advanced families and in more advanced stamens, it has progressively shortened becoming more globose. The primitive stamen was laminar, with two pairs of sporangia borne on either the adaxial or abaxial surface. From this simple stamen, the slender stamen with marginal pairs of sporangia is developed. The dorsiventral form is lost and the specialised anther of the higher families is more or less four-angled and the filament terete. The number of sporangia in the anther is usually four, when there is less than four, this represents a reduction from the basic four. The two-sporangiate types are considered more advanced than the four-sporangiate types. (Eames, 1961).

The following discussion on the stamens of the Dipterocarpaceae is concentrated on the following points:

A. The protrusion of the connective; B. Vasculature and C. Suggested general evolutionary trends.

A. *The protrusion of the connective.*

The prominent connectives of the Dipterocarpaceae was mentioned by Parkin (1951). It was suggested that the continuation of the connective beyond the anther as a sterile tip in the Magnoliaceae may have ancestral significance. He further suggested a comparison of the vestige with the sterile, pointed extremity of the Bennettitean microsporophyll. Among the polypetalous families with produced connectives are the Magnoliaceae, Annonaceae, and Nymphaeaceae. However, according to Canright (1952), developmental studies of flowers in other families have shown that the anther normally develops very early in floral ontogeny, but that protrusion of the connective does not take place until just before anthesis. Thus it seems to suggest that extreme protrusion of the anther apex is a specialised rather than a primitive character.

Parkin also suggested that the prolongation of the connective may have biological value as it is quite possible that the protrusion, may have been extended and elaborated in one way or another to assist in pollination. Howard (1948) observed that in a subsection of the native West Indian species of *Magnolia* (*Magnoliaceae*), the connective is produced to a setaceous tip which is usually the length of the thecae. The setaceous tip plays a very important role in the distribution of pollen in this group of species. In the flower bud, the connective

tips are forced against the gynoecium and soon becomes firmly embedded in the fleshy gynoecial tissue. Hence, stamens are held by the connective in the reversed position, an advantageous position for pollen distribution. Parkin (1951) suggested that the dipterocarps should receive some attention in this respect.

Connective protrusions of various lengths were observed in all the species studied. Only in the Red Meranti group of *Shorea*, eg. *S. sericea*, inappendiculate stamens are present. The fleshy, clavate appendages seen in *Doona*, (Fig. 7; Plate 1B), *Parashorea malaanonan* (Fig. 14a), *Pentacme malayana* (Fig. 15), *Vatica nitens* (Fig. 31d; Plate 1H) seem to indicate that they are more primitive according to Hallier's (1903; cited in Parkin, 1951) definition of the primitive stamen. Extremely long, filiform, subulate appendages which may be setose or glabrous, are present in *Dipterocarpus* (Fig. 5), *Hopea* (Fig. 12), Meranti Pa'ang group of *Shorea* (Fig. 21; Plate 1F), *Upuna* (Fig. 28) and *Anisoptera curtisii* (Fig. 2b, c). It appears that they may have some bearings to the pollination mechanisms. It would seem, therefore, that the stamens of these genera represent the more advanced forms. The appendages usually have no vascular tissue.

B. *Vasculature*

Stamens of the dipterocarp species studied are supplied with a single vascular bundle which traverses the filament, enters the connective, terminating blindly near the apex. Sometimes it enters the distal appendage, eg. *Dipterocarpus* (Fig. 5), *Doona* (Fig. 7), *Parashorea malaanonan* (Fig. 14a), *Vatica* (Fig. 31d; Plate 1H). Branching within the connective is observed in the stamens of the Red Meranti group of *Shorea*. The common one trace condition was considered to have arisen by reduction in number of traces (Eames, 1961).

Stamen bundles are seen in the Balau group and the Red Meranti group of *Shorea, Hopea, Dryobalanops*. Usually the staminal bundle divides to give rise to three branches, each serving a stamen, eg. members of the Balau group of *Shorea* (Plate 1E) (e.g. *S. exelliptica, S. foxworthyi, S. seminis*); *Hopea nutans, Dryobalanops oblongifolia*, or the bundle divides into five vascular traces as in *S. sericea*.

C. *Suggested general evolutionary trends*

Species of the Dipterocarpaceae studied seem to show certain specialisations. The following evolutionary trends in stamens are suggested:

1. Elongation of appendage to connective and gradual shortening or loss of appendage.
2. Elongation and tapering of the upper part of the filament.
3. Development of hairs.
4. Development of anther sacs with apical and basal portions produced into appendages.
5. Reduction in number of sporangia.
6. Shortening of sporangia from linear oblong to ovate or subglobose.
7. Connective tissue becoming narrow and constricted; reduction in connective tissue in both apical and basal portions of anthers.

A diagram (Diagram 1) illustrating the probable course of evolution of the stamens in the Dipterocarpaceae have been drawn out, based on the morphology of the stamens studied and on the evolutionary trends listed above. Representative members of certain genera have been selected: *Cotylelobium burckii, Hopea nutans* (taken as representative of those with longer appendages in *Hopea, Shorea talura* of Meranti Pa'ang group of *Shorea, Shorea resina-nigra* of Meranti Damar Hitam group, *Shorea hemsleyana* of Red Meranti group (taken as representative of the group excluding *S. parvifolia, S. sericea* and *S. kunstleri*).

S. parvifolia (Fig. 27e) seems to be the basic form in the genus *Shorea* because of the short appendage, broad and short filament and elliptic oblong sporangia. From this basic form is the Balau group (Fig. 18; Plate 1E) with its longer filament and its appendage projects abaxially, leading on to the Meranti Pa'ang group (Fig. 21; Plate 1F) with long produced recurved appendage. The tendency is also towards the loss of appendage as in the Red Meranti group (Fig. 26, 27) eg. *S. sericea* or reduction to thin needle-like appendage as in *S. resina-nigra* (Fig. 22d) of the Meranti Damar Hitam group. Diagram 2 illustrates the probable course of evolution of stamens in the genus *Shorea*.

The stamens of *Hopea* are very alike certain members of *Shorea* except that they display an increased elongation of the appendage which are filamentous and setose. *Anisoptera curtisii* has stamens which are very similar to *Upuna* with reference to their long appendages . *Vatica wallichi* (Fig. 31a, b) seems to have stamens nearer to that of *Shorea*. *Vatica nitens* (Plate 1H) with its clavate appendage could be the primitive form.

The progressive elongation of stamen filaments is apparent in the *Hopea* and *Shorea* species, especially the Meranti Damar Hitam group eg. *S. resina-nigra* and *S. maxima;* also in the Red Meranti group, eg. *S. hemslevana, S. leprosula, S. sericea, S. curtisii, S. lepidota*. The elongation of stamen filaments in more specialised flowers can have either one or two different functions (Stebbins, 1974). In wind-pollinated flowers, it places the dehiscing anthers well above the level of the perianth and so increases the efficiency of pollen dispersal. In flowers pollinated by nectar-seeking insects or other animal vectors, elongate filaments place the anthers in such a position that pollen is dusted onto particular parts of the animals' body during its visit. *Shorea sericea*, with its long and twisted filaments is very likely to be wind-pollinated. Adnation of stamen filaments to the corolla tube is a common specialisation as seen in *S. resinosa, S. gratissima, Hopea sangal*. The adaptive value of the epipetalous condition was probably the precise positioning of the anthers with respect to the stigma and the insect pollinators (Stebbins, 1974).

In *Dipterocarpus oblongifolius*, there is an outer ring of staminodes (Fig. 5c) The presence of staminodes that are homologous with stamens and apparently derived from them is characteristic of many flowers that are highly specialised for insect pollination (Stebbins, 1974). The long filiform appendages of *Anisoptera, Dipterocarpus, Hopea,* the Meranti Pa'ang group of *Shorea* and *Upuna* which may be setose or glabrous, as mentioned earlier, seems to be highly evolved structures for assisting in pollination. The stamens of these genera may be regarded as more advanced, in this respect. Moreover, the Balau group of *Shorea* (Plate 1E) have appendages which are barbate. These bristles may serve to brush off pollen from insect visitors. The long appendages of *Hopea* (Fig. 12) are usually minutely setose, eg. *H. nutans, H. beccarianna, H. apiculata*. Setaceous nature of the appendages may cause stamens to cling onto the insects' body and

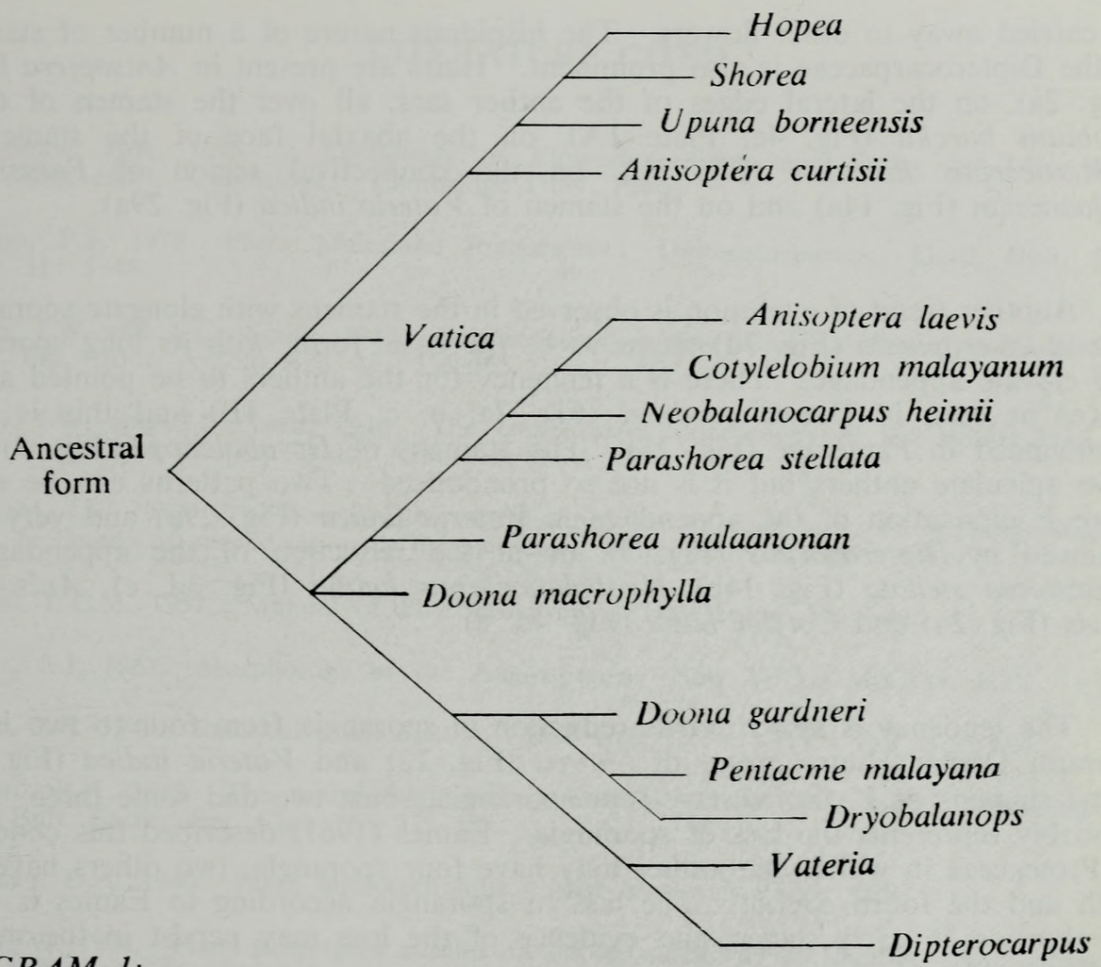


DIAGRAM 1:

Hypothetical evolutionary trends of stamens in the family of Dipterocarpaceae

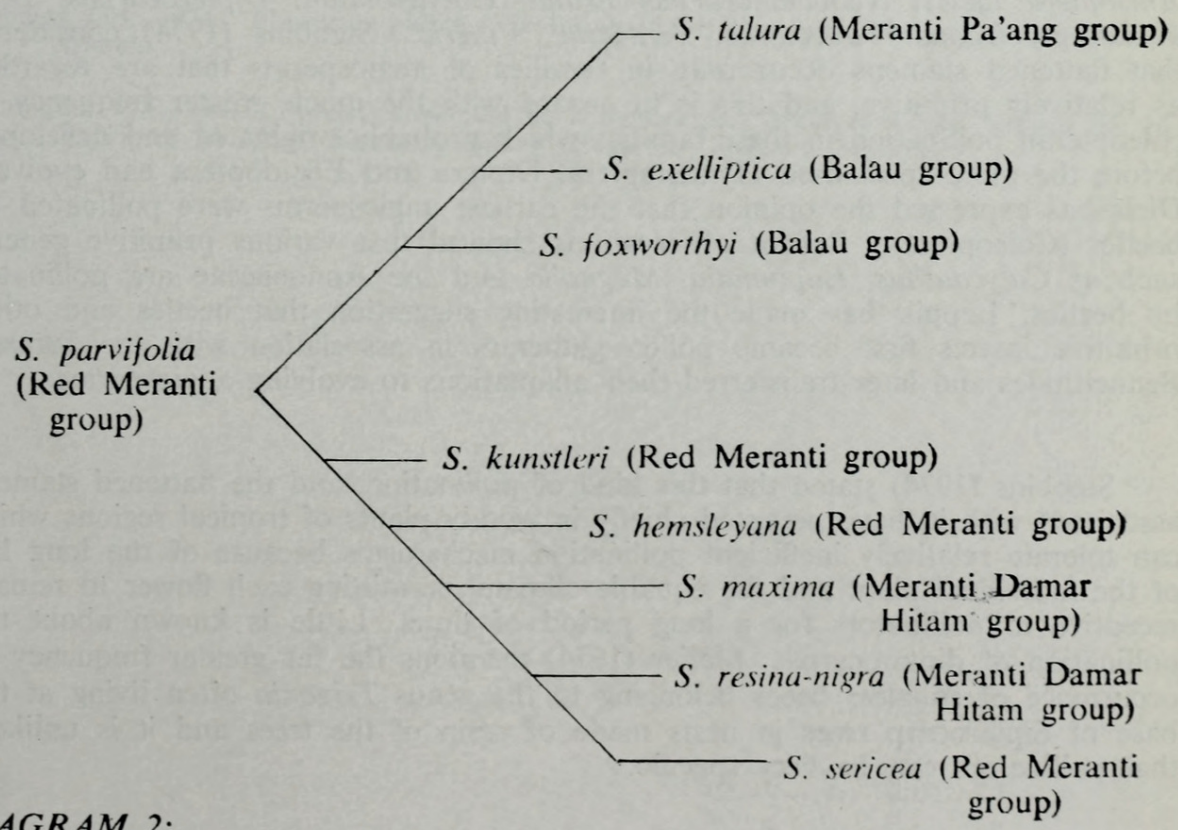


DIAGRAM 2:

Hypothetical evolutionary trends of stamens in the genus Shorea

be carried away to other flowers. The hispidous nature of a number of stamens of the Dipterocarpaceae is also prominent. Hairs are present in *Anisoptera laevis* (Fig. 2a), on the lateral edges of the anther sacs, all over the stamen of *Cotylelobium burckii* (Fig. 4e; Plate 1A), on the abaxial face of the stamen of *Dipterocarpus kunstleri* (Fig. 5b); on the connectival region of *Parashorea malaanonan* (Fig. 14a) and on the stamen of *Vateria indica* (Fig. 29a).

Another trend of evolution is observed in the stamens with elongate sporangia. *Doona macrophylla* (Fig. 7d) seems to be the basic form, with its long sporangia and clavate appendage. There is a tendency for the anthers to be pointed at the apices as seen in *Doona gardneri* (Fig. 7a, b, c; Plate 1B) and this is most pronounced in *Pentacme* (Fig. 15). The stamens of *Dryobalanops* (Fig. 9) also have apiculate anthers but it is not so pronounced. Two patterns can be seen: there is elongation of the appendage in *Vateria indica* (Fig. 29a) and very pronounced in *Dipterocarpus* (Fig. 5), or in the reduction of the appendage in *Parashorea stellata* (Fig. 14b), *Neobalanocarpus heimii* (Fig. 3d, e), *Anisoptera laevis* (Fig. 2a) and *Cotylelobium* (Fig. 4d, e).

The tendency is also towards reduction in sporangia from four to two in the Meranti Damar Hitam group of *Shorea* (Fig. 22) and *Vateria indica* (Fig. 29). Some stamens of *V. indica* have four sporangia, some two and some three. This probably represents the loss of sporangia. Eames (1961) described this condition in Proteaceae in which one anther may have four sporangia, two others have two each and the fourth sterile. The loss of sporangia according to Eames is often by abortion in early stages, and evidence of the loss may persist in the mature anther.

The family contains a number of members with flattened stamens eg. *Anisoptera laevis, Neobalanocarpus heimii, Cotylelobium, Dipterocarpus, Dryobalanops, Doona, Parashorea, Pentacme, Vateria.* Stebbins (1974) considered that flattened stamens occur only in families of angiosperms that are regarded as relatively primitive, and this is in accord with the much greater frequency of coleopteran pollination in these families which probably originated and developed before the more specialised Hymenoptera, Diptera and Lepidoptera had evolved. Diels has expressed the opinion that the earliest angiosperms were pollinated by beetles (Coleoptera). Recent observations showed that various primitive genera, such as *Calycanthus, Eupomatia, Magnolia* and the Annonaceae are pollinated by beetles; Leppik has made the interesting suggestion that beetles and other primitive insects first became pollen gatherers in association with the Jurassic Bennettitales and later transferred their adaptations to evolving angiosperms.

Stebbins (1974) stated that this kind of pollination, and the flattened stamens associated with it, have persisted chiefly in woody plants of tropical regions which can tolerate relatively inefficient pollination mechanisms because of the long life of the individual plant and the equable climate, permitting each flower to remain receptive to pollinators for a long period of time. Little is known about the pollination of dipterocarps. Meijer (1974) mentions the far greater frequency of occurrence of stingless beees belonging to the genus *Trigonia* often living at the base of dipterocarp trees in nests made of resin of the trees and it is unlikely that pollinators can be very specific.

LITERATURE CITED

Airy-Shaw, H.K. 1973. A Dictionary of Flowering Plants and Ferns, by J.C., Willis (8th edit.). Cambridge: Cambridge Univ. Press.

Ashton, P.S. 1978. Flora Malesiana Precursores: Dipterocarpaceae. Gard. Bull. Sing. 31: 5–48.

Bailey, I.W. and A.C., Smith. 1942. Degeneriaceae, a new family of flowering plants from Fiji. Jour. Arnold Arb. 23: 356–365.

Bailey, I.W. and C.F., Nast. 1943. The comparative morphology of the Winteraceae. I. Pollen and stamens. Jour. Arnold Arb. 24: 340–346.

Canright, J.E. 1952. The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialisation in the stamens. Amer. Jour. Bot. 39: 484–497.

Croizat, L.C.M. 1952. Manual of Phytogeography. The Hague: W. Junk.

Eames, A.J. 1961. Morphology of the Angiosperms. New York: McGraw Hill.

Foster, A.S. 1949. Practical plant anatomy (2nd ed.). New York: Van Nostrand.

Howard, R.A. 1948. The morphology and systematics of the West Indian Magnoliaceae. Bull. Torrey Bot. Club 75: 335–357.

Johansen, D.A. 1940. Plant microtechnique. New York: McGraw Hill.

Meijer, W. 1974. Plant geographic studies on Dipterocarpaceae in Malesia. Ann. Missouri Bot. Gard. 61: 806–818.

Parkin, J. 1951. The protrusion of the connective beyond the anther and its bearing on the evolution of the stamen. Phytomorphology 1: 1–8.

Stebbins, G.L. 1974. Flowering plants. Evolution above the species level. London: Edward Arnold.

Symington, C.F. 1943. Forester's Manual of Dipterocarps. Malayan Forest Record no. 16. (Reprinted in 1974. Kuala Lumpur: Penerbit Universiti Malaya).

APPENDIX

LIST OF VOUCHER HERBARIUM SPECIMENS FOR STUDIES

1. *Anisoptera curtisii* Dyer.

   Gunong Angsi, Negri Sembilan, Malaya: *F.S. Watson* (*CF No. 742*), April 1916.

   Bt. Bank F.R. Trengganu, Malaya: *Y.C. Chan* (*FRI 25067*), 15 May 1976.

2. *Anisoptera laevis* Ridl.

   Ulu Gombak FR, Selangor, Malaya: *C.F. Symington* (*KEP 47004*), 31 August 1938.

3. *Balanocarpus curtisii* King = *Hopea minima* Sym. Waterfall, Penang, Malaya: *C. Curtis 1406*, March 1901.

4. *Balanocarpus heimii King* = *Neobalanocarpus heimii* Ashton, Malaya:

   F.C. Yong (*KEP 98875*), 11 May 1963. FRI Kepong, Malaya: *Collector unknown* (*KEP 98870*).

5. *Cotylelobium burckii (Heim)* Heim.

   Aup, Sibu, Sarawak: *J. Wight* (*SAR A0416*), 14 June 1938.

6. *Cotylelobium malayanum* V.Sl.

   Sungei Morai, Singapore: *J.S. Goodenough 4630*, 18 July 1890.

7. *Dipterocarpus gracilis* Bl.

   Ulu Gombak F.R., Selangor, Malaya: *K.M. Kochummen s.n.*, 22 April 1965.

8. *Dipterocarpus kunstleri* King

   Jerangau S.L. Dungun, Malaya: *K.M. Kochummen* (*KEP 76663*), 28 July 1955.

9. *Dipterocarpus oblongifolius* Bl.

   Kechau River, Pahang, Malaya: *M. Hashim (C.F. No. 695)*, 1 June 1916. FRI Kepong, Malaya: *Z. Ramli* (*KEP 99075*), 29 April 1965.

   Gunong Tahang, Pahang Malaya: *Md. Haniff & Md. Nor 8032*, 20 June 1922.

   Kepong, Malaya, *K.M. Kochummen 97742*, 12 May 1961.

10. *Doona gardneri* Thw.

    Ceylon: *Thwaitesii s.n.*, 1919.

11. *Doona macrophylla* Thw.

Ceylon: *Thwaitesii 3713.*

12. *Dryobalanops aromatica* Gaertn. f.

Kuching Reserve, Selangor, Malaya: *Ahmad 5047*, 20 Sept. 1920.
FRI Arboretum, Kepong, Malaya: *F.S.P. Ng* (*FRI 6320*), 28 March 1972.

13. *Dryobalanops oblongifolia* Dyer

Kuantan, Pahang, Malaya: *J.G. Watson* (*CF Field No. 3250*), 21 May 1919.
FRI Arboretum, Kepong, Malaya: *F.S.P. Ng s.n.*, 28 March 1972.

14. *Hopea apiculata* Sym.

Field 12A FRI, Kepong, Malaya: *Motan* (*KEP 80225*), 15 March 1955.

15. *Hopea beccariana* Burck

Govt. Hill, Penang, Malaya: *C. Curtis 1398*, July 1888.

16. *Hopea mengarawan* Miq.

Temerloh, Pahang, Malaya: *Hamid* (*C.F. 4621*), 10 Dec. 1919.

17. *Hopea nutans* Ridl.

FRI Arboretum, Kepong, Malaya: *S. Chelliah* (*KEP 98355*), 17 March 1972.

18. *Hopea odorata* Roxb.

FRI Arboretum, Kepong, Malaya: *F.S.P. Ng* (*FRI 6325*), 30 March 1972.

19. *Hopea sangal* Korth.

Batu Gantong, Penang, Malaya: *Md. Haniff* (*C.F. No. 3715*), 5 June 1918.

20. *Parashorea malaanonan* (Blanco) Merr.

FRI Arboretum, Kepong, Malaya: *F.C. Yong* (*KEP 99624*), 5 April 1962.

21. *Parashorea lucida* (Miq.) Kurz

Bt. Naga F.R. Malaya: *V.P. Borges* (*KEP 5611*), 4 Oct. 1921.

22. *Parashorea stellata* Kurz

Bt. Naga Reserve, Perak, Malaya: *V.P. Borges 5611*, 4 Oct. 1921.

23. *Pentacme malayana* King

Pulau Rabana, Perlis, Malaya: *M.R. Henderson 23107*, 25 Nov. 1929.

24. *Shorea acuminata* Dyer

FRI Arboretum, Kepong, Malaya: *Z. Ramli* (*KEP 98352*), 17 March 1965.

25. *Shorea curtisii* Dyer

Bt. Timah F.R. Singapore: *Ngadiman* (*S.F. No. 34784*), 5 Sept. 1938.

26. *Shorea exelliptica* Meijer

FRI Arboretum, Kepong, Malaya: *Y.C. Chan* (*FRI 18197*), 4 June 1976.

27. *Shorea foxworthyi* Sym.

FRI Arboretum, Kepong, Malaya: *F.S.P. Ng* (*FRI 22180*), 12 March 1976.

28. *Shorea gratissima* Dyer

Bot. Gardens, Singapore: *H. Keng & Jumali s.n.*, May 1977.

29. *Shorea hemsleyana* (King) King ex Foxw.

FRI Kepong Malaya: *Y.C. Chan* (*KEP 115740*), 22 Jan. 1972.

30. *Shorea kunstleri* King.

Parit Reserve, Kinta, Perak, Malaya: *M.L. Weber 13714*, 18 Nov. 1927.

31. *Shorea lepidota* (Korth.) Bl.

Pasoh F.R.N.S. Malaya: *Y.C. Chan* (*FRI 23894*), 7 April 1976.

32. *Shorea leprosula* Dyer

Bt. Timah Reserve, Singapore: *Ngadiman* (*S.F. No. 37251, Tree No. 275*), 16 Oct. 1939.

33. *Shorea maxima* (King) Sym.

FRI Arboretum, Kepong, Malaya: *F.S.P. Ng* (*FRI 6326*), 30 March 1972.

34. *Shorea ovalis* (Korth.) Bl. = *S. sericea* Dyer

FRI Arboretum, Kepong, Malaya: *F.C. Yong* (*KEP 99988*), 14 June 1963.

35. *Shorea parvifolia* Dyer

FRI Arboretum, Kepong, Malaya: *Ahmad* (*KEP 99392*), 6 April 1961.

36. *Shorea resinosa* Foxw.

FRI Kepong, Malaya: *Y.C. Chan* (*FRI 18193*), 24 Feb. 1976.

37. *Shorea resina-nigra* Foxw.

FRI Arboretum, Malaya: *K.M. Kochummen* (*KEP 98876*), 5 May 1963.

38. *Shorea seminis* (de Vriese) V. Sl.

Sarawak: *Yakup S79*, 25 Sept. 1958;

J. Singh (*SAN 60875*), 10 May 1967; *Rehal S9581*, 26 August 1957.

Sandakan, Borneo: *A. Bakar 36214*, 8 May 1963.

39. *Shorea sericea* Dyer

Govt. Hill, Penang, Malaya: *Md. Haniff 3760*, 24 June 1918.
Temerloh, Pahang, Malaya: *Hamid 5475*, 11 Dec. 1920.

40. *Shorea talura* Roxb.

FRI, Kepong, Malaya: *Collector unknown s.n.*, 11 Feb. 1963.

41. *Upuna borneensis* Sym.

Sarawak: *Moksin S1917*, 13 August 1955.

42. *Vateria indica* Linn.

Yellapur, Bombay: *N.L. Bor. 9671*, 26 April 1939.

43. *Vatica nitens* King

Perak, Malaya: *F.S.P. Ng* (*FRI 21000*), 28 Jan. 1972.

44. *Vatica ridleyana* Brandis

Meranta Avenue, Bot. Gdns, Singapore: *M.R. Henderson* s.n., 13 March 1931.

45. *Vatica wallichi* Dyer

Lawn 2, Bot. Gdns., Singapore: *C.X. Furtado* (*S.F. No. 37446*), 27 Nov. 1941.

Singapore: *J. Sinclair* (*S.F. No. 10696*), 10 June 1962.
FRI Kepong Malaya: *Mat Asri* (*FRI 21682*), 27 August 1976.