Studies in the *Trichilia* - *Walsura* complex (Meliaceae)

by

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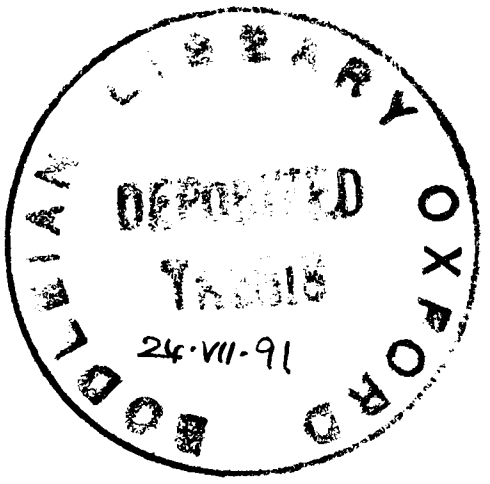

A thesis submitted for the degree of Doctor of Philosophy
in the University of Oxford
Michaelmas Term 1990.

ABSTRACT

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Generic delimitation within the Trichilieae (Meliaceae) is considered, with particular reference to the Trichilia P. Browne - Heynea Roxb. ex Sims - Walsura Roxb. complex. Original investigations of leaf-surface micromorphology, palynology and fruit anatomy are made of species of each genus of the tribe and an isoenzyme study is made of species of Trichilia, Heynea and Walsura. The accounts of these studies are extensively illustrated with photographs, scanning-electron-micrographs and annotated drawings. Seed dispersal systems are briefly considered including original field observations of a species of Walsura. In the light of the data revealed by these studies, inter-generic relationships are discussed.

The Indo-Malesian genus Walsura is taxonomically revised and the closely related new genus Pseudoclausena is segregated from it and described. Within Walsura, a new section (Ruswala) and three new species (W. dehiscens, W. pachycaulon and W. sarawakensis) are described and one new combination is made (W. trifoliolata ssp. acuminata). The new genus consists of one new species (P. chrysogyne), formerly W. chrysogyne (Miq.) Bakh.f, and W. velutina Ridley is reduced to a new forma of it. Keys are given for the identification of all taxa and the species are illustrated by drawings and (in some cases) by photographs.

A cladistic analysis is made of all the species of Walsura, Pseudoclausena and Heynea, taking Trichilia as the outgroup. This, together with the findings of the above studies and published data indicate that Heynea should be considered a distinct genus in the alliance of Walsura. A key for the identification of these four genera is given. The other genera of the tribe are briefly considered and all are maintained as distinct. The great diversity of fruit structures within the tribe provides particularly good characters for the segregation of these genera.

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CHAPTER 1

INTRODUCTION

1. Introduction to the tribe.

The Meliaceae is a tropical to sub-tropical family in the order Sapindales (Cronquist, 1981). It consists of c. 575 species in 51 genera and most of these species are trees, with few shrubs (Mabberley, 1987). The largest genera are Aglaia Lour. (c. 100 spp., currently being revised by C. Pannell), Trichilia P. Browne (c. 89 spp., de Wilde, 1968; Pennington & Styles, 1981; Cheek, 1989), Dysoxylum Blume (c. 75 spp., currently being revised by D. Mabberley), Chisocheton Blume (51 spp., Mabberley, 1979) and Guarea (40 spp., Pennington & Styles, 1981).). These five genera thus contain over half of the species of the family.

De Candolle (1824) provided a more comprehensive and detailed revision of the Meliaceae than any previous author and was also the first to divide the family into tribes. He established the Melieae, Trichilieae and Cedreleae. His Trichilieae includes Trichilia, Ekebergia, Heynea and Guarea and is characterised by a fruit with 1 or 2 seeds per loculus, exalbuminous unwinged seeds and an inverted embryo with thick cotyledons. De Jussieu (1830) had only two tribes (viz. Melieae & Trichilieae, Cedreleae being excluded as a distinct family) in his treatment of the Meliaceae but Hooker (1862) reinstated Cedreleae and included a fourth, viz. Swietenieae. Trichilieae here includes

Dysoxylum, Chisocheton, Epicharis, Cabralea, Sandoricum, Aglaia, Milnea, Lansium, Amoora, Synoum, Guarea, Dasycoleum, Ekebergia, Walsura, Heynea, Beddomea, Moschoxylon, Odontandra, Trichilia, Owenia and Carapa and is defined by united filaments, 1- or 2-ovulate loculi, and unwinged exalbuminous seeds with thick, often fused, cotyledons.

Baillon (1875) and C. de Candolle (1878) both reviewed the family, largely following Hooker's classification with some small amendments to the Trichilieae, e.g. Baillon reduced Walsura to Heynea and de Candolle removed Carapa to the Swietenieae. Harms (1896), in his first account of the Meliaceae, also followed Hooker closely, but reduced Heynea to Walsura. However, whilst maintaining the broad (24 genera) conspectus of the tribe, in his second account (1940) he reinstated Heynea as a distinct genus and gave the most comprehensive treatment of the tribe (& family) then available. Kribs (1930) proposed a re-classification of the family based on wood anatomical characters but none of his conclusions affected the state of the Trichilieae.

The next, and most recent, generic revision of the family was that of Pennington & Styles (1975), much of it based on Pennington's (1965) D.Phil. thesis. Here tribal delimitation within subfamily Melioideae is considerably re-organised. The Trichilieae loses many of its genera to other tribes, while Pterorhachis and Cipadessa are moved in from the Turraeeae and certain recently established genera (viz. Pseudobersama, Lepidotrichilia, Astrotrichilia and Malleastrum) are incorporated. Within the Melioideae (which is characterised by naked buds and the fruit being a capsule, berry or drupe with unwinged seeds), Pennington & Styles have seven tribes, viz. Turraeeae, Melieae, Vavaeeae, Trichilieae, Aglaieae, Guareeae and Sandoriceae, the last two being newly

described. None of these, however, is sharply distinguished. The Trichilieae is particularly diverse morphologically, e.g. in leaf, flower and fruit features, and there does not seem to be one single good character to distinguish it. A number of the 16 features of the tribe given by Pennington & Styles need to be taken collectively to key it out. Nevertheless, the circumscription of the tribe by Pennington & Styles is here taken as a working basis. This includes the following genera (in the order given by them): Trichilia P.Browne, Pseudobersama Verdcourt, Pterorhachis Harms, Walsura Roxb., Lepidotrichilia (Harms) J.F.Leroy, Malleastrum (Baill.) J.F.Leroy, Ekebergia Sparrm., Astrotrichilia (Harms) J.F.Leroy, Owenia F.Muell. & Cipadessa Blume.

2. Heynea and generic delimitation within the Trichilieae.

When considering the affinities and relationship between Trichilia and Walsura, one is confronted with the old problem of what to do with the two Indo-Malesian species of Trichilia, formerly constituting the genus Heynea Roxb. ex Sims. The taxonomic history of these species can be summarised thus:

Browne	(1756):	Trichilia validly published.
Roxburgh	(1814):	Heynea (H.trijuga & H.quinquejuga) nom.nud. & Walsura nom. nud.
Sims	(1815):	H.trijuga validly published (+ illustration).
Roxburgh	(1832):	Walsura (W.piscidia & W.robusta) validly published.
Hiern	(1875):	Heynea and Walsura maintained as distinct genera.
Kurz	(1875):	Heynea species reduced to Walsura.
Baillon	(1875):	Walsura species reduced to Heynea.

Harms (1896): Heynea species reduced to Walsura, Harms erroneously arguing that Walsura should have precedence.

Harms (1940): Heynea reinstated as a distinct genus.

Bentvelzen (1962): Heynea reduced to Trichilia.

Pennington & Styles (1975): With reservations, Bentvelzen's reduction maintained.

Various other species of Heynea have been described (mostly between 1830 and 1863) but Bentvelzen, in the last revision of these species, reduced all of those which do not belong to Walsura (see Chapter 6) to one or other of the two Indo-Malesian Trichilia species, T.connaroides (W.& A.) Bentv. and T.sinensis Bentv. No objection is raised here against Bentvelzen's reduction of the various species of Heynea to two species. However, the question of whether the reduction of Heynea to Trichilia should be maintained needs re-examination since: (i) Bentvelzen's reasons for the reduction are open to question (see below); (ii) in many features, the genus seems intermediate between Trichilia and Walsura and its status therefore has implications for the status of the larger genus Walsura; (iii) modern investigative techniques, e.g. scanning-electron microscopy and chemotaxonomy (not available to Bentvelzen), can reveal additional data on which to base taxonomic decisions.

Excluding the two Indo-Malesian species, Trichilia is a large and highly variable genus with 19 species in tropical Africa (De Wilde, 1968; Cheek, 1989) and about 70 species in the Neotropics (Pennington & Styles, 1981). They are mostly sub-canopy or canopy trees, many of value for their timber. Walsura is a genus of about 16 tree species in the Indo-Malesian region (see Chapter 6).

Until all the evidence is presented to allow a decision to be made about the status of the two Asian Trichilia species, in this thesis, they will be referred to as Heynea for convenience. The synonomy, following Bentvelzen (1962), is therefore:

Trichilia connaroides (W.& A.) Bentvelzen

.....

var. connaroides .

forma connaroides ..... Heynea trijuga Roxb. ex Sims

forma glabra .

.....

var. microcarpa ..... Heynea trijuga var. microcarpa Pierre

Trichilia sinensis Bentvelzen ..... Heynea velutina How & Chen

The question is therefore whether to maintain Trichilia, Heynea and Walsura as distinct genera or whether to extend the range of Trichilia to the Indo-Malesian region, and even to include the Walsura species.

Floral differences between the three genera are small or insignificant (Pennington & Styles, 1975, and see Chapter 8) and Bentvelzen's principal reason for reducing Heynea was the same reason previous authors had given for segregating Heynea from Walsura, that it (like the Trichilia species) posseses a dehiscent fruit. This feature has recently been observed in Walsura however

(see Chapter 4). This character he backed up with three lesser characters viz. presence of bitter substances and glands in the leaves and absence of wood vessels from the pith of the twig. These minor characters will be discussed more fully in Chapter 8. The reduction has a rather shaky basis therefore, especially in view of the biogeographic differences between Trichilia and the Asian genera. This then is the nub of the problem to be tackled here, but the status of these three genera and the characters employed to decide their fate may necessarily determine how the other small genera of the Trichilieae (especially the other Asian genus, Cipadessa) are to be regarded.

3. The current project.

For a complete understanding of the relationship between Walsura and Heynea and its allies, it was considered essential to prepare a monographic account of Walsura as the last revision was that of de Candolle (1878) and since then something in excess of 95% of specimens currently available for study have been collected. Little attempt has previously been made to deal with synonymy within the genus and new undescribed species have recently been identified. The completed revision is presented in Chapter 6.

With a range of modern investigative techniques available, and the opportunity to break new ground in the study of the Meliaceae by investigating features of the plants not previously studied in detail or at all (viz. micro-features of the leaf surface (Ch. 2), pollen morphology (Ch. 3), fruit anatomy (Ch. 4) & isoenzymes (Ch. 5)), it was decided to undertake a study across the tribe, with particular emphasis on the Trichilia - Heynea - Walsura complex. The

identification of the nature of the fruit dehiscence in these species (including that in Walsura) was considered particularly important. The characteristics, including geographical distributions, of the genera of the tribe will be considered in Chapter 8, along with the data from the present study.

CHAPTER 2

LEAF SURFACE

INTRODUCTION

Leaf-surface features are second only to those of the flower and fruit in value and usage for taxonomic studies (Stace, 1984). Indeed for identification purposes, they are often more valuable since they are usually present for a far greater part of the plant's life cycle. Their value in taxonomic work has long been demonstrated, e.g. trichomes in the Gramineae (Metcalfe, 1960) and in the Solanaceae (Roe, 1971); stomatal characters in the Magnoliaceae and related families (Baranova, 1972); papillae in the Aizoaceae (Reule, 1937). Leaf surface features have thus been shown to be of great value in primary taxonomic decisions and in the identification of sterile or fragmentary material.

Even though the effort involved in preparing material for microscopy is generally greater than that for studying macro-morphological features, it is still necessary to take measures to avoid undersampling and not picking up the full range of variation of a particular feature. Stace (1965) and Dilcher (1974) have between them shown how trichome and stomatal density and distribution, cuticle thickness, epidermal cell anticlinal wall patterns and cuticular striations can all vary with environmental conditions.

Cutler (1982) has shown that in Aloe species (Liliaceae) from South Africa, cuticular sculpturing (i) is under strong genetical control, (ii) varies little within species, (iii) varies little with habitat, (iv) differences between species reflect the accepted phylogenetic arrangement of the group. Lavier George (1936) also found that cuticular features provide good characters for the separation of certain Madagascan Philippia species (Ericaceae). Dunn, Sharma and Campbell (1965) examined a wide range of dicotyledons (226 species) and concluded that xerophytic species tend to have far more ornately sculptured cuticles than do mesophytic ones. However, there are few data on mesophytes from the wet tropics, an exception being, for example, Rao's observations (1963) on the cuticular ornamentation of Hevea brasiliensis (Adr.Juss.) Muell.Arg. (Euphorbiaceae).

Papillae are projections of the outer periclinal wall of the epidermal cells and include any ornamentations it may have. They seem to have been little used for taxonomic purposes, largely it seems because (as with striate sculpturing of the epidermis) for many taxa they are not a constant character, but their production is much influenced by environmental factors (Solereder, 1908; Goris, 1910; Baas, 1970; Wilkinson, 1979). Reule (1937) however recognised seven distinct types of papillae in 81 species of Aizoaceae and felt able to use them taxonomically.

Due to their degree of specialisation and their widespread occurence in the angiosperms, trichomes have been intensely studied since the early days of microscopy (Behnke, 1984). Today, trichome characters are very commonly employed in systematic work. Rollins and Banerjee (1975) utilised

diversification from a single cell to various types of trichome as a basis for a phylogenetic reconstruction of Lesquerella (Cruciferae), and sub-tribal classification of the Phaseoleae (Leguminosae) is largely supported by distinct trichome types (Lackey, 1978).

Leaf-surface features can broadly be split into 'macro', i.e. those capable of being assessed by the naked eye (e.g. presence or absence and density of pubescence), and 'micro', for which a hand lens, light microscope (LM) or scanning electron microscope (SEM) is required (e.g. trichome type). Whilst many 'macro' features of the leaf surface have been noted in the Trichilieae, in the normal course of taxonomic descriptions and revisions (e.g. De Wilde, 1968; Pennington & Styles, 1975 & 1981), very few microscopical observations have been made. In their accounts of the family, Solereder (1908), Metcalfe & Chalk (1950 & 1979), Pennington (1965) and Pennington & Styles (1975 & 1981) make very basic microscopical observations. In view of the paucity of data, it was decided to make a detailed study of 'micro' features in the Trichilieae. The object was to determine those features which may be of taxonomic value. The study was of materials from across the tribe with an emphasis upon the species of the Trichilia - Heynea - Walsura complex. Since this was also the first group within the Meliaceae to be investigated in this way, it was hoped that the findings might suggest avenues of investigation in other parts of the family, particularly if good taxonomic characters could be recognised here.

MATERIALS AND METHODS

Most of the material used in the investigation was taken from herbarium specimens but fresh material was also available (at Oxford) from six species (viz. *Walsura tubulata* Hiern, *Heynea trijuga* Roxb. ex Sims, *Trichilia emetica* Vahl, *T.dregeana* Sond., *Ekebergia capensis* Sparrm., *Pterorhachis zenkeri* Harms) for comparison. A total of 126 specimens was examined under SEM and in those species known to be highly variable in other (macro) characters (e.g. *T.dregeana*) several specimens of each were examined. One to several specimens of *Walsura*, *Heynea* and African *Trichilia* species were examined. For logistic reasons, it was not possible to examine all other species (particularly the New World *Trichilia* spp.) but where a selection had to be made, macro-morphological diversity and geographical range were taken into account. Emphasis has been given to character quality rather than size or density per unit of leaf area as it was soon apparent that the latter varied considerably within species and with age of leaf. Throughout this investigation and unless otherwise stated or defined, the terminology used is in accord with that recommended by Wilkinson (1979).

Prior to the investigation proper, a range of leaf material from across the tribe was examined, using the methods detailed below. Specimens were taken from all parts of the fully expanded leaf or, in the case of divided leaves, of a distal lateral leaflet. It was determined that all potentially useful characters occurred on the abaxial surface of the leaf and that these would be covered if an area of lamina at least 1 cm X 1 cm square was taken from the middle region of the leaf/leaflet, cut in such a way that it

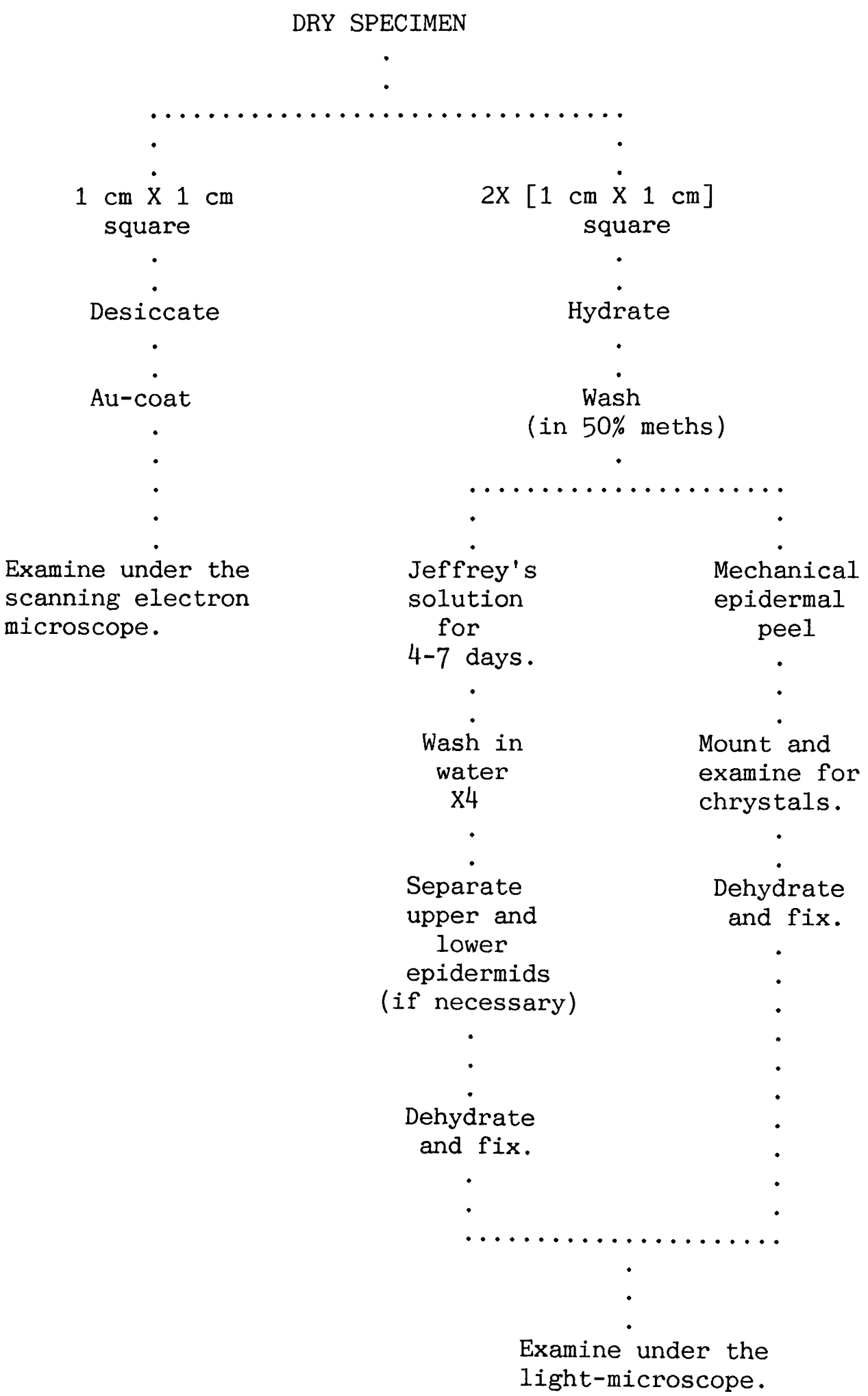
included a section of midrib along one side. A list of specimens used is appended (Appendix 1).

1. Fresh material

The freshly-cut squares of lamina were fixed in a 2.5% gluteraldehyde solution buffered with a Na-K-phosphate buffer, then post-fixed in a 1% osmium tetroxide solution in the same buffer (Juniper et al., 1970; Koek-Noorman and Berendsen, 1985), dehydrated through an alcohol series, the alcohol replaced by acetone, and critical-point-dried (Hayes, 1973; Juniper & Jeffree, 1983). The fixing stops all metabolic activity and preserves cellular components from chemical degradation. In critical point drying, the solvent (in this case acetone) is replaced by liquid carbon dioxide in a pressure bomb. The bomb is sealed and its temperature raised to the 'critical point' of 31°C when the liquid changes to gaseous carbon dioxide at the same volume. The gas is released and the specimen is dry. This method avoids the physical damage rendered to tissues by surface tension forces in other methods of drying.

Slightly larger areas of lamina were also taken for epidermal isolation. Mechanical epidermal peels, from both surfaces of the leaf, were taken by scraping the epidermis away from the pallisade and mesophyll layers beneath using a razor blade (or by tearing it away using forceps, whichever proved easier). These were then desiccated through an alcohol series (50%, 75%, 95%) and mounted without staining for examination under the LM.

FIG. 2.1 Preparation of dried herbarium material for microscopical investigation.



Epidermal preparations were also produced chemically. The tissue was placed in Jeffrey's solution (O'Brien & Mc Cully, 1981) which is a 1:1 mixture of 10% aqueous chromium (VI) oxide and 10% nitric acid. It is left in this strong oxidising solution for between one and four days until the two epidermides are just falling free and the other leaf contents falling away as débris. With experience a preparation consisting of the cuticle and epidermal cell layer (with no pallisade or mesophyll cells, as is often the case with mechanical peels) or of the cuticle only can be made. Time seems to be the critical factor, but for particularly tough leaf material it may help to put the specimen into fresh Jeffrey's solution after two days. When ready, the specimen is washed several times in water, to remove all traces of oxidant, dehydrated through an alcohol series and then mounted (in pure glycerin and sealed with "Glyceel"*) without staining for examination under the LM.

2. Dried herbarium material

(see FIG. 2.1 for summary)

Squares were taken directly from the herbarium specimens for examination under SEM. It was decided not to wash the material since this would bring about partial rehydration and its associated drying problems (as above) and since most of the extraneous matter on the leaf surface was fungal hyphae

* Glyceel is a trade name of British Drug Houses.

(often penetrating the leaf surface through stomatal apertures), washing would be of limited use in removing it.

Two further samples from each specimen were also taken and gently rehydrated by soaking in a weak aqueous detergent solution for two to three days (or a little longer for some particularly tough leaves). They were then washed twice in a 50% aqueous solution of ethanol and one subjected to the Jeffrey's solution treatment (as above) and the other peeled mechanically. The mechanical peel was then investigated under the LM for the presence of sub-epidermal crystals and then, together with the chemical isolates, dehydrated, fixed and mounted (in pure glycerin and sealed with "Glyceel") without staining for examination under the LM.

N.B. The material had to be examined for crystals before dehydration and fixing since these partly chemical processes are liable to dissolve or physically dislodge the crystals which, at this stage, will be only loosely attached to the inner-side of the epidermis.

LM investigation consisted of examination under 100X, 400X and 1000X (oil immersion) with a Zeiss bench microscope. Features observed and recorded (by photography with a Nikon FE2 SLR 35mm camera attached directly on to an eyepiece of the microscope or by freehand drawing) included:

1. epidermal cell shape and size;
2. shape, size and orientation of guard and subsidiary cells;
3. composition of trichomes (cell number)

SEM investigation consisted of mounting the specimens on Cambridge-type aluminium stubs using epoxy resin (Araldite) and coating them with a thin layer of gold in a 'Polaron SEM Coating Unit E5000'. Coating at 200 mA and 1 kV for 2.5 minutes under a vacuum of 0.2 torr gave a gold coating of c.250 nm thick.

They were then examined in a Cambridge Steroscan 150 machine at Oxford and micrographs were made. Features observed included:

1. epidermal cell type (simple or papillate);
2. cuticular sculpturing;
3. external shape of stomatal apparatus;
4. trichome type and sculpturing;
5. detail of epicuticular substances (e.g. wax).

OBSERVATIONS

Using the methods described above, a comprehensive picture of the leaf surface can be built up for any one specimen, from either fresh or dried material.

Care has to be exercised in the interpretation of what is seen, since any chemical or physical preparation is liable to distort the leaf surface and produce artifacts. Various measures, such as critical point drying of fresh

FIG. 2.2

1. Striae wings radiating from a stoma in W.pinnata (Luang 21733; Sarawak). SEM.

2. Striae wings radiating from a stoma in C.baccifera (Cult.: Iowa). SEM.

3. Striae in concentric rings around stomata in E.capensis - non-papillate leaf (Clements 656; Malawi). SEM.

4. Low power view of leaf undersurface in E.capensis - non-papillate leaf (Clements 656; Malawi). SEM.

5. Striae radiating from the stomata in P.mossambicensis (Sem Sei S1387; Tanzania). SEM.

6. Concentric ring sculpturing in E.capensis as seen in epidermis isolated from a non-papillate leaf (Styles 294; Uganda). Light-microscopy.

7. Papillate cells encircling a stoma in W.trifoliolata (Simpson 9223; Ceylon). SEM.

8. Papillate cells encircling a stoma in H.trijuga (Pennington 7877; Sabah). SEM.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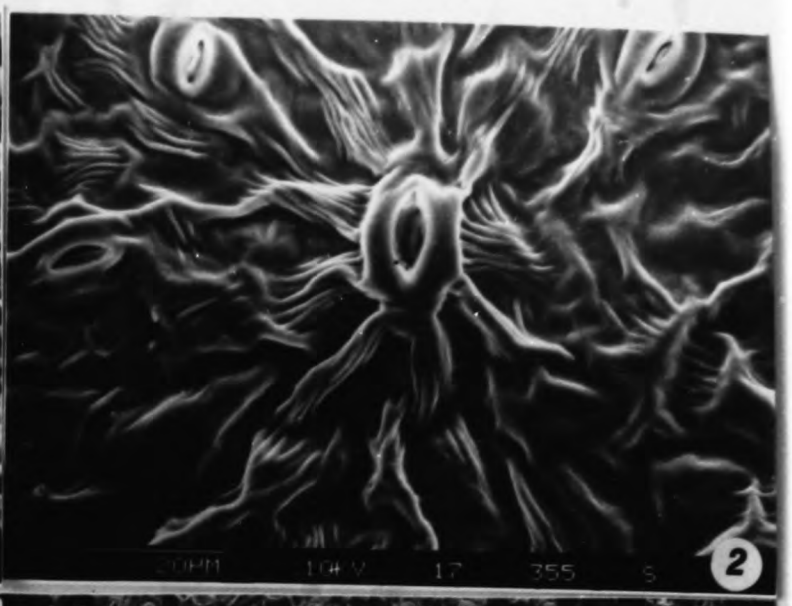
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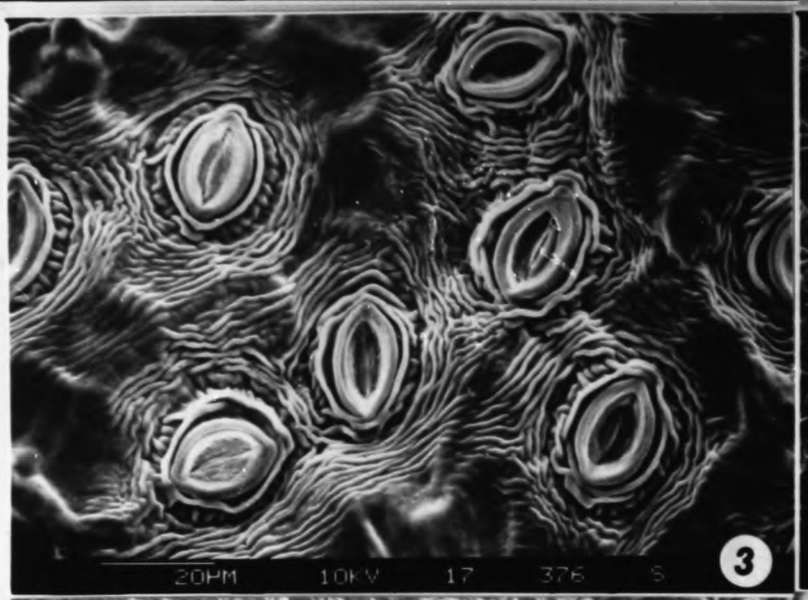
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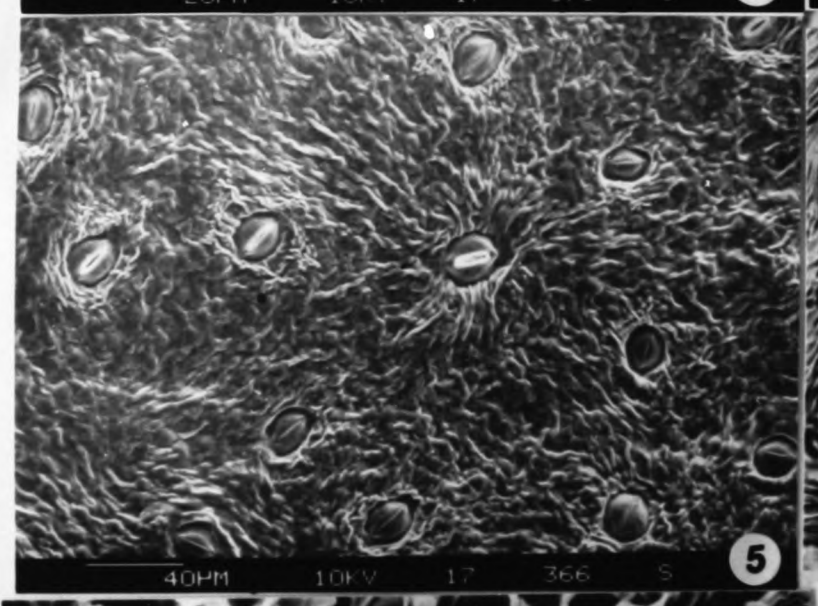
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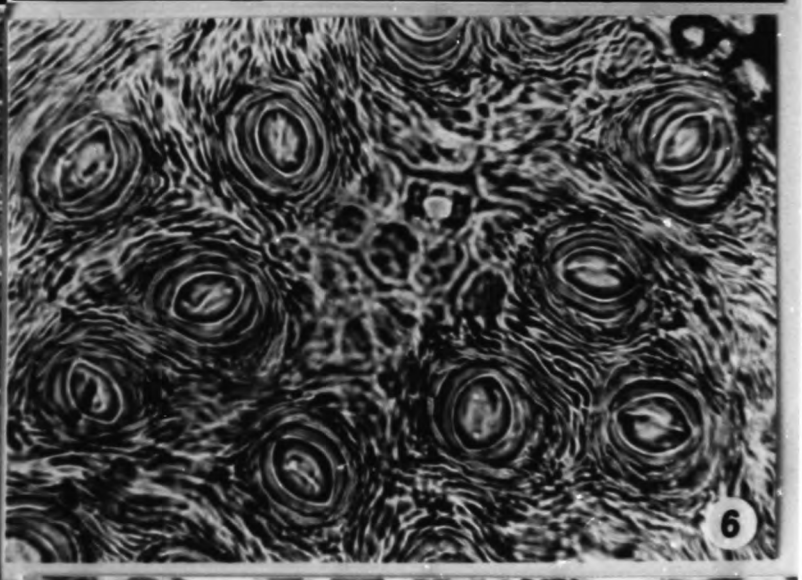
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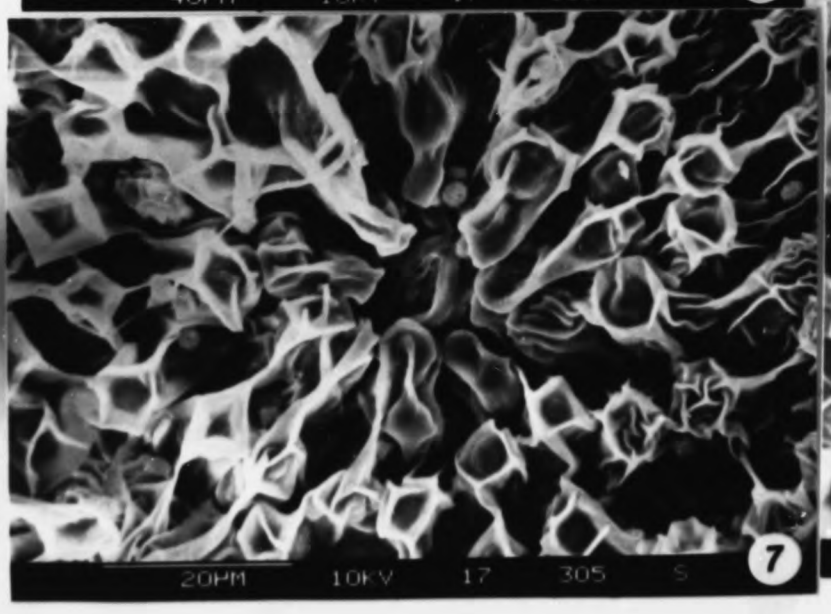
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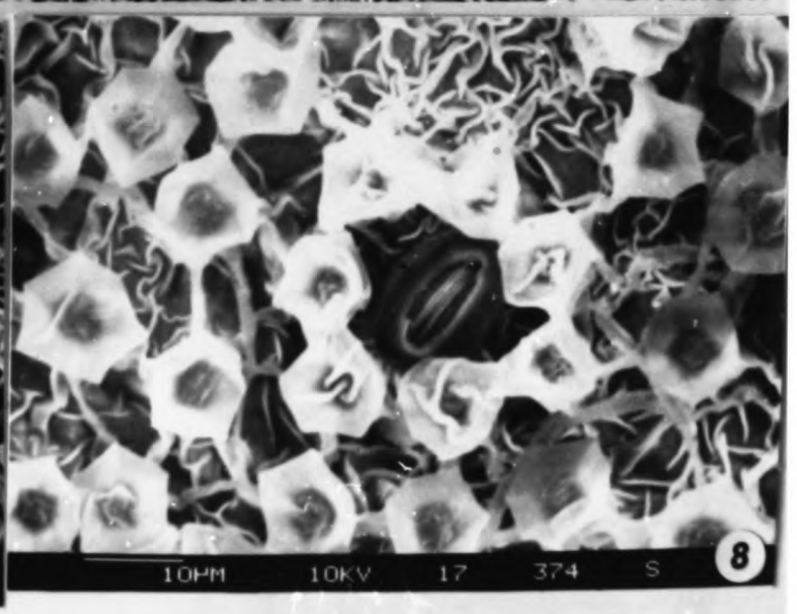
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FIG. 2.3

1. Low power view of the undersurface of a papillate leaf in E.capensis (Styles 290; Uganda). SEM.

2. Papillate cells encircling a stoma in E.capensis (Styles 290). SEM.

3. Trichomes on the leaf of H.trijuga (Saradet 427; Thailand). SEM.

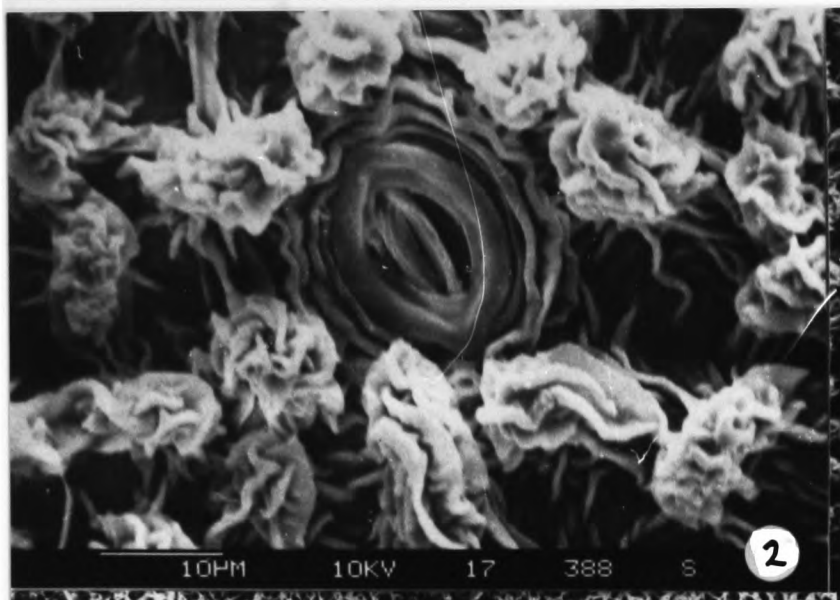
4. Detail of trichome sculpturing in H.trijuga (Saradet 427; Thailand). SEM.

5. Trichomes in T.emetica (Styles 254; Uganda). SEM.

6. Detail of trichome sculpturing in T.emetica (Styles 254; Uganda). SEM.

7. Trichomes as seen in isolated epidermis of T.dregeana (Cult.; Oxford Botanic Garden). Light-microscopy. Mag.: X130.

8. Trichomes as seen in isolated epidermis of H.trijuga (Saradet 427; Thailand). Light microscopy. Mag.: X200.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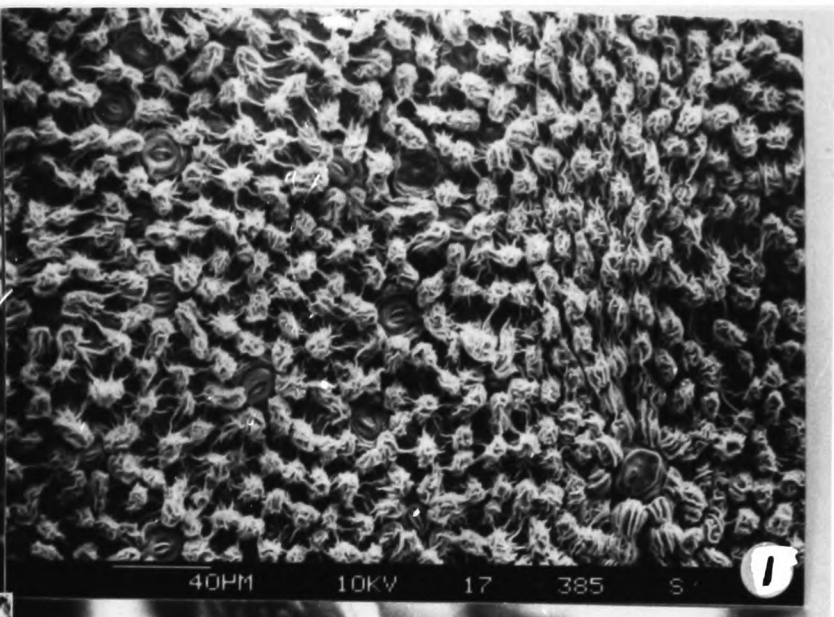
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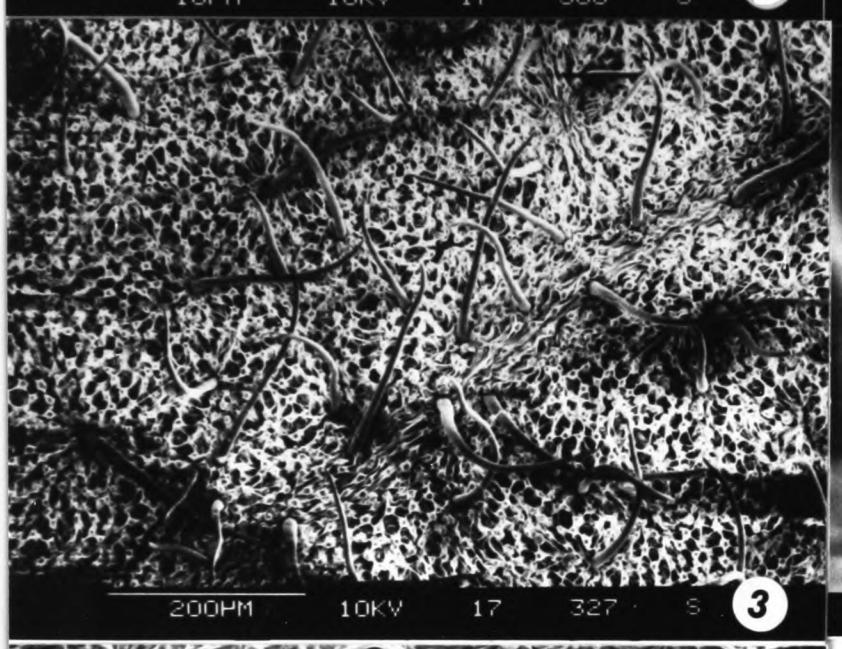
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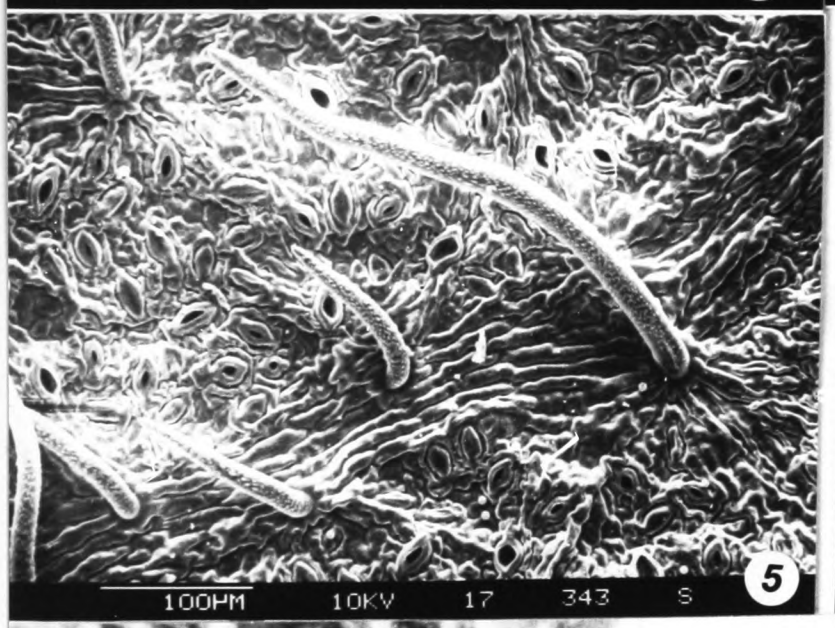
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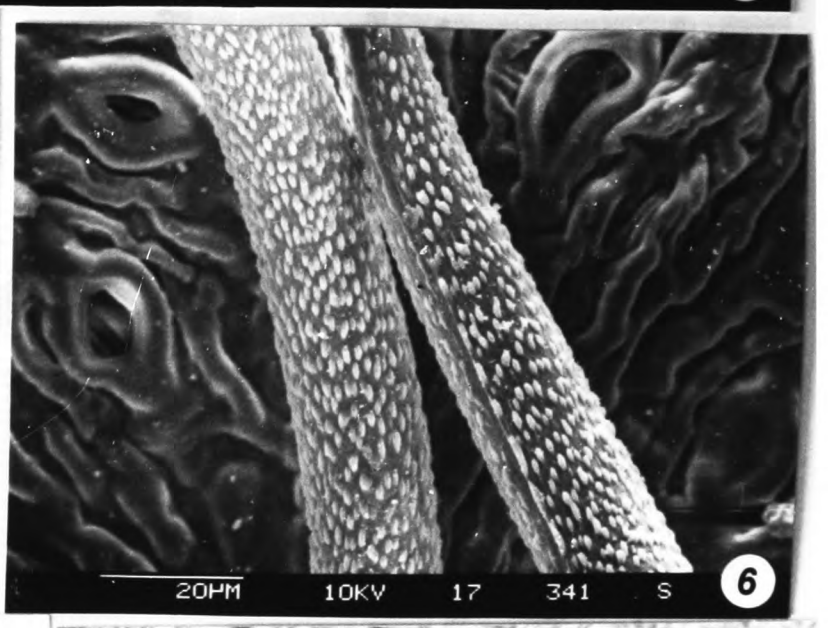
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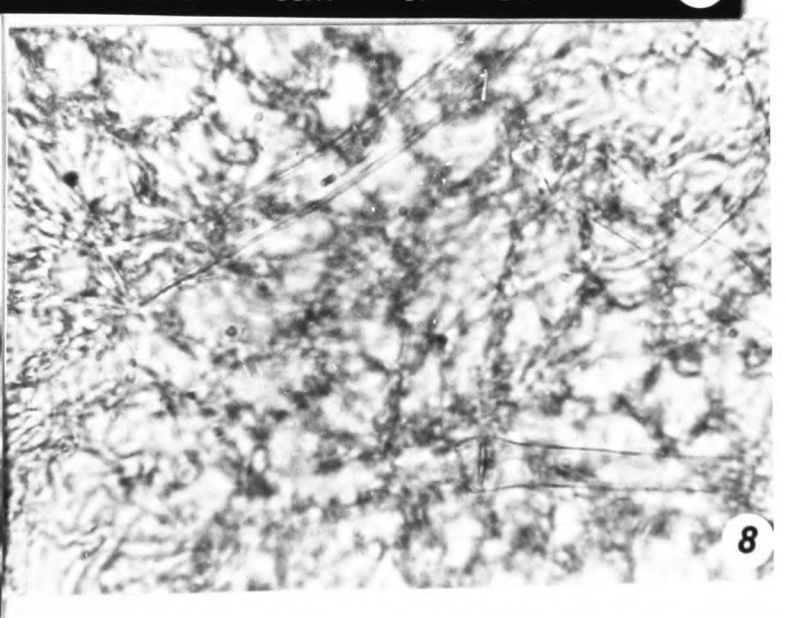
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material and minimal preparation of herbarium material for SEM, were employed to help combat this. The greatest distortion however is likely to be from the initial drying of the leaves to make herbarium specimens. For this reason, the six species available as fresh material were examined at the same time as herbarium specimens of the same species, and in two cases of the same plants. No significant differences were noted in any feature of the leaf surface. At least in the Trichilieae, leaf surface features preserve very well in the herbarium.

Upon examination of the initial range of species from across the tribe, it was found that, with the exception of certain Ekebergia species (see below), the adaxial surface provided no interesting or potentially useful characters. It is simply a smooth surface with venation prominent to varying degrees, and this varies considerably between fresh and herbarium material. It was therefore decided to concentrate the investigation on the abaxial surface for all further specimens.

1. Striae

Striate sculpturing of the cuticle was observed in species of Trichilia, Heynea, Walsura, Cipadessa, Ekebergia and Pseudobersama, but not constantly in any one genus or species. The striae are generally localised in the cuticle immediately above stomatal subsidiary cells and occasionally extend as wings between adjacent stomata. Two basic forms of striae arrangement were observed. In W.pinnata Hassk. and C.baccifera (Roth) Miq. (FIG. 2.2) the striae occur in wings radiating from the outer ledges of the stomatal

FIG. 2.4

1. Two-armed trichome in W.trifoliolata (Simpson 9223; Sri Lanka). SEM.

2. Two-armed trichome in isolated epidermis of W.trifoliolata (Simpson 9223; Sri Lanka). Light-microscopy. Mag.: X 275.

3. Simple prostrate trichome in W.tubulata (Cult. Oxford Botanic Garden). SEM of critical-point-dried fresh material.

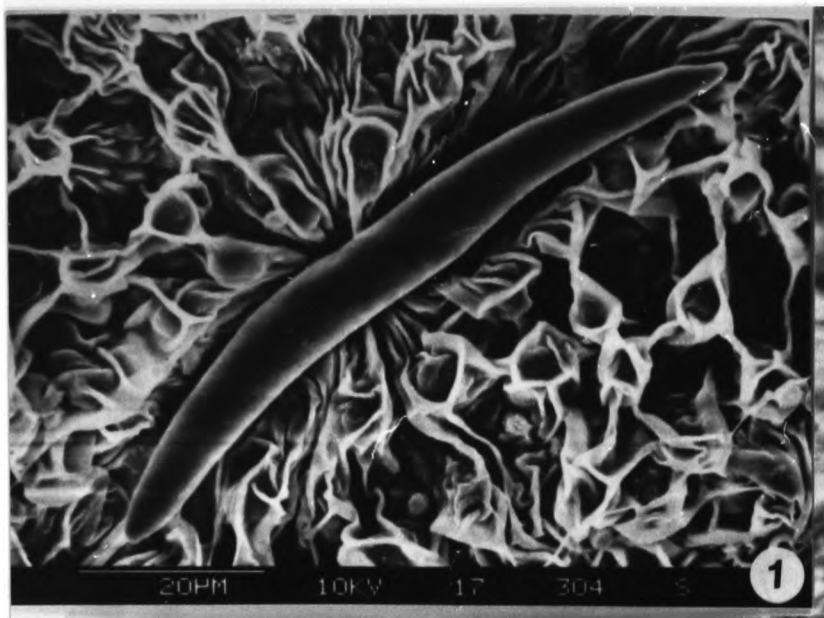
4. Simple prostrate trichome in isolated epidermis of W.tubulata (Cult. Oxford Botanic Garden). Light-microscopy. Mag.: X 575.

5. Low power view of undersurface of leaf in W.chrysogyne (Tan & Wright 27267). SEM.

6. Low power view of isolated epidermis (with trichomes remaining) of W.chrysogyne (Tan & Wright 27267). Light-microscopy. Mag.: X 48.

7. Detail of one trichome in W.chrysogyne (Tan & Wright 27267). SEM.

8. Detail of one trichome in isolated epidermis - to show multicellular construction - in W.chrysogyne (Tan & Wright 27267). Light-microscopy. Mag.: X 250.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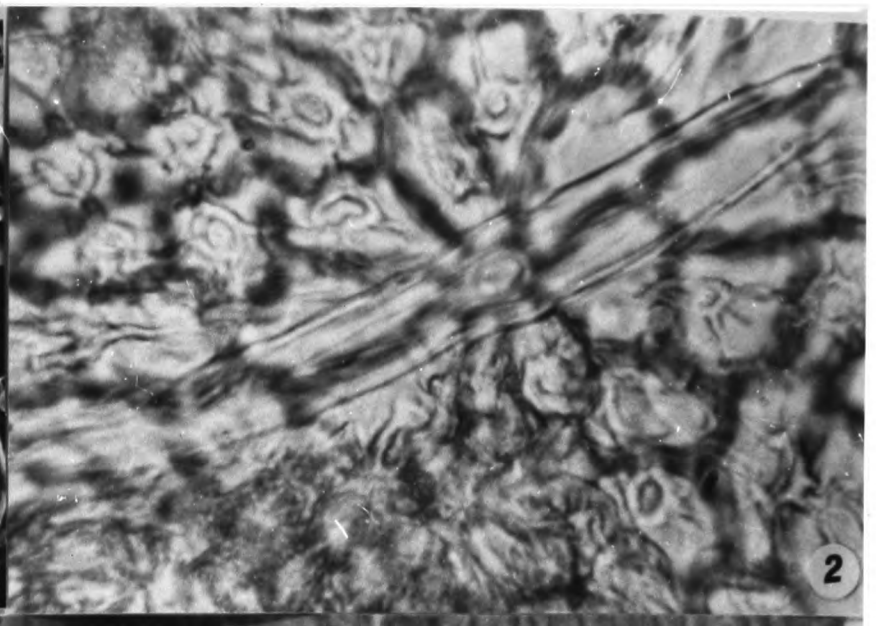
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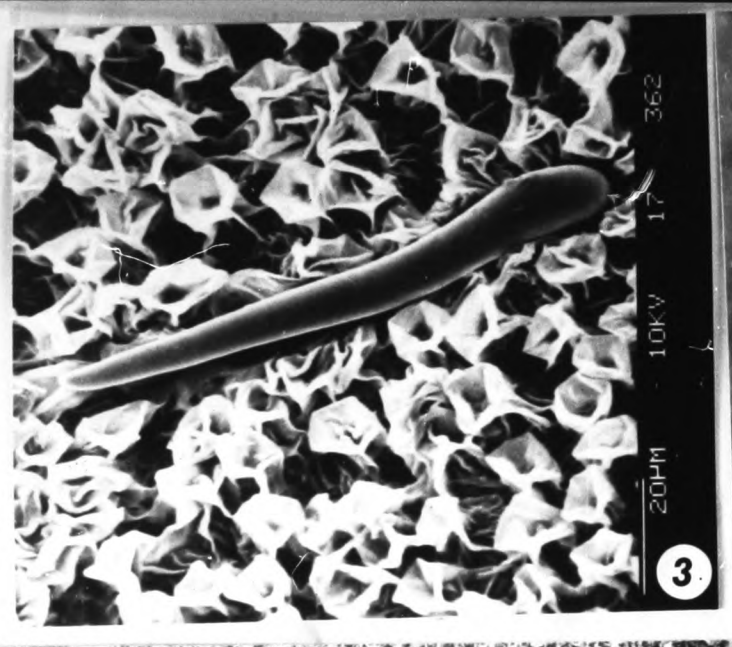
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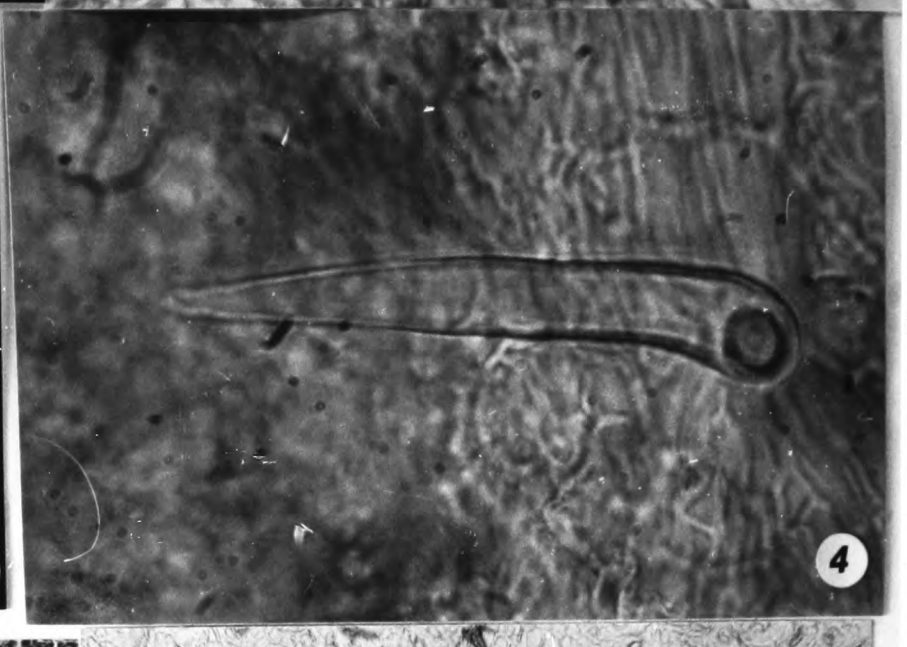
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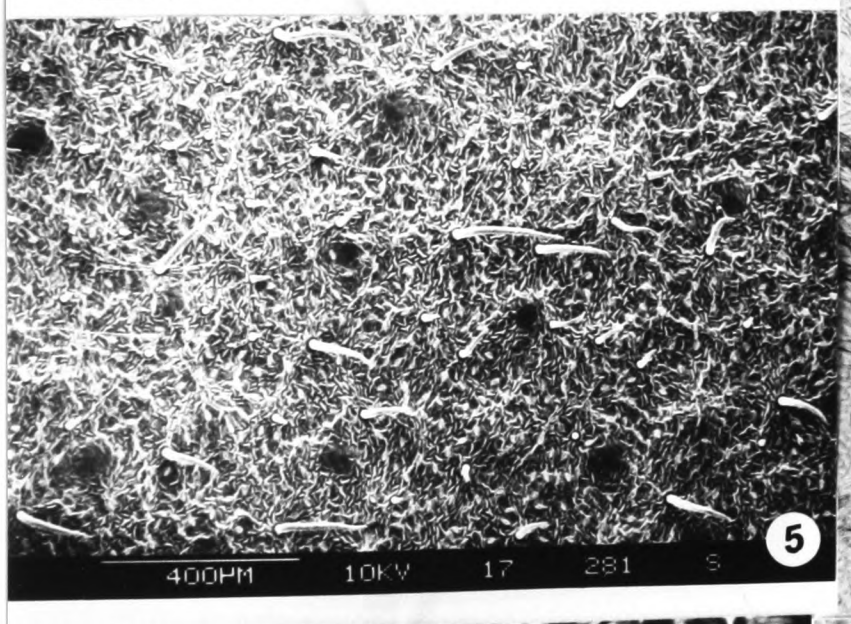
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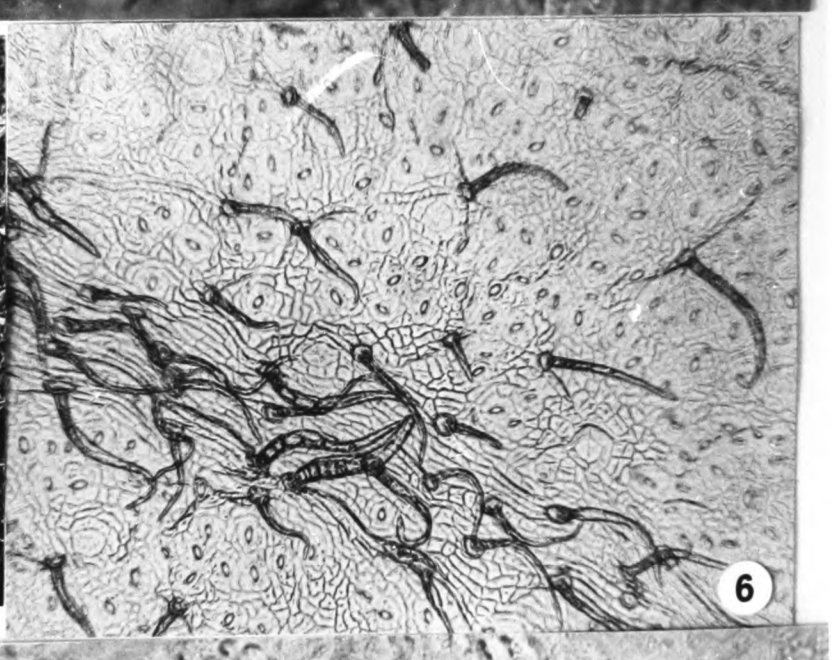
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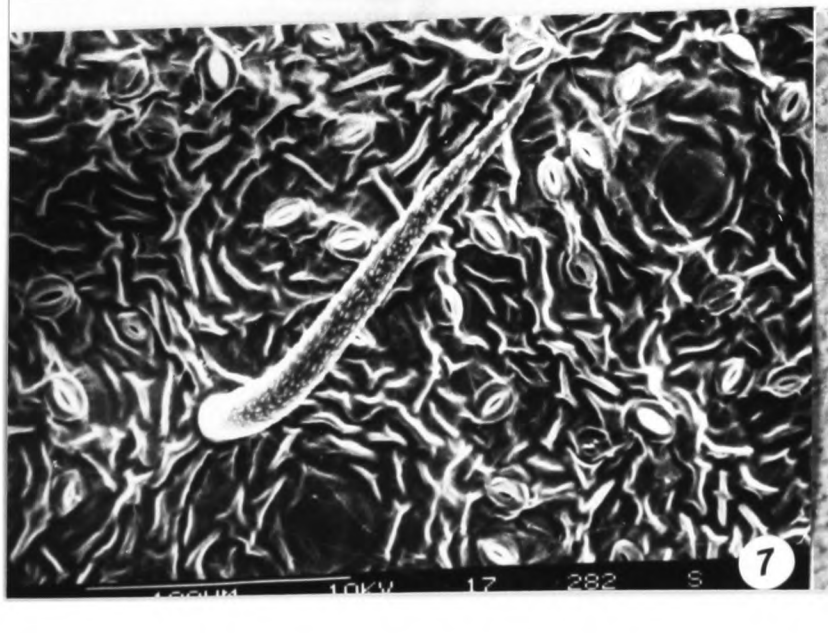
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FIG. 2.5

1. Low power view of undersurface of leaf of L.volkensii (Styles 179; Uganda). SEM.

2. Detail of stellate and simple trichomes in L.volkensii (Styles 179; Uganda). SEM.

3. Simple trichomes in C.baccifera (Cult: Iowa). SEM.

4. Detail of part of trichome in isolated epidermis of C.baccifera (Cult: Iowa). Note cross-cell walls. Light-microscopy. Mag.: X 200.

5. Surface view of one stomate in W.trifoliolata (Simpson 9223; Ceylon). SEM.

6. Surface view of one stomate in T.dregeana (Styles 206; Uganda). SEM.

7. Surface view of one stomate in O.vernicosa (McWhirter 7; Queensland). SEM. Note wax deposits on surface of epidermis.

8. Surface view of one stomate in P.mossambicensis (Sem Sei S1387; Tanzania). SEM.


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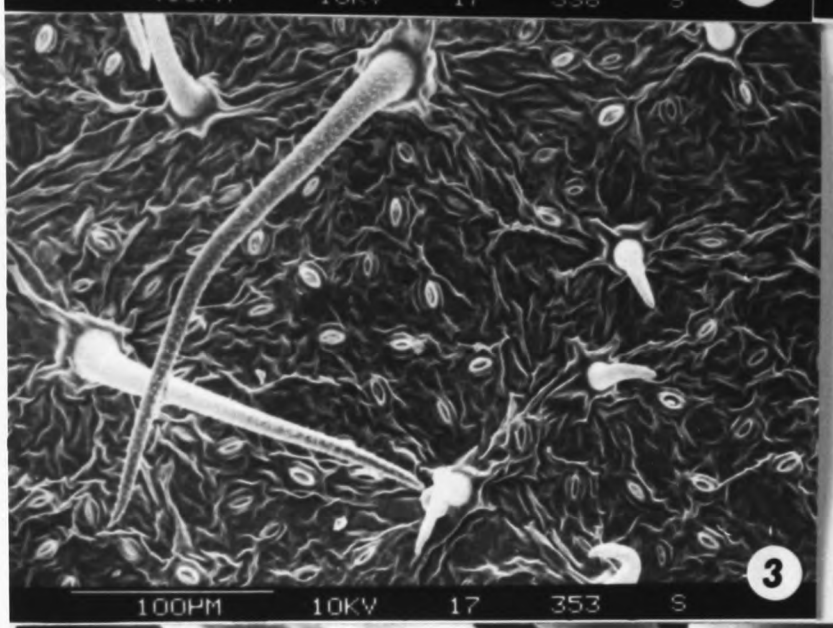
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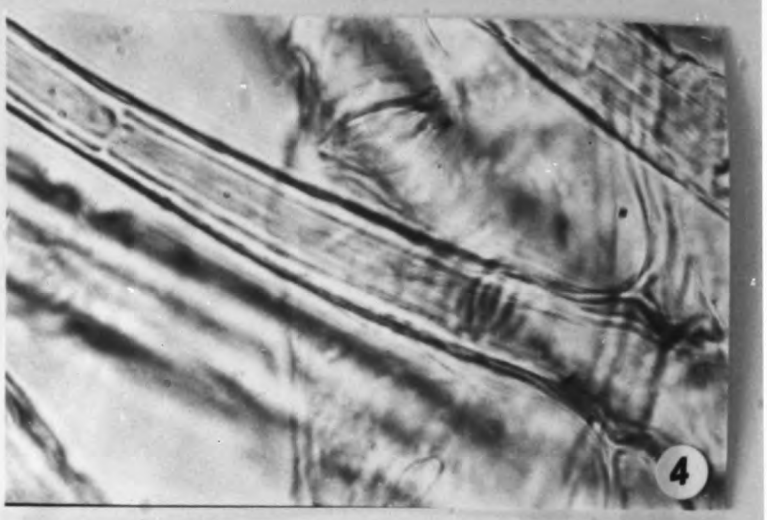
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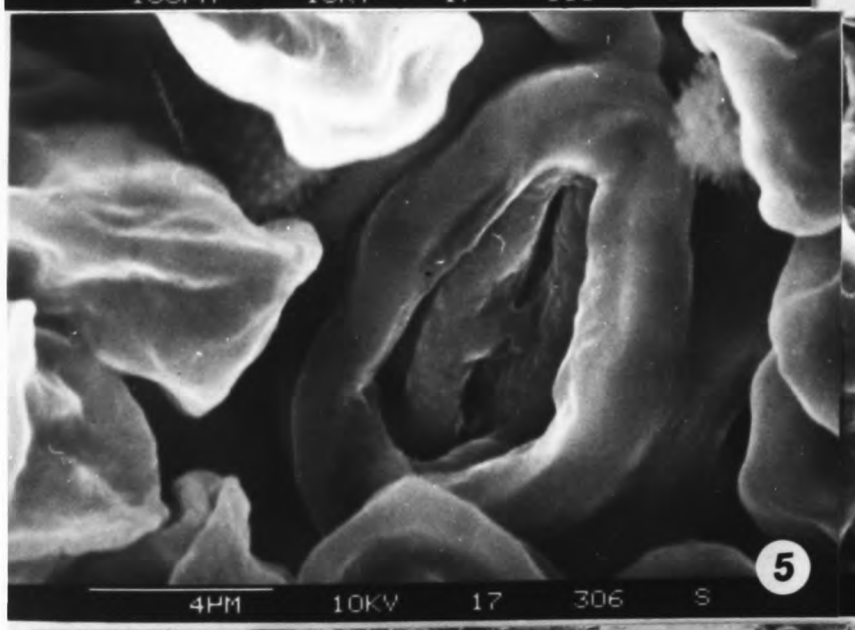
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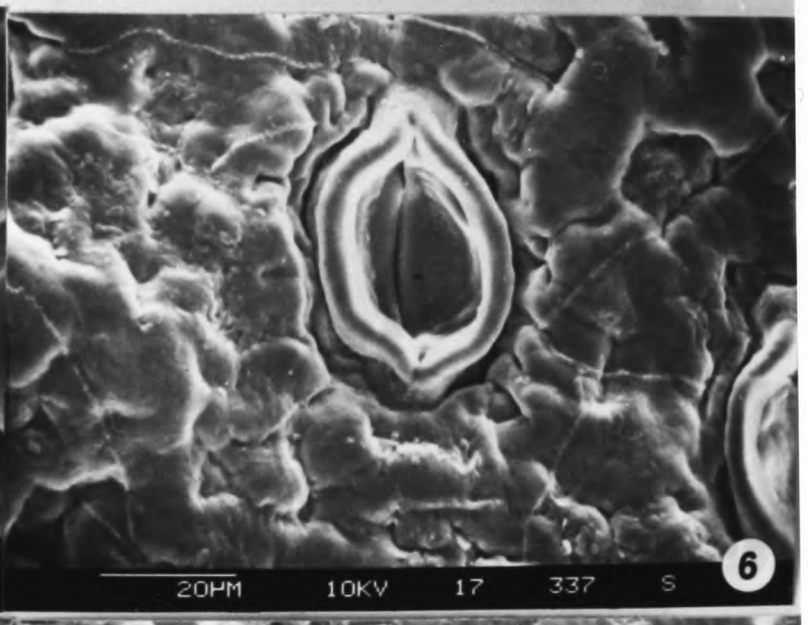
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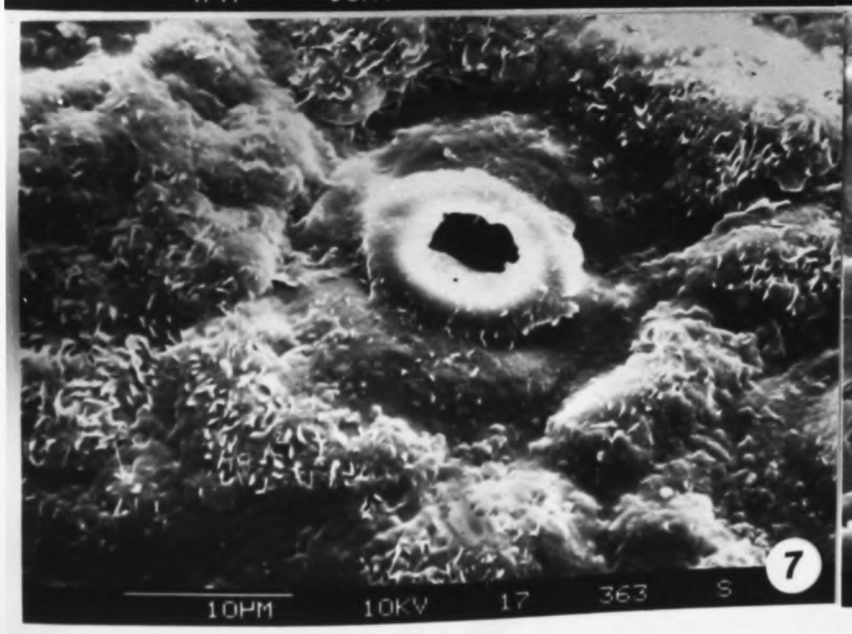
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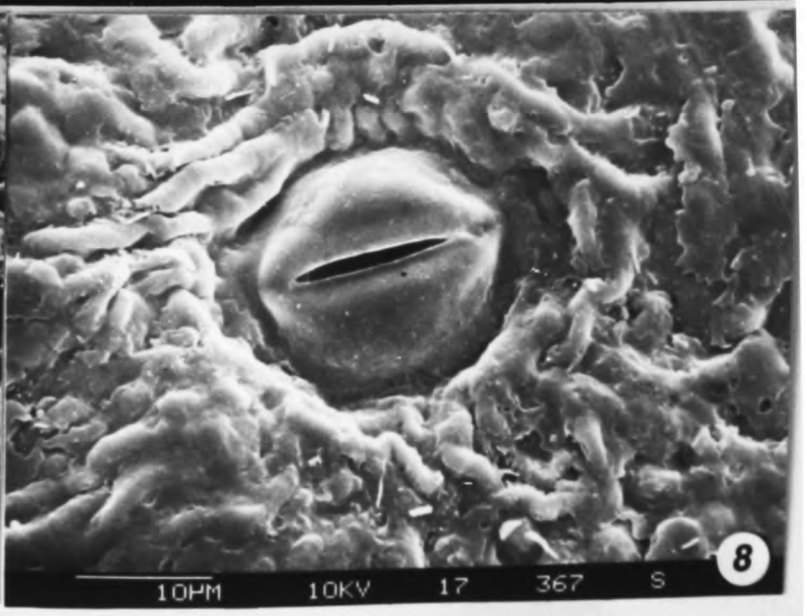
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guard cells. In Ekebergia spp. (FIG. 2.2) they were observed as two to eight concentric rings encircling the guard cell pair. In P.mossambicensis (Sim) Verdcourt (FIG. 2.2) the striae are in one to four concentric rings or radiate from all around the guard cell pair (not as wings), but here the striae are not nearly as pronounced as in the other genera.

Those genera with papillate epidermis (see below) show some difference in cuticular sculpturing on the papillae. In Walsura and Heynea the cuticle is shaped so as to give each papilla a cup-shaped apex (FIG. 2.2). In Ekebergia spp. the papilla has a frilly striate pattern (FIG. 2.3).

2. Papillae

Papillae here are treated as distinct from trichomes. Whilst there is no clear general distinction between papillae and unicellular trichomes (Wilkinson, 1979), it is quite simple, in the Trichilieae, to make a distinction on the basis of height to (basal-) width ratio and also on the basis of cuticular sculpturing. Foliar papillae in the Trichilieae have a height to width ratio of less than 1:2 and have a striate cuticle whereas foliar trichomes have a considerably greater ratio (the lowest being 1:5 in species of Owenia) and a smooth or verrucose cuticle.

Papillae are less widely distributed in the tribe than striae and also show a higher degree of constancy in any one species or genus. The epidermal cells concerned seem to be always mono-papillate but the position of the papilla on/in the cell can be influenced by the position of the cell.

3. Trichomes

These are here classified as distinct from papillae (see above) but nevertheless a wide range of trichome types is found within the tribe. The features of the trichomes in each genus or genus group are here summarised:

(i) Astrotrichilia, Lepidotrichilia, and Pterorhachis:

(FIG. 2.5)

stellate;

multicellular (each arm being one cell);

multi-angulate;

sessile or very shortly stalked;

surface smooth.

The stellate trichomes may have as few as five arms but the greatest number of arms counted was thirty-five in a specimen of P.zenkeri (Oxford Botanic Garden cultivated). Very occasionally, simple unicellular trichomes (of the type found in Malleastrum etc. below) are seen amongst the stellates, but when they occur they are very sparse. L.volkensii often has trichomes on the adaxial leaf surface also.

(ii) Malleastrum, Pseudobersama, Ekebergia, Trichilia and Heynea:

(FIG. 2.3)

simple;

unicellular;

erect to decumbent;

surface verrucose.

In a few species of New World Trichilia, stellate hairs of the above type are found and in a few other species (of sect. Moschoxylum) 2-armed trichomes (of the sort found in certain Walsura spp.) occur, but in all other members of the genus, the trichomes fall into the present group (see Pennington, 1981). Adaxial surface trichomes also seem common in E.senegalensis and E.benguelensis.

(iii) Cipadessa:

(FIG. 2.5)

simple;

usually unicellular but 2- and 3- celled trichomes are occasionally seen;

N.B. These trichomes (and those of Walsura spp., below) are considered multicellullar (and not merely septate) since the transverse wall is clearly an extension of the exterior cell wall, whether the cell boundaries are visible at the surface of the trichome or not.

+/- erect;

surface verrucose.

(iv) Walsura chrysogyne:

(FIG. 2.4)

simple;

multicellular;

FIG. 2.6

1. Low-power view of undersurface of leaf in O.vernicosa (Symon 7172; Queensland). SEM.

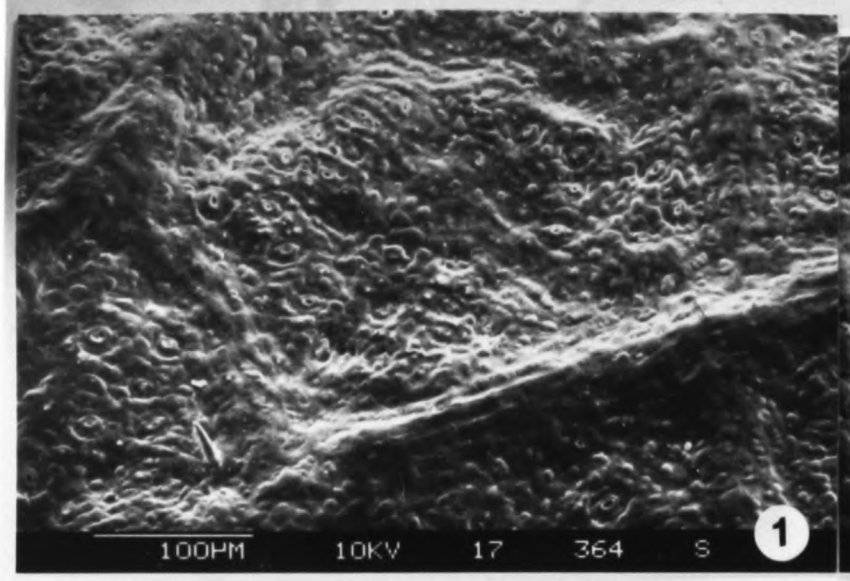
2. Undersurface of leaf in O.acidula (McWhirter 10; Queensland). SEM.

3. Low-power view of undersuface of leaf in O.reticulata (Symon 6898). SEM.

4. Detail of leaf surface in O.reticulata. Note globular wax deposits. (Symon 6898). SEM.

5. Undersurface of leaf in W.trichostemon, showing several two-armed trichome hairs and one glandular body. (Ohn Shwe 5037; Burma). SEM.

6. Detail of glandular body. (Ohn Shwe 5037; Burma). SEM.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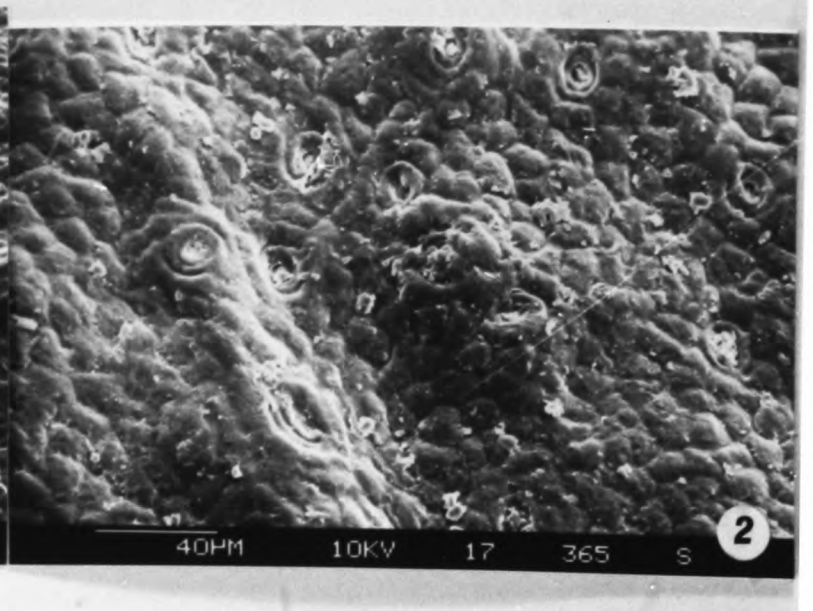
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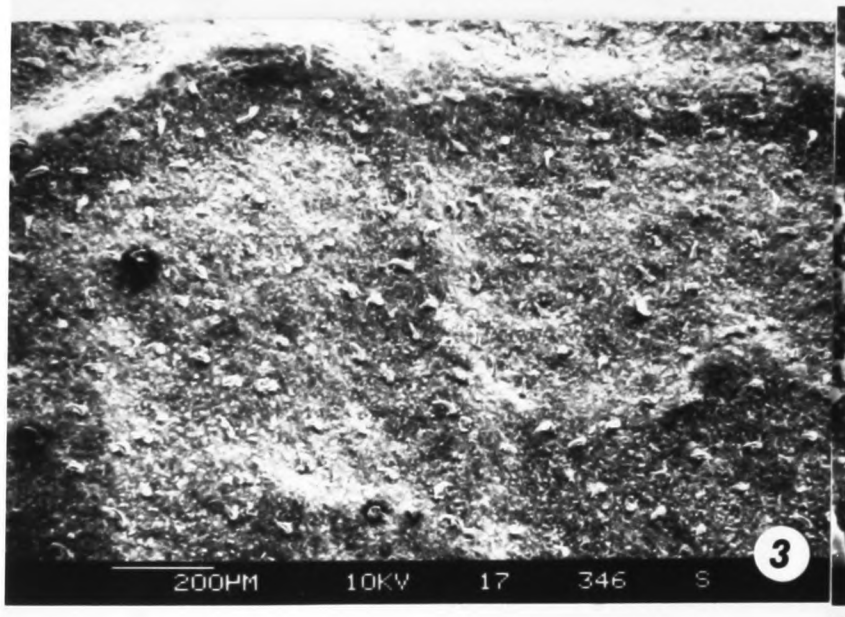
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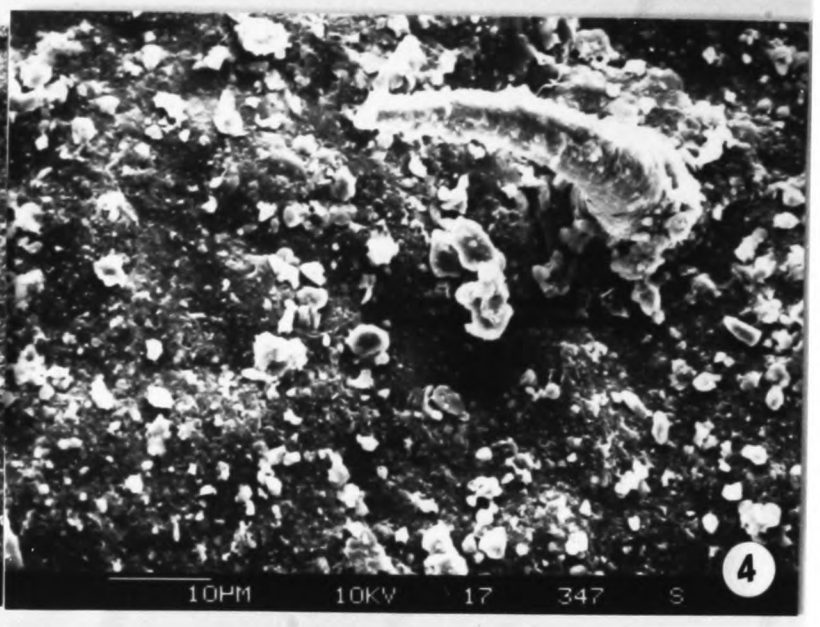
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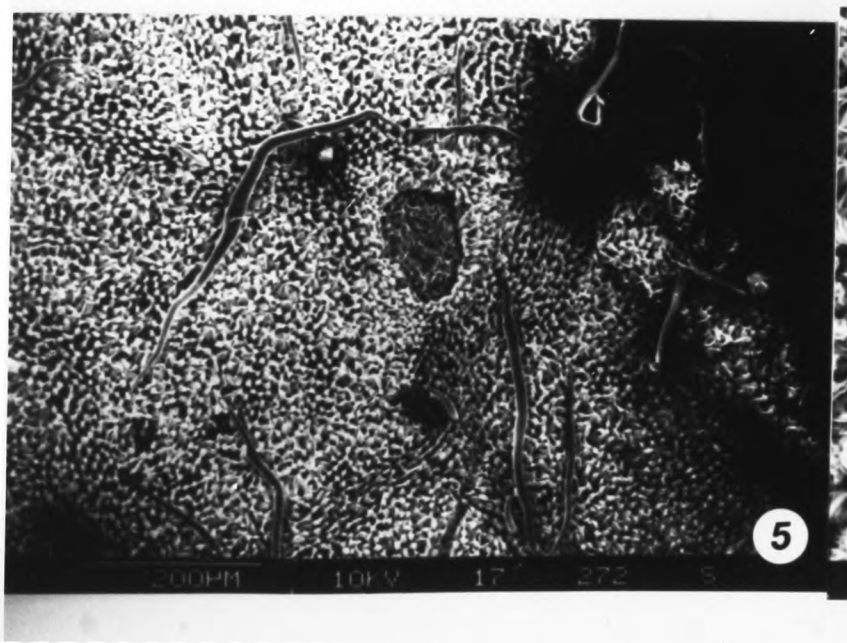
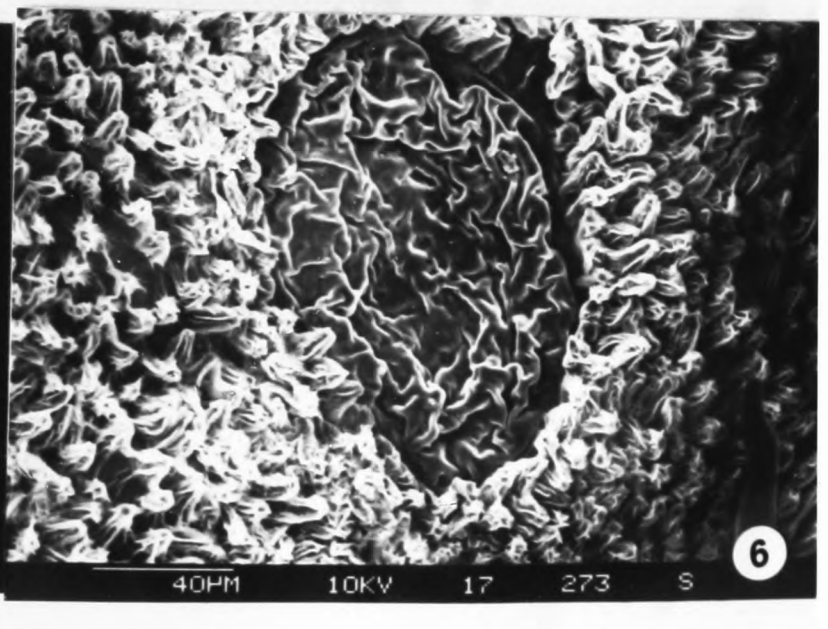

200µM 10KV 17 272 S
5


40µM 10KV 17 273 S
6

+/- erect;

surface verrucose.

Very occasionally, the trichomes are aggregated to form compound stellates which are very fragile at the base and are easily broken off.

(v) Walsura (excl. W.chrysogyne):

(FIG. 2.4)

simple or (in W.trifoliolata (Adr.Juss.) Harms, W.trichostemon Miq. and W.gardneri Thw.) 2- or (rarely) 3-armed trichomes mixed with the simple ones;

unicellular (all types);

N.B. The trichomes have been investigated in various planes and no transverse walls have been observed in the 'stalk' or 'arm' parts.

prostrate to procumbent;

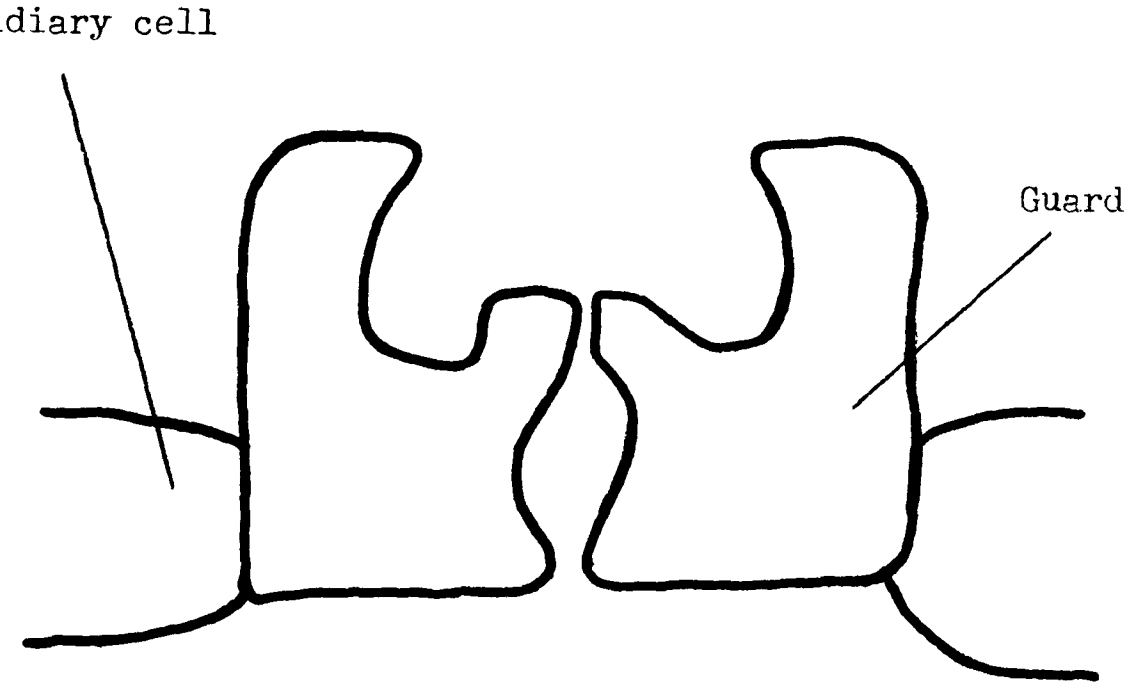
surface smooth or sparsely verrucose.

(vi) Owenia:

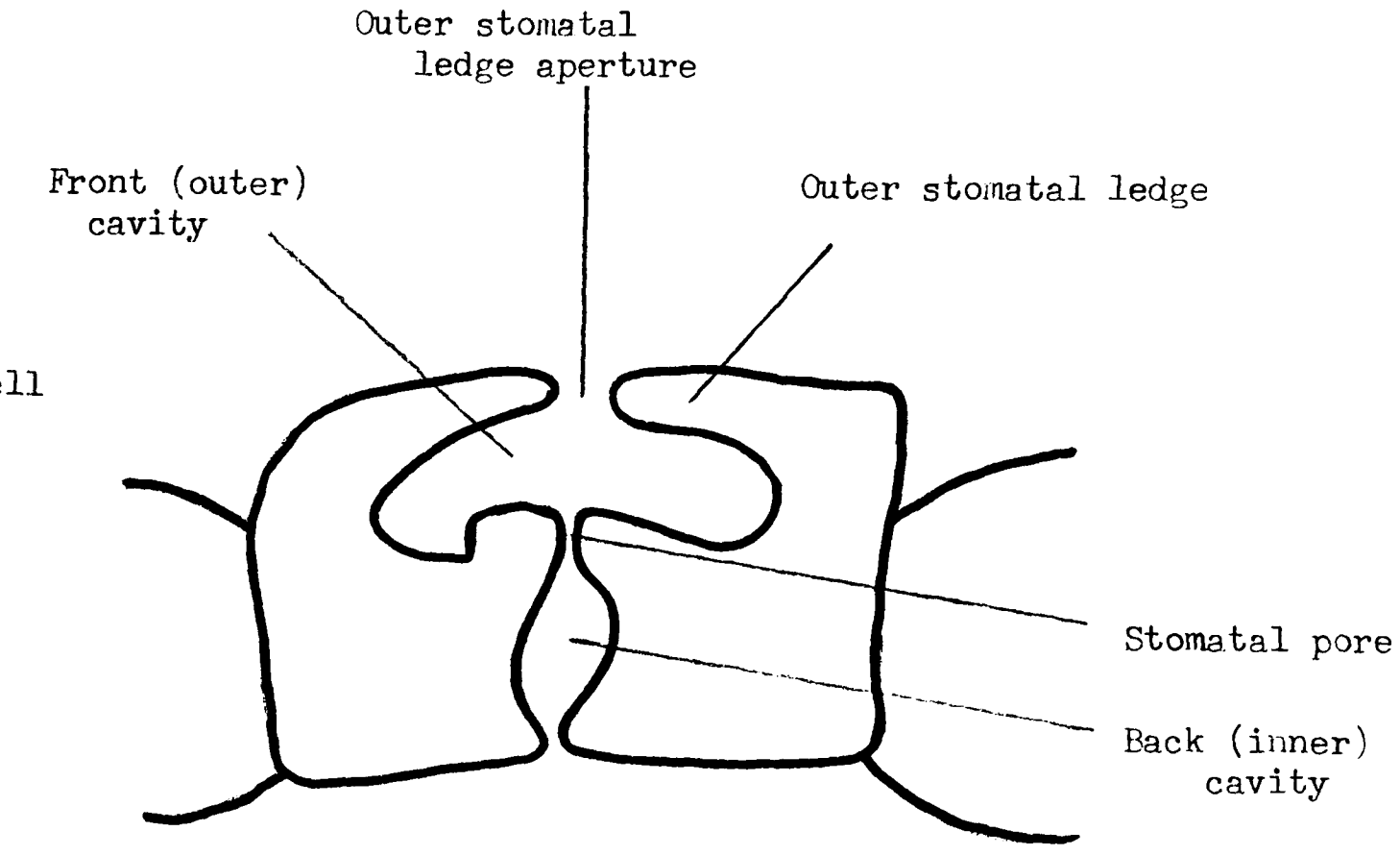
(FIG. 2.6)

Trichomes in this genus are sparse or absent (in any one species). If present they are very short, being c. 50 um long cf. an average T.emetica Vahl trichome of 500 um length, and are erect to decumbent and more or less smooth.

FIG. 2.8 THE TWO EXTREMES OF STOMATAL TYPE FOUND IN THE TRICHILIEAE



Erect outer stomatal ledge type.



Horizontal outer stomatal ledge type.

Apart from presence or absence of verrucose sculpturing, density and direction of patterning (e.g. random or in longitudinal or spiral lines) varies considerably within each species or genus. Throughout the tribe, where verrucae occur they are usually longitudinally elongate on the trichome.

4. Stomatal apparatus

The stomatal apparatus is taken to include the subsidiary cells. For explanation of terms see Wilkinson (1979) and FIG. 2.8. The stomata found in this tribe range between:-

(i) Those found in Walsura, Heynea, Cipadessa, Ekebergia and some species of Trichilia with erect outer stomatal ledges and usually wide outer stomatal ledge apertures. (FIG. 2.5)

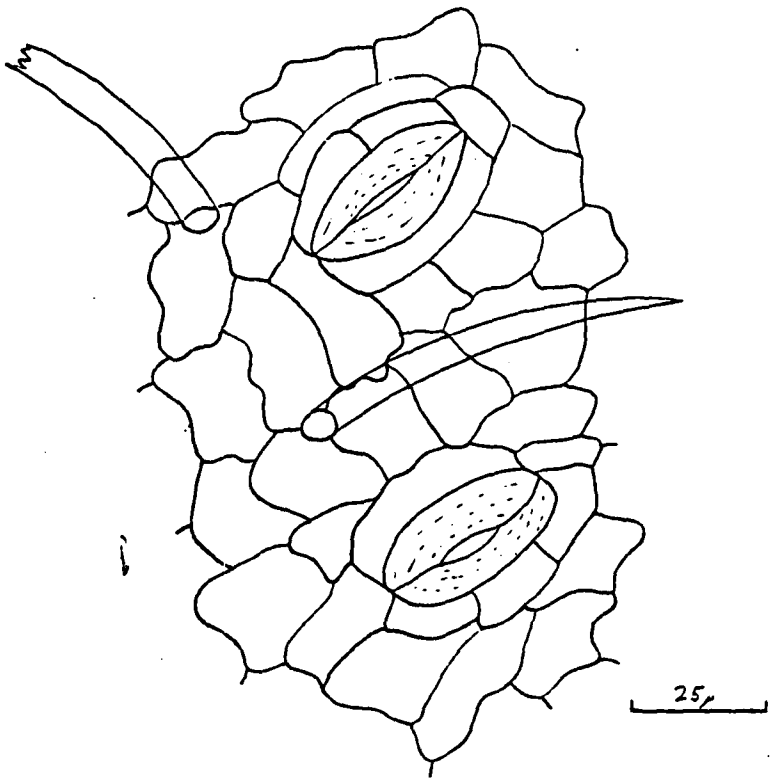
and

(ii) Those found in Owenia, Malleastrum and Pseudobersama with more or less horizontal outer stomatal ledges and usually narrow outer stomatal ledge apertures. (FIG. 2.5)

The former tend to have the outer stomatal aperture raised higher above the surrounding cells (excluding papillae) than the latter.

Congo.
Liben 3343.

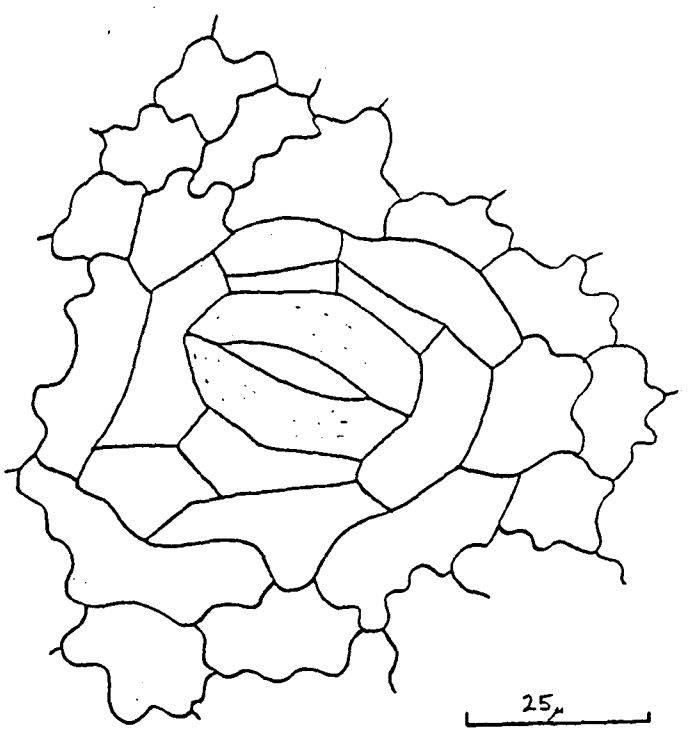
Trichilia welwitschii
C.DC.



A

Natal.
Ross 1270.

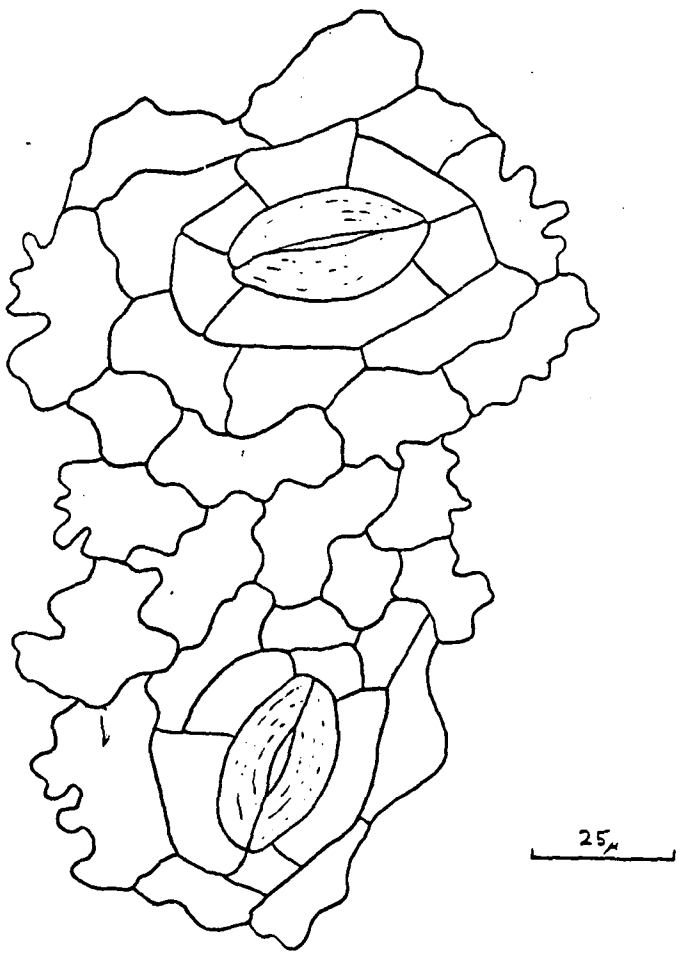
Trichilia dregeana
Sonder



B

Fresh Mat. - Wytham
BTS/FW

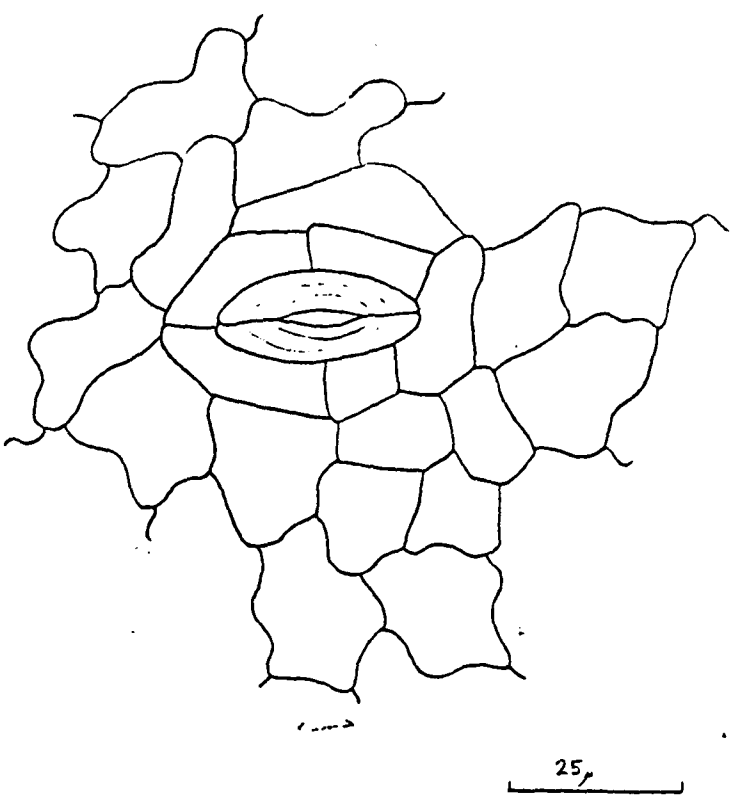
Trichilia emetica
Vahl.



C

Ivory Coast.
De Wilde 751.

Trichilia monadelpha
(Thonn) J.J. De Wilde

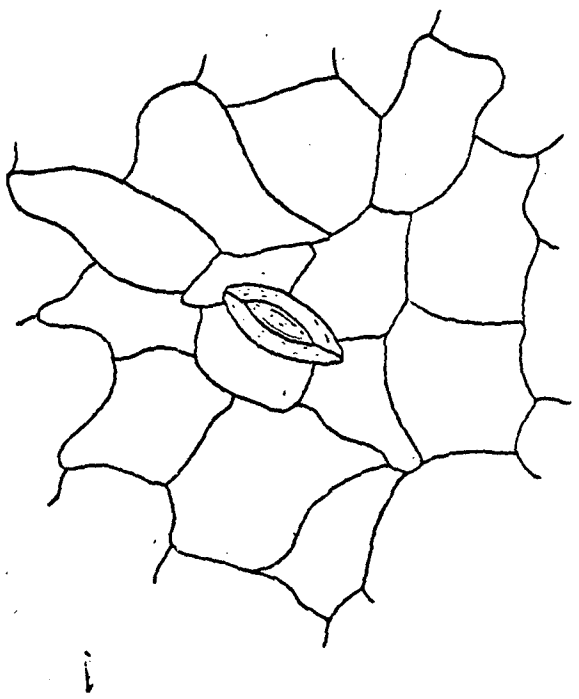


D

FIG: 2.9 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

Costa Rica
Hartshorn 1395.

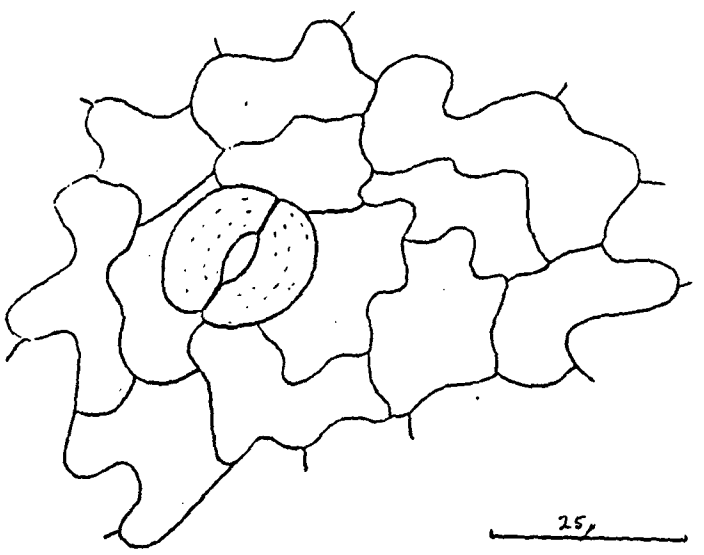
Trichilia glabra
L.



A

Uganda.
Styles 14.

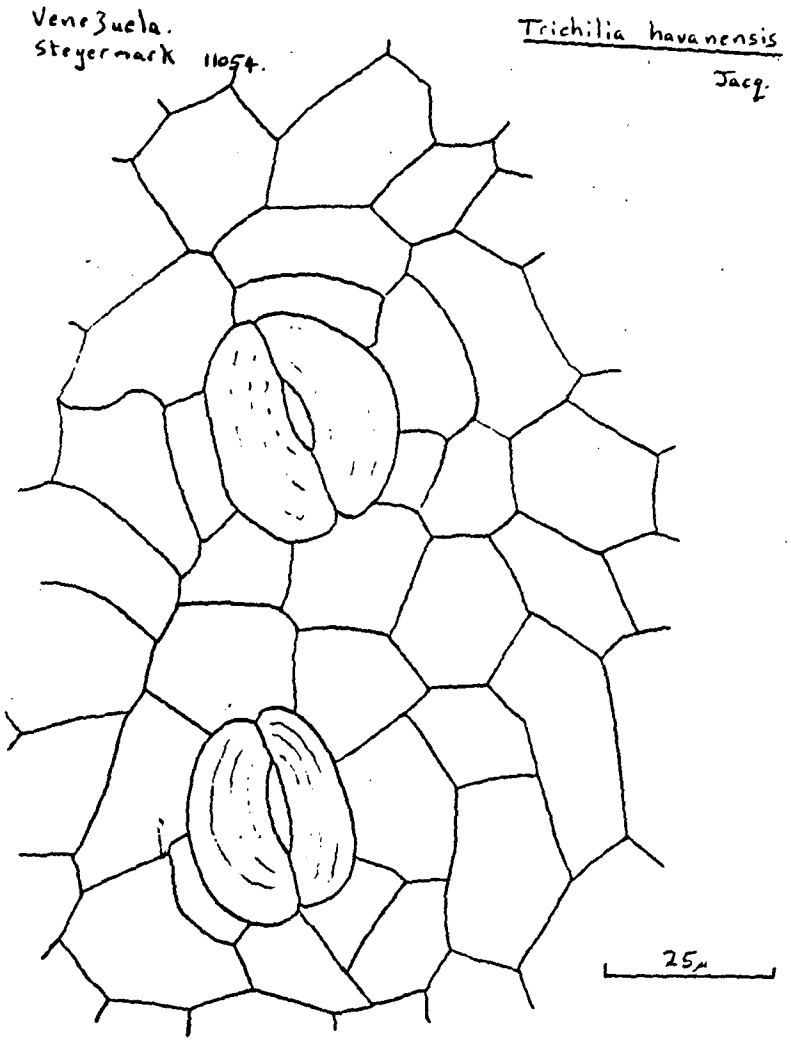
Trichilia prieuriana
A.Gr. Juss



B

Venezuela.
Steyermark 110544.

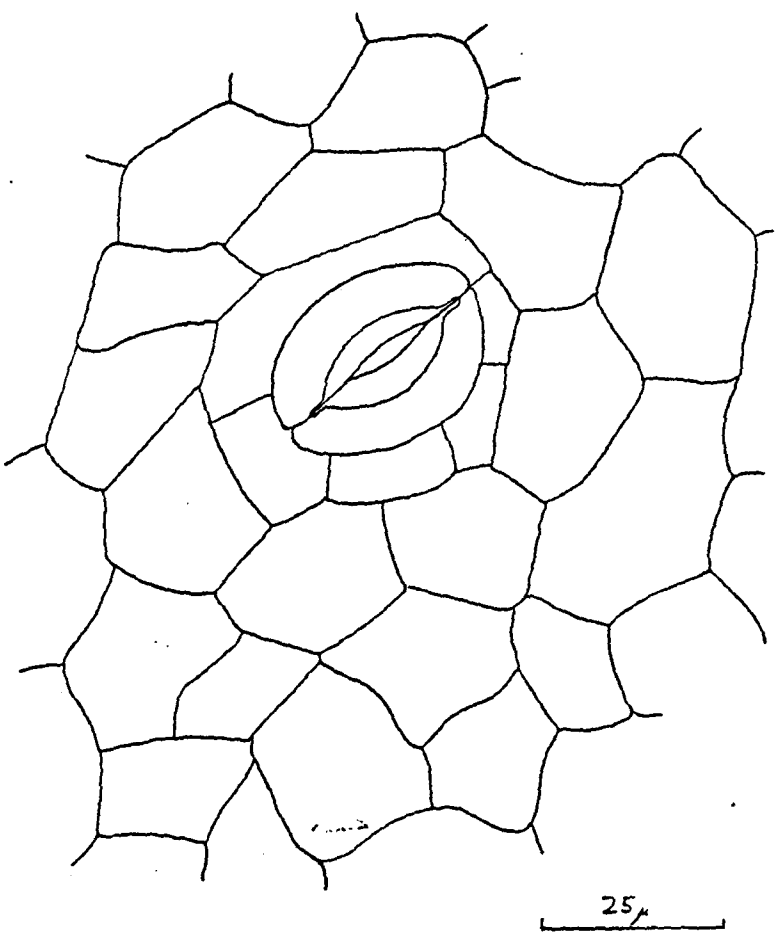
Trichilia havanensis
Jacq.



C

Brazil.
Prance + Silva 58256.

Trichilia pallida
Sw.

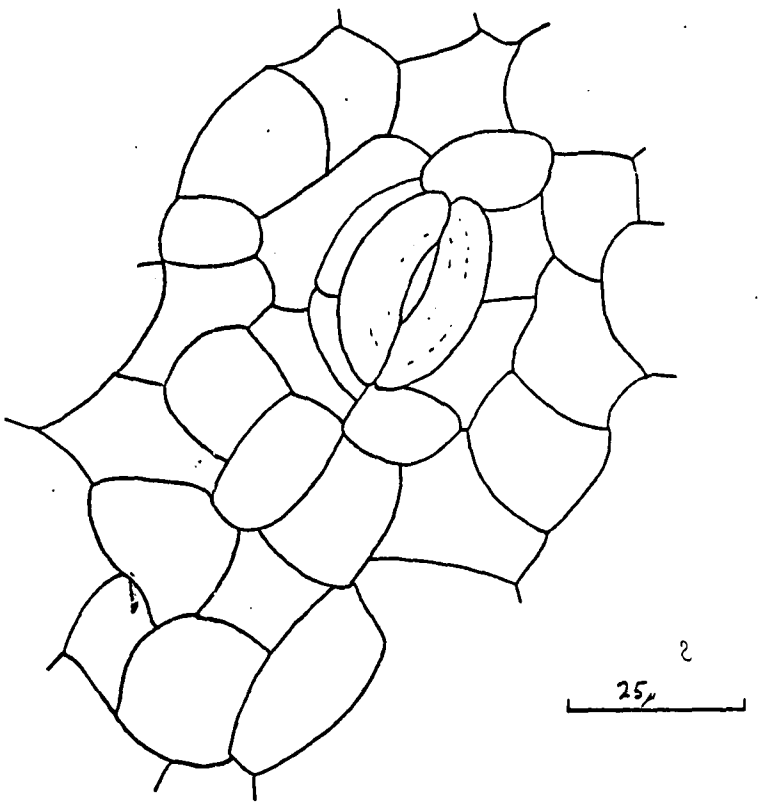


D

FIG: 2.10 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

Aldabra.
Woodell 7403.

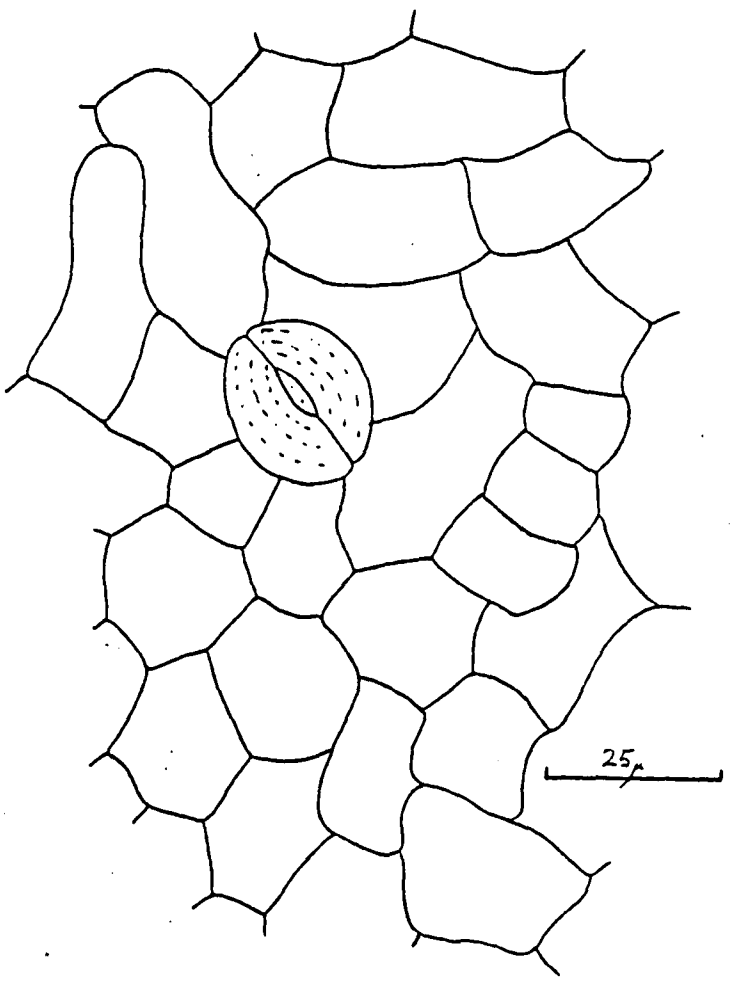
Malleastrum sp.



A

Madagascar.
Mabberley 825.

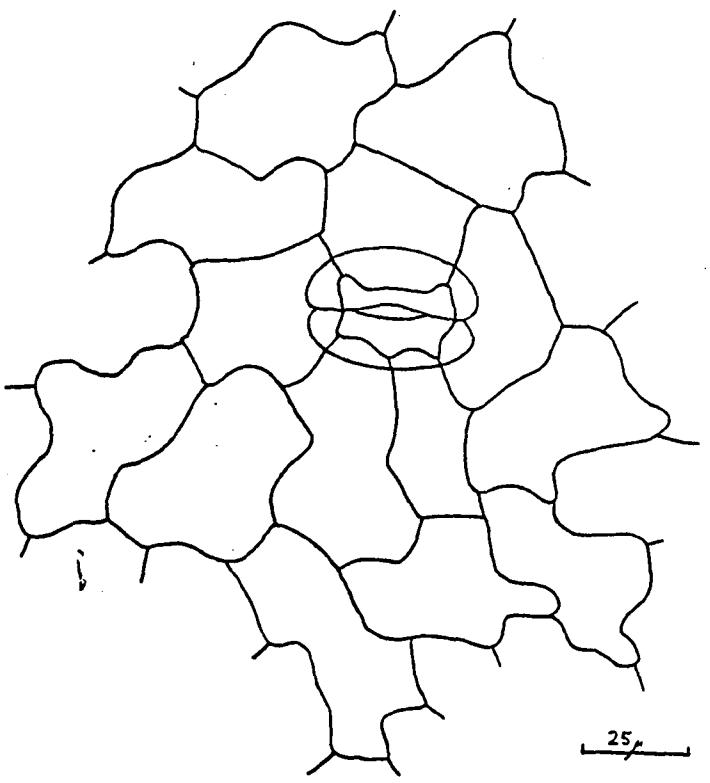
Astrotrichilia sp.



B

Fresh Mat.
Oxford Botanic Gardens.

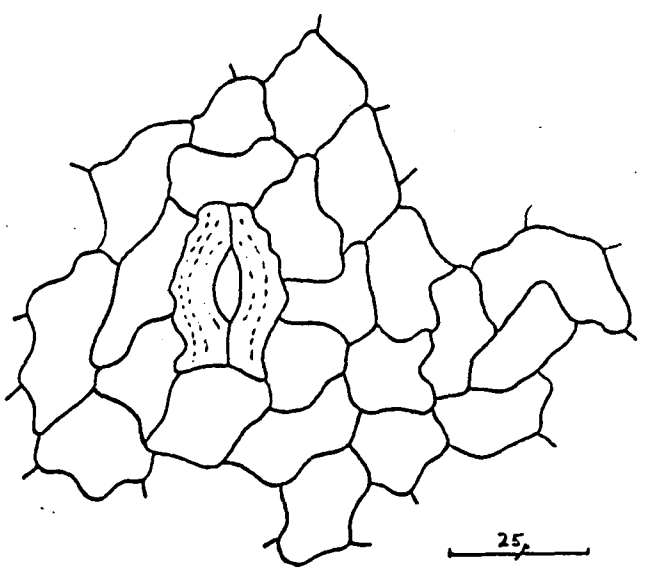
Pterorhachis Zenkeri Harms



C

Congo.
Gurtzwiller 3629.

Lepidotrichilia volkensii (Gürke) J.F.Leroy.

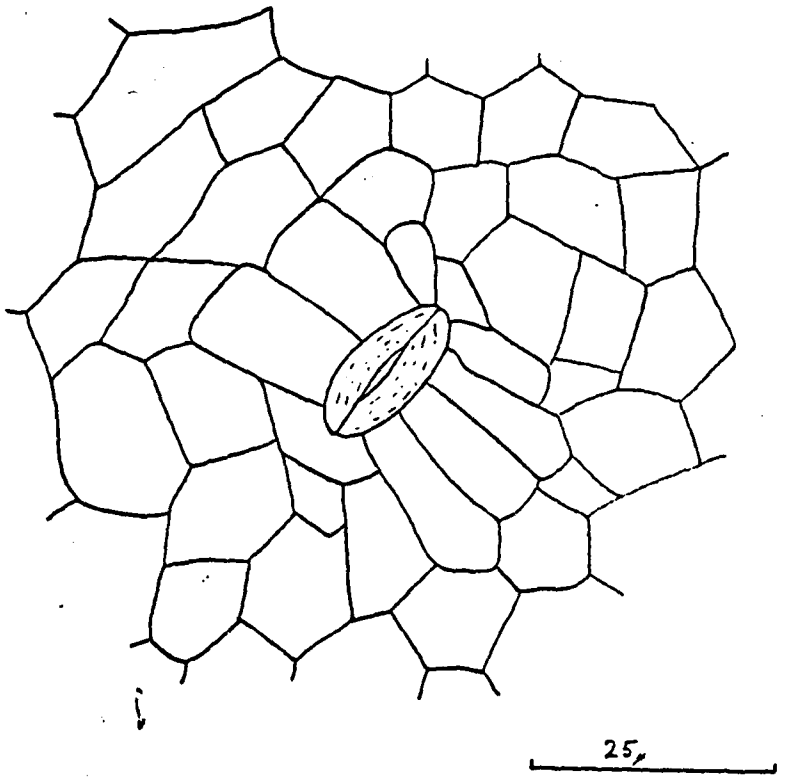


D

FIG: 2.11 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

Sarawak.
Luang 21733.

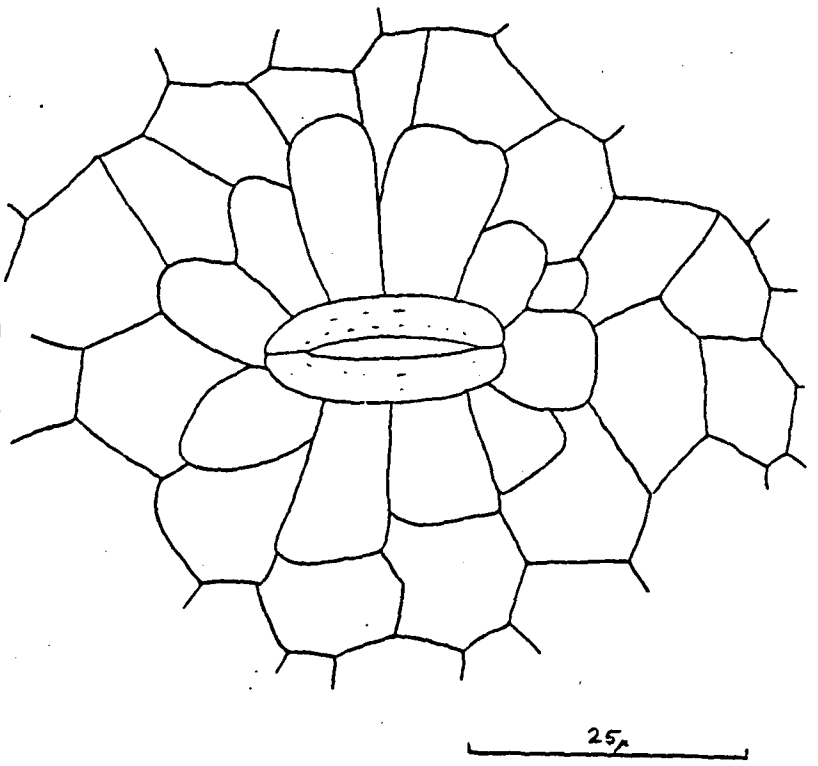
Walsura pinnata
Hassk.



A

Sabah.
Hey et al 61654.

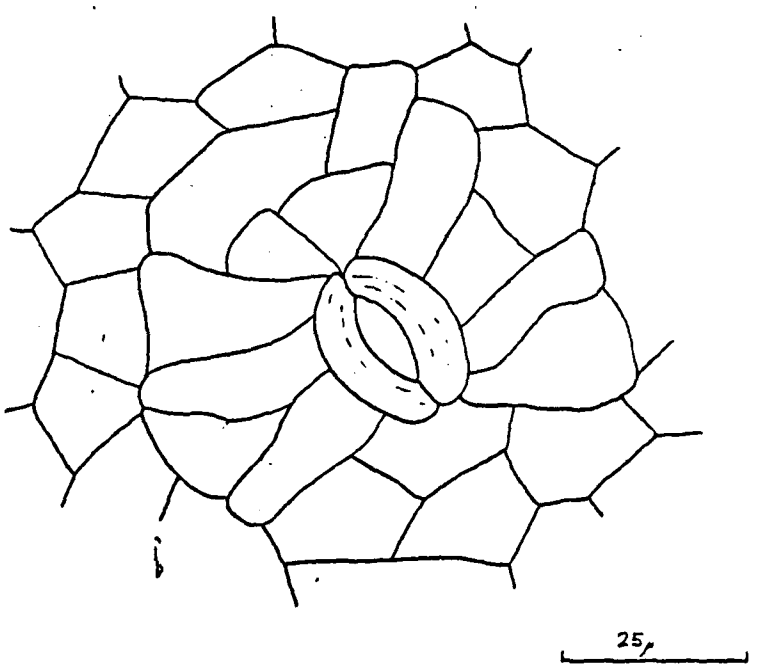
Walsura pinnata
Hassk.



B

Sabah.
Fedelis 88314.

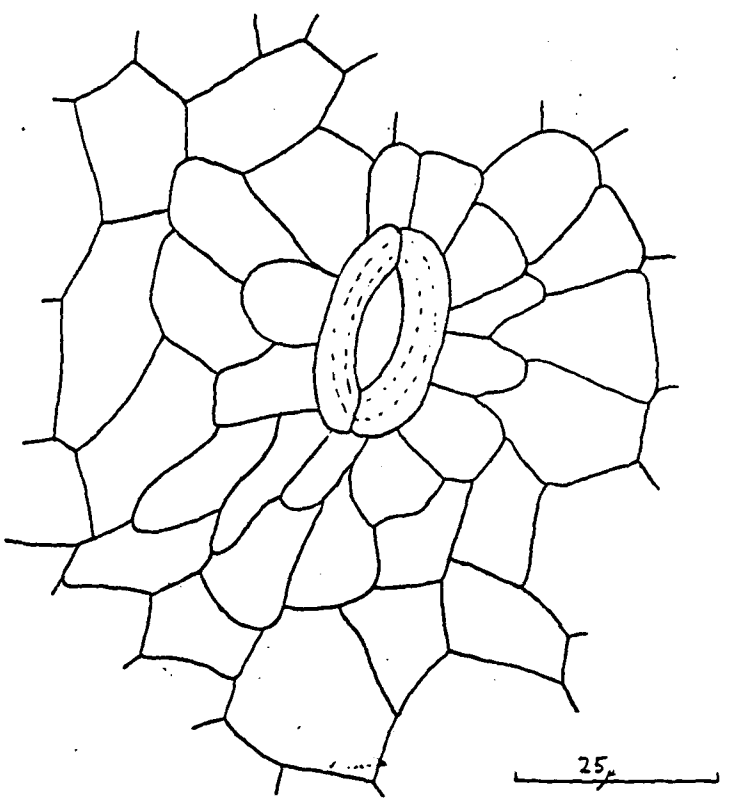
Heynea trijuga
Roxb. ex Sims



C

Thailand.
Saradet 427.

Heynea connaroides W+A.

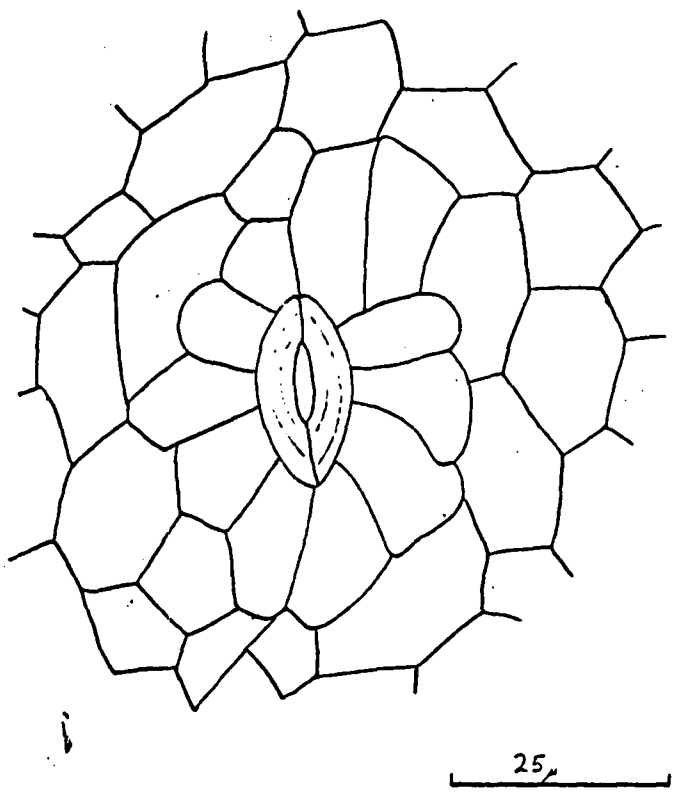


D

FIG: 2.12 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

Fresh mat.
Oxford Botanic Garden.

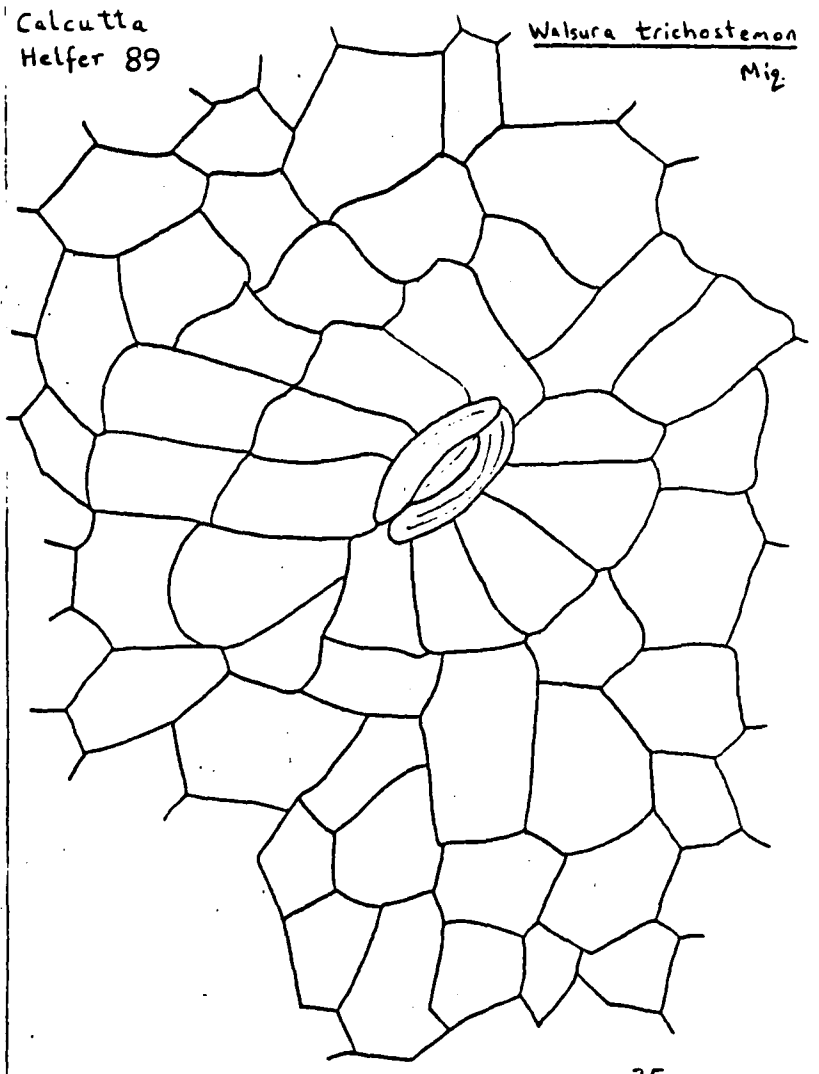
Walsura tubulata
Hiern.



A

Calcutta
Helfer 89

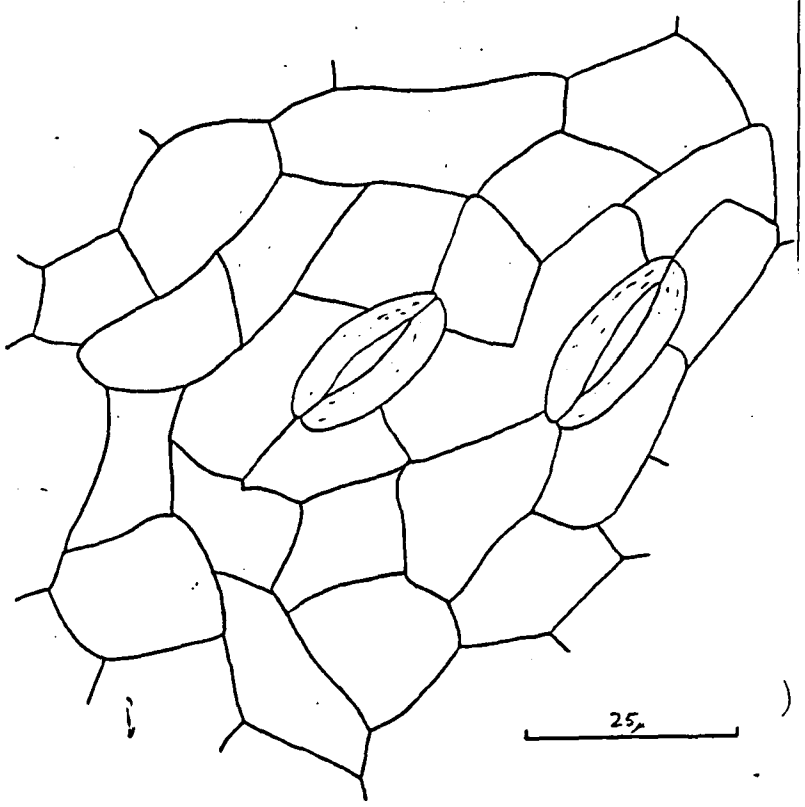
Walsura trichostemon
Miq.



B

Iowa (cult).

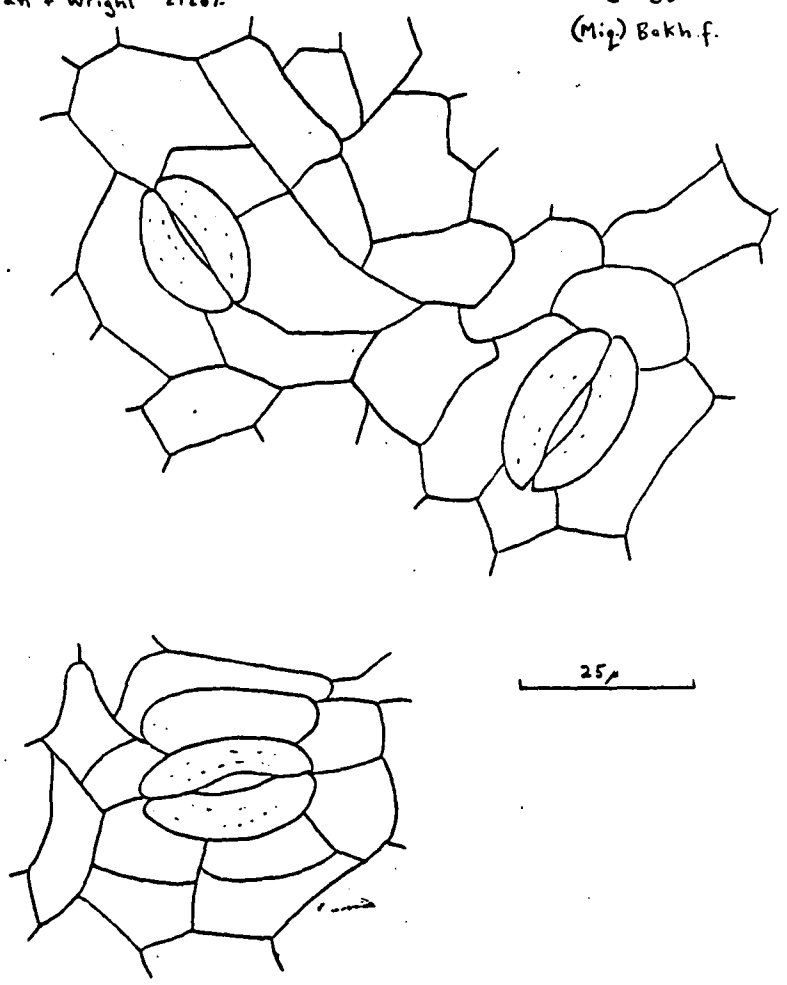
Cipadessa baccifera
(Roth) Miq.



C

Sarawak.
Tan + Wright 27267.

Walsura chrysogyne
(Miq.) Bakh.f.



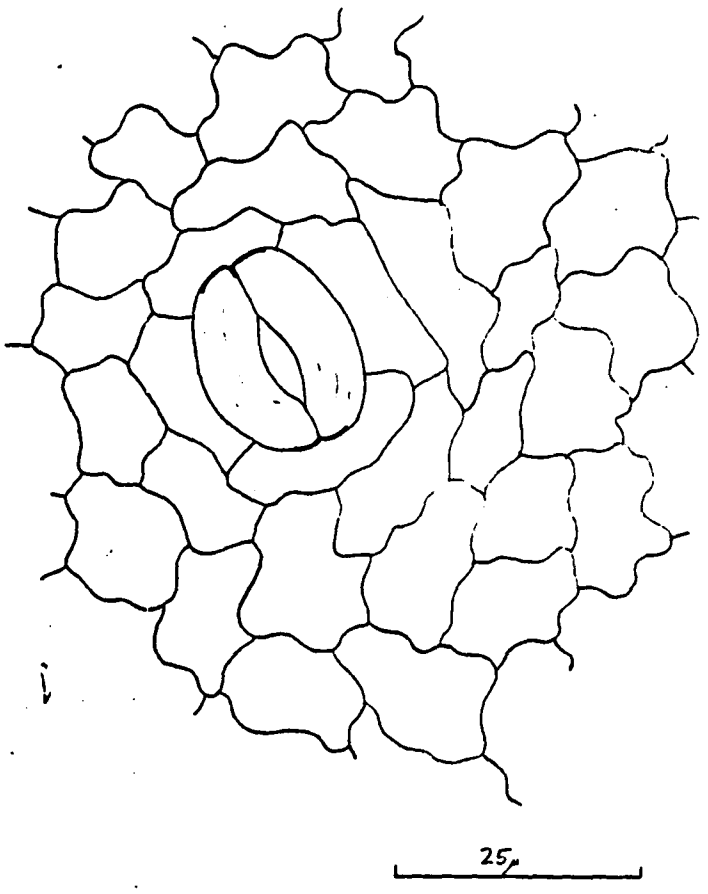
♀ tree.

D

FIG: 2.13 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

Tanzania.
Sem Sei S 1387.

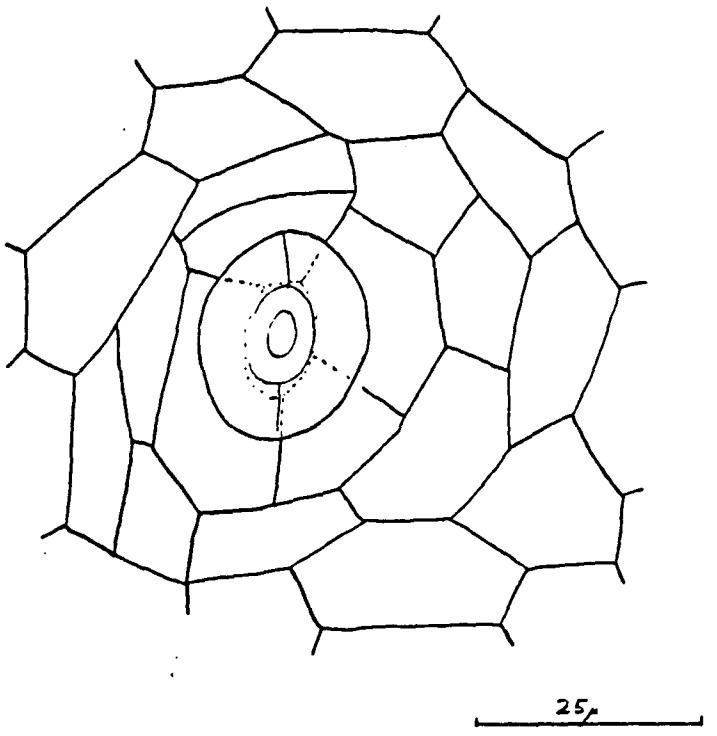
Pseudobersama mossambicensis
(Sim) Verdcourt.



A

Queensland.
Mc Whirter 7.

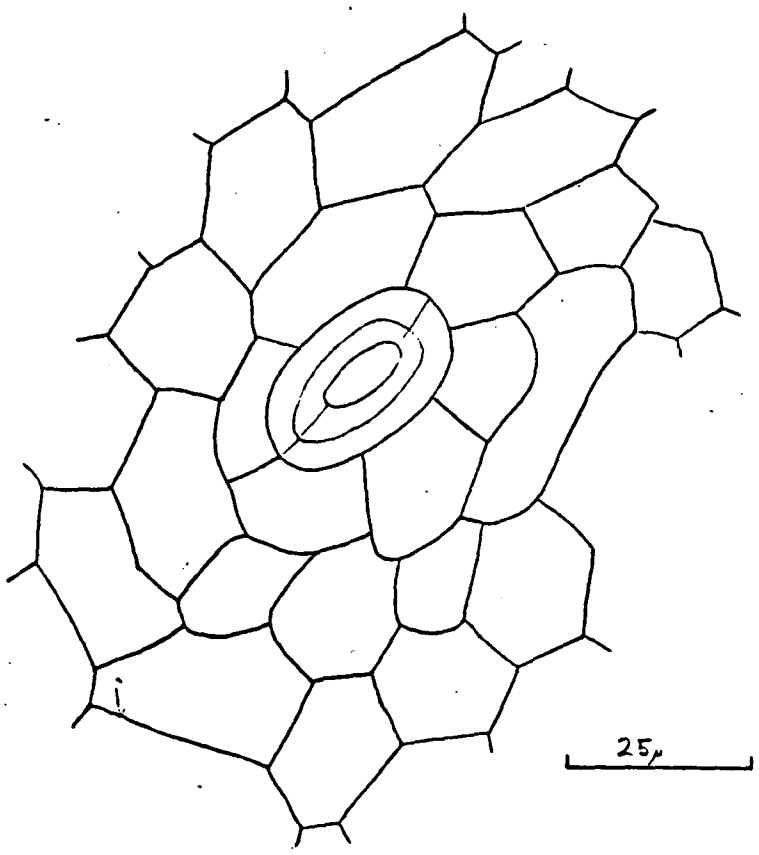
Owenia venosa
F. Muell.



B

Uganda
Styles 294.

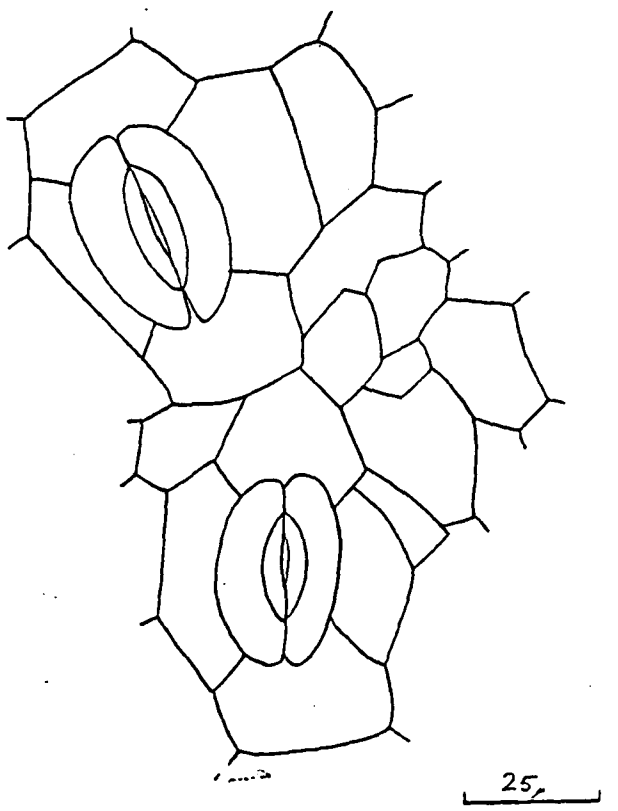
Ekebergia capensis
Sparrm.



C

Fresh mat. – Wytham.
BTS/FW 523

Ekebergia capensis Sparrm.



D

FIG: 2.14 STOMATAL SUBSIDIARY CELL ARRANGEMENTS

All other species and genera fall somewhere in between these two extremes and within Trichilia practically the whole range between the two extremes can be observed. Those species of Walsura (excluding W.chrysogyne et al., see Chapter 6) and Heynea are always of the erect outer stomatal ledge type.

Subsidiary cell arrangement was also investigated (FIGS. 2.9-2.14). Walsura (excl. W.chrysogyne et al.) and Heynea were found to differ from all other genera with their actinocytic (sensu Stace, 1965) arrangement and W.chrysogyne differed in its paracytic arrangement. All other genera are anomocytic, or sometimes approaching paracytic.

One other interesting feature, noted only in Pseudobersama, is the presence of very thin T-pieces, i.e. thickenings of the cell wall at the stomatal poles (FIG. 2.14).

5. Epicuticular wax

In the tribe, epicuticular wax deposits seem to be restricted to Owenia, all species of the genus having wax deposits to some degree. In O.vernicosa F. Muell. they occur as small flakes or short cylinders and in O.reticulata F. Muell. and O.acidula F. Muell. as much larger globules (FIG. 2.6).

6. Glandular bodies

Small (100-310 um diam.) circular black bodies were seen in species of Walsura (excluding W. chrysogyne et al.), Heynea and Ekebergia. They are +/- level with the surrounding epidermal cells or a little prominent and are located within 1-3 mm of the midrib, between the costae. In W.dehiscens T.Clark ined. they also occur on either side of the costae. The glands are largest and most conspicuous in W.monophylla Elmer ex Merrill. Occurrence within Ekebergia and Heynea seems sporadic but most species of Walsura have them, to some degree, in all specimens (FIG. 2.6).

These glands have been observed in a plant of W.tubulata (see Chapter 6) to be secreting a colourless, sweet, nectar-like liquid and seem to be extra-floral nectaries.

Lersten & Pohl (1985) report the presence of extra-floral nectaries on leaves of Cipadessa baccifera . They occur on the abaxial surface of the primary rachis and, rarely, on the abaxial surface of the petiole and leaflet midrib, but were never observed on the lamina. From Lersten & Pohl's description and illustrations, these nectaries seem very similar to the glandular bodies observed, in the present study, on the lamina in species of Walsura, Heynea & Ekebergia.

DISCUSSION

(i) Taxonomy

The leaf cuticle in 8 genera of mangroves (in the families Combretaceae, Rhizophoraceae and Avicenniaceae) was investigated by Stace (1965) and that of certain species of Anacardiaceae by Wilkinson (1979) and both concluded that whilst cuticular striations may provide a reliable character in one taxon, it may be useless in another (even if closely allied) taxon. It seems that in the Trichilieae the latter is the case, with considerable variability within species and genera. The only exceptions are those species with a papillate epidermis, where the papillae always have a cuticular sculpturing of some sort (viz. Walsura, Heynea and Ekebergia).

Solereder (1908) and Metcalfe & Chalk (1950) recognised the occurence of papillate abaxial epidermis in the leaves of Ekebergia, Heynea and Walsura, and the present study has not recorded foliar papillae in any other genus of the Trichilieae. In Heynea and Walsura (excluding W.chrysogyne) papillae occur in all specimens of all species examined (from W.trifoliolata in the 'dry zone' of Sri Lanka to W.pinnata in very wet regions of Borneo). Their presence seems be an excellent taxonomic character, and very useful for distinguishing these species from Trichilia and W.chrysogyne. Whilst papillae occur in all species of Ekebergia, only in one did they occur in all specimens examined, and so seem of little use as a character for delimiting the genus, or indeed the species. The possibility of the character being sex-linked was soon dismissed as male and female specimens of each species were examined. Without details of habitats (sufficient data

FIG. 2.7 Abaxial leaf papillae and trichomes occurring in 175 FHO Ekebergia specimens.

SPECIES	Number of specimens examined	Character	Number of specimens with character	% of specimens with character
E.capensis Sparrman	89	Papillate	15	17
		Papillate + trichomes	2	2
		Trichomes + non papillate	2	2
E.senegalensis Adr.Juss.	34	Papillate	24	71
		Papillate + trichomes	4	12
		Trichomes + non papillate	0	0
E.benguelensis Welw. ex.C.DC.	52	Papillate	52	100
		Papillate + trichomes	29	56
		Trichomes + non papillate	0	0

are rarely given in specimen notes) it is difficult to say if papillae production is more under genetical or environmental control. It is perhaps not unreasonable to hypothesise however that E.senegalensis may have a lower gene-switching threshold for papillae production than E.capensis, and this might also be reflected in the facility to produce trichomes (see FIG. 2.7).

Despite the work on trichomes mentioned in the Introduction, no-one yet seems to have examined them, in any detail, across the family. Solereder (1908) and Metcalfe & Chalk (1950) made a few observations about hair types in a few genera (whether simple or stellate) and Pennington & Styles (1975) noted indumentum types in each genus of the family. Pennington (1981) made more detailed observations about trichomes in New World Trichilia species but still there are no high-power microscopical observations. The present study has demonstrated a wide range of trichome types in the Trichilieae and they seem to provide good characters for the division of the tribe into genus groups and, in some cases, genera.

Stomatal apparatus is also widely used taxonomically (e.g. Stace, 1965; Baranova, 1972; Raju and Rao, 1977). Barthlott (1981) stated that in woody plants from the humid tropics, the epidermal cell outline is likely not to be manifest on the surface. This is generally the case in the Trichilieae but, with the preparations described above and high power L.M., the shape of guard and subsidiary cells can be clearly seen, in addition to stomatal surface features seen under S.E.M. Outer stomatal ledges and apertures seem to be of limited value taxonomically within the Trichilieae, but subsidiary cell arrangement provides another very good character for segregating

	STRIAE			PAPILLAE		TRICHOMES							STOMATAL APPARATUS						WAX		GLANDS	
	Pres.	Wings	Conc. rings	Absent	Pres.	Simple	2-armed	Stell.	Uni-cell.	Multi-cell.	Smooth	Verru-cate	Erect ledge	Inter-mediate ledge	Horiz. ledge	Anomo-cytic	Para-cytic	Actino-cytic	Absent	Pres.	Absent	Pres.
TRICHILIA	★			★		★			★			★	★	★		★			★		★	
PSEUDOBERSAMA	★		★	★		★			★			★			★	★			★		★	
PTERORHACHIS				★				★		★	★			★		★			★		★	
HEYNEA	★				★	★			★			★	★					★	★			★
WALSURA (excl. W.chrysogyne)	★	★			★	★	★		★		★	★	★					★	★			★
W.chrysogyne et al.				★		★		★		★		★	★				★		★		★	
LEPIDOTRICHILIA				★				★		★	★			★		★			★		★	
MALLEASTRUM				★		★			★			★			★	★			★		★	
EKEBERGIA	★		★	★	★	★			★			★	★			★			★			★
ASTROTRICHILIA				★				★		★	★			★		★			★		★	
OWENIA				★		★			★		★				★	★				★	★	
CIPADESSA	★	★		★		★				★		★	★			★			★		★	

FIG. 2.15 Summary table of useful leaf surface characters.

See text for details of characters / character states.

★ = presence of that character / character state.

Walsura (excluding W.chrysogyne) and Heynea from the rest of the tribe. Once again, W.chrysogyne differs in its paracytic arrangement. The presence of T-pieces in Pseudobersama seem to be a good distinguishing character for that genus too. Singh and Kundu (1962) found this character very useful at species level in Digitalis (Scrophulariaceae).

Epicuticular wax seems to be a good character for distinguishing Owenia, as it occurs in all species within and nowhere else without the genus. O.vernicosa is further distinguished by its characteristic granule form.

The glandular bodies of Walsura, Heynea and Ekebergia are not particularly useful taxonomically but do, along with the papillae, suggest certain affinities between these three genera. The "secretory cells" noted by Solereder (1908) in members of the Trichilieae, and by Pennington (1981) in species of Trichilia are internal features of the leaf (located at the boundary between the spongy and palisade mesophyll), visible if the leaf is held up to a strong light. Their function is unknown and are considered to be quite different from the surface glands observed here which seem to be extra-floral nectaries.

The useful leaf surface characters considered above are summarised in FIG. 2.15.

CHAPTER 3

PALYNOLOGY

INTRODUCTION

Pollen as a source of taxonomic characters has long been appreciated (e.g. Brown, 1810) but it was not widely employed until Erdtman (1934) had developed the acetolysis technique for revealing exine morphology in greater detail (see below). Nair (1965) made some observations on pollen morphology in three western Himalayan species of Meliaceae (viz. *Azadirachta indica* Adr.Juss., *Toona ciliata* M.Roemer. & *Melia azaderach* L.) but Erdtman (in his monumental *Pollen Morphology and Plant Taxonomy*, 1952 a 1966) was responsible for probably the earliest published systematic study of the family's pollen. In addition to a family description, he gave brief descriptions of twenty-seven species in eighteen genera. From the Trichilieae, only *T.dregeana* Sond. and *L.volkensii* (Gürke) Leroy are represented however. Pennington (1965) examined (by light-microscopy) pollen grains of two-hundred meliaceous species , including representatives from all the Trichilieae genera. He concluded that pollen characters are chiefly of value in circumscribing the family and that, for the most part, the differences between genera are slight. These observations were incorporated into Pennington & Styles (1975).

Pennington did not however employ scanning electron microscopy (in its infancy in the 1960s) which can reveal features of exine morphology previously unknown (Heywood, 1968; Jones, 1970; Blackmore, 1984). The fine detail of exine sculpturing, particularly, is difficult or impossible to determine with the light-microscope alone. Pennington was only able to make preliminary observations on the aperture apparatus of these grains. Such data are now needed to help determine generic limits in the tribe. With material of almost all species of Trichilieae available at Oxford (most, especially of the American Trichilia species, having been collected since 1970), a detailed study of pollen across the tribe was commenced employing light and scanning electron microscopy, with emphasis on the species of the Trichilia - Heynea - Walsura complex.

MATERIALS AND METHODS

(including a new pollen preparation technique)

An initial investigation was made of those slides used by Pennington (1965). These (at the Forest Herbarium, Oxford) were largely prepared by him as an extension of Meliaceae pollen slides prepared by G.T.Prance at Oxford in the early 1960s. However, since grains are prone to deformation to varying degrees with different preparations and mounting media (Reitsma, 1969) it was decided to base this study solely on newly prepared material using uniform methods.

Anthers were taken from male or hermaphrodite flowers on herbarium specimens at FHO. Extra material was also obtained through the kindness of Dr. Brian Styles, from his pickled flower collection at the Oxford Forestry Institute. A list of materials used, and of grain sizes for many specimens, is appended (App. 2).

Acetolysis is conventionally carried out in accordance with Erdtman's (1943, 1952) method, i.e. heating the pollen in a mixture of nine parts acetic anhydride to one part sulphuric acid. Here, however, for convenience due its more ready availability, glacial acetic acid was used instead of the anhydride. This is an acceptable alternative (Moore & Webb, 1987).

It was found necessary to heat the mixture in the water-bath for four to five minutes in order to remove all the cytoplasm and external proteinaceous material. This treatment did not seem to deform the grain exine (by comparison with untreated material). Following this, the pollen was subjected to the following series of washes:

(i) Glacial acetic acid.....to displace the sulphuric acid

(ii) Distilled water.....to remove the acids

(iii) " " ..... " " " "

(iv) " " ..... " " " "

(v) 50% Industrial Methylated Spirits.....to dehydrate

(vi) 75% " " " ..... " "

(vii) 100% " " " ..... " "

It is in the method of washing that the new technique differs from the standard (Erdtman) technique. Conventionally, after acetolysis , the mixture is transfered to a centrifuge tube and the whole centrifuged for ten to fifteen minutes. The supernatant is decanted, the first wash added, the pellet re-suspended and the tube centrifuged again. This is repeated for each wash until a final anhydrous suspension in IMS (or acetone) is obtained.

In the new method, the acetolysis mixture is put into a 2.5" white porcelain evaporating dish and allowed to cool (under a petri-dish lid or in a fume-cupboard). During this time, all the solids will have settled to the bottom of the dish. The supernatant is then removed with a pipette, held at an angle of c.30° to the horizontal so as not to disturb the solids on the bottom. The first wash is then added and the solids mixed into it using the pipette. It is then left for about 5 minutes by which time the solids have settled again. The process is repeated for each wash. If for some reason (e.g. surface tension or air bubbles) some grains are remaining at the surface, the addition of the smallest amount of detergent quickly releases them.

The beauty of this technique is that the whole process can be conducted under a dissecting microscope and , at 40X magnification, the individual grains can be discerned. It is therefore possible to tell immediately after acetolysis.

(i) if there are any unbroken anthers, which can then be teased apart with forceps and the grains released;

(ii) if there is any pollen in the preparation at all;

(iii) the amount of pollen present;

(iv) if the pollen 'was' fertile, it usually being possible at 40X to discern if the grains are a good shape or are collapsed (i.e. the usual state of infertile grains).

Another advantage of the technique is that at any stage in the washing sequence, debris from the anthers (which is often considerable) can be removed, either with forceps or by deft use of a micro-pipette. The effect of having large quantities of debris in the preparation are painfully apparent under the SEM, since not only do they cast shadows on free grains and congregate around them as the IMS evaporates (see below), but bits of debris also charge readily under the electron beam and tend to jump about the stub. All this is avoided using the sedimentation technique. With the traditional technique, if centrifugation is not quite long enough or if grains have clung to the side of the tube, most of the grains can be lost in the supernatant. Constant monitoring of the grains in the new method prevents such losses. The new method is still completed in less time than the old one.

This new method is quite different from that of Ding Hou (1969). Ding Hou's technique utilizes very small quantities of chemicals and relies on the chemical properties of the acetolysis mixture when in contact with ethyl alcohol to remove the pollen grains from the acids. This is quite unlike the solely mechanical sedimentation technique described here. Ding Hou's method is, however, simple and quick and may well have been a better method to use here. I had, however, perfected my own method before his came to my

attention. Both seem preferable to the conventional centrifugation technique, at least when dealing with small quantities of material.

A few drops of pollen in IMS suspension are then put on to an SEM stub and allowed to dry in dust-free conditions. Care has to be taken here to prevent the grains clumping together as the IMS evaporates and this is done by gentle teasing apart using clean mounted needles in the latter stages of evaporation. Another sample of pollen in IMS is taken and dried down. A small piece of glycerol jelly on a mounted needle is brushed against the pollen a few times and then put on to a clean polished microscope slide. A drop of safranin stain (in IMS) is added and a cover slip put on top. The whole is then gently heated over a soft flame until the jelly melts and (pushed down by the weight of the cover slip) forms a thin layer and a permanent pollen slide. The exine of these grains is quite thick (see below) and there seems to be no appreciable damage due to acetolysis or dehydration. The grains of many taxa require critical-point-drying, but the grains of the species of the Meliaceae seem mechanically very strong and do not require this treatment.

The SEM stubs were gold-coated in a 'Polaron SEM Coating Unit E5000' at Oxford to give a gold coating of c.250 nm thick (see Chapter 2 for details) and examined at the Royal Botanic Gardens, Kew (Palynology Unit) using a Hitachi S-510 SEM. The slides were examined and photographed at Oxford using a Zeiss bench microscope. All grain measurments were made using a calibrated eye-piece graticule at 1000X magnification (oil-immersion). Not all species of each genus were investigated (particularly in Trichilia) but when representative species had to be selected, the geographical

distribution, variety in macro-characters and the comments of authors (e.g. Pennington and Styles, 1981, and De Wilde, 1968, for Trichilia) were taken into account.

As it was often quite difficult to distinguish between male and female flowers (especially in the early stages of the study, because of unfamiliarity with the flowers of this group), anthers of female flowers were occasionally acetylised. It is only when the material is observed under the microscope, and the grains seen to be deformed and not viable (i.e. aborted), that one can be certain that the material is from a female inflorescence. This problem caused a certain amount of time to be wasted in the early stages, but did establish unequivocally the sex of the specimen under investigation. This is particularly useful when considering other characters (e.g.in the leaf surface) which may be sex-linked. Confirmation that deformed grains were in fact aborted was obtained by the use of a stain mixture containing Malachite green, acid fuchsin & orange G (Alexander, 1969) on selected specimens (prior to analysis).

The terminology used here mainly follows that recommended by Reitsma (1970), who also gives a very useful glossary of palynological terms, and Moore & Webb (1978).

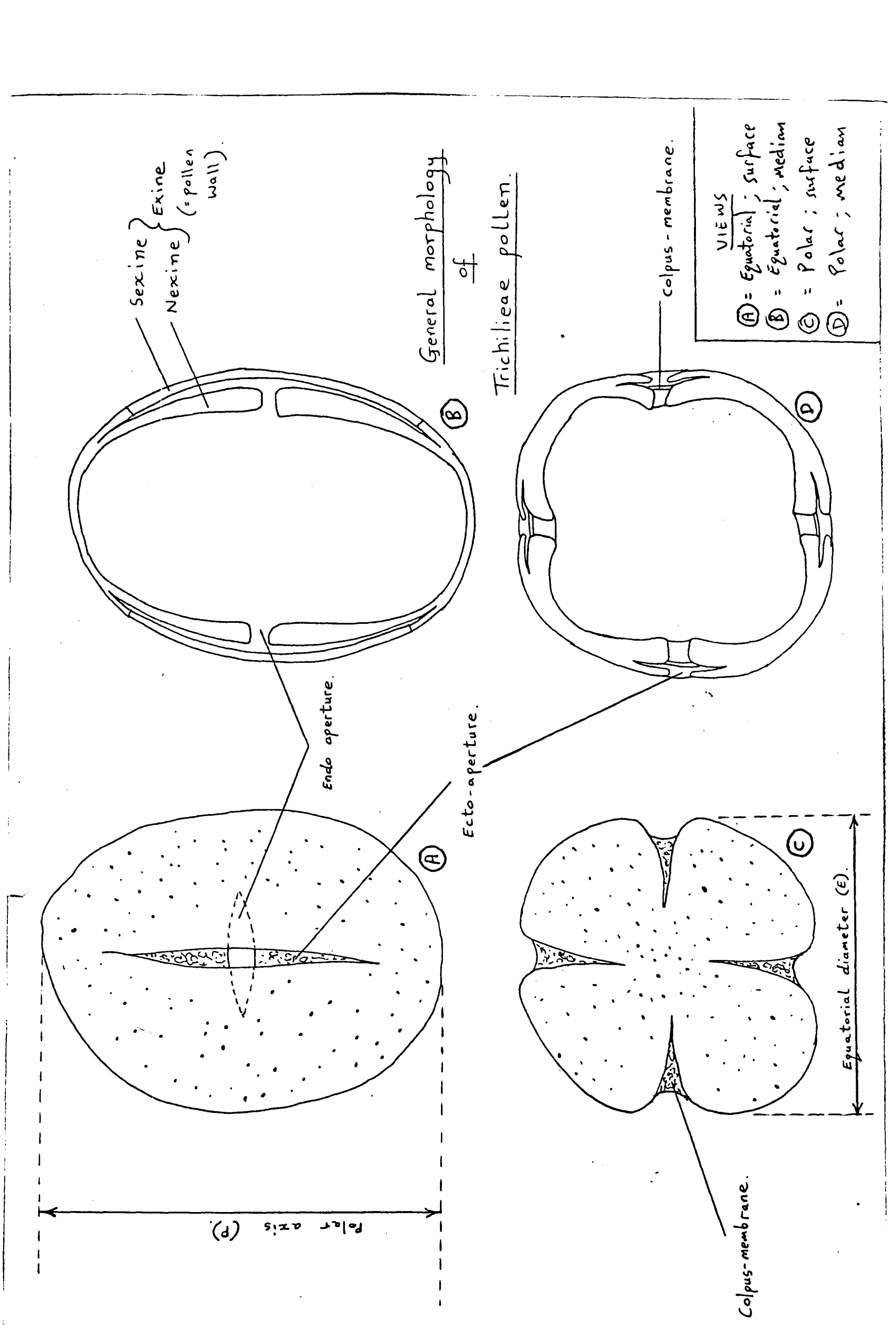


FIG: 3.1/A GENERALISED DIAGRAM OF POLLEN MORPHOLOGY IN THE TRICHILIEAE.

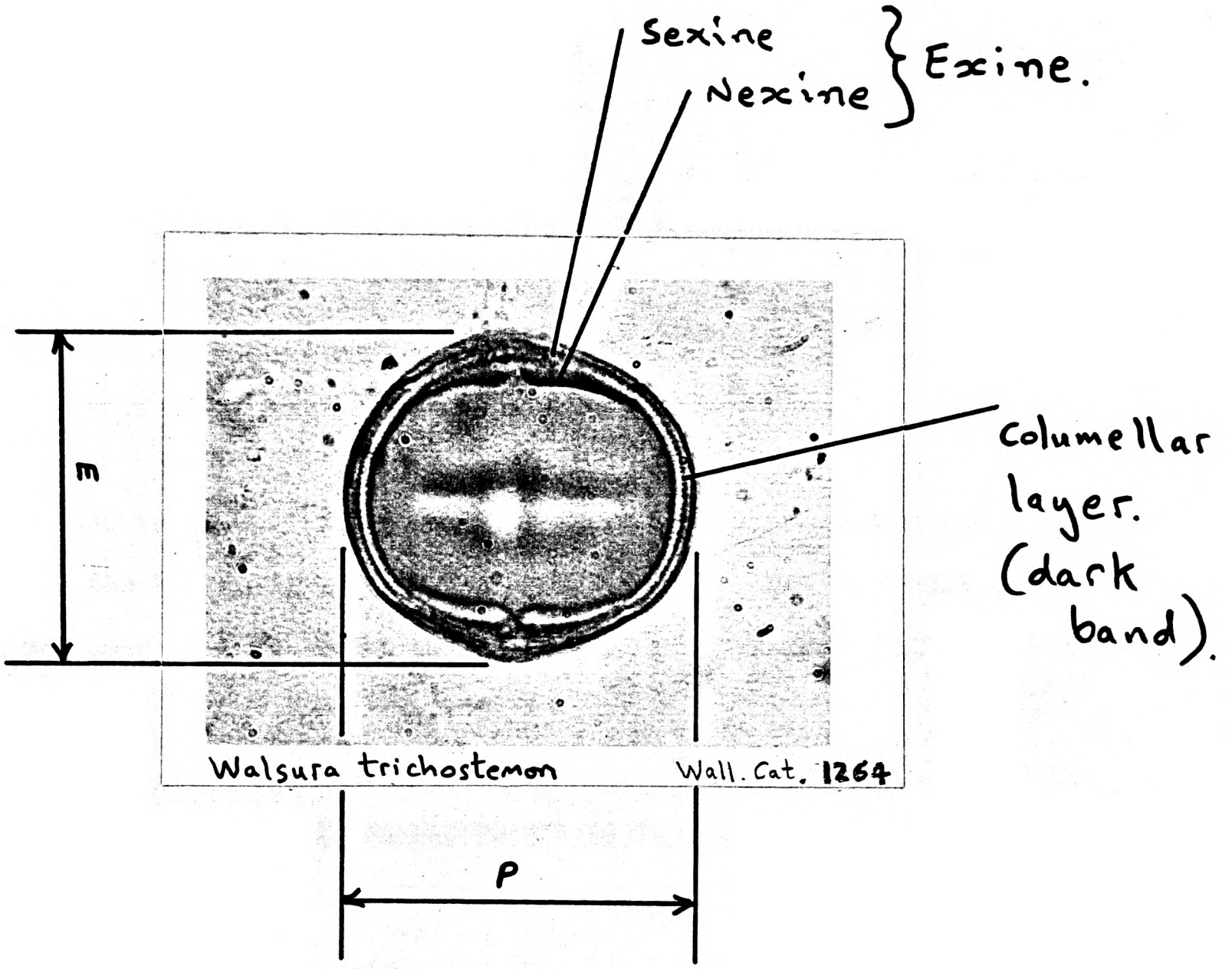


FIG. 3.1/B Photomicrograph of Walsura sp. pollen grain to show exine layers. Grain seen in equatorial view and focus at median plane.

It is not possible to distinguish between the sexine and the nexine (except in the immediate vicinity of the compound aperture) under the light-microscope. The columella is a component of the sexine only.

GENERAL DESCRIPTION

(See FIGS. 3.1/A & 3.1/B)

The following is a general description of the Trichilieae pollen grain:

Single; generally apolar (occasionally polar); (3)-4-(5)-zono-colporate; never syncolpate.

Shape: Prolate-spheroidal to sub-prolate (sensu Erdtman, 1952)

Semi-erect to adequate (sensu Reitsma, 1970)

Size: Polar axis, P= 22 - 59 um; equatorial diameter, E= 18 - 56 um.

The outline in equatorial view ranges from elliptic to almost circular. The sides of the longer grains, though usually convex, can be almost flat for most of their length. The poles are usually rounded also, but can be more or less flat.

The outline in polar-view ranges from circular, with slight indentations where the ecto-apertures occur, to strongly 3-, 4- or 5- (depending on the number of apertures) angular.

The exine is quite thick: 2 - 3 um at the poles (the narrowest points). The nexine can be of constant thickness throughout or, in some species, diminishes gradually to nothing towards the poles, and/or (in most species) increases in thickness in the region of the apertures. The abrupt increase in nexine thickness here can give the appearance of internal lips on the inner side of the endo-aperture.

The sexine is not distinguishable from the nexine under the light-microscope (except perhaps in the immediate vicinity of the compound-aperture), but a columellar layer within the sexine is often seen under light-microscopy. The outer layer of the sexine (i.e. that above the columellae) may be perforated by micro-puncta, which are clearly visible under SEM. The micro-puncta vary in size and density from species to species and occasionally appear as if not fully formed, but merely as slight depressions in the outer exine surface. They are sometimes randomly distributed over the grain surface or may be arranged in simple patterns (e.g. in lines, as in Owenia spp.).

The apertures are compound and are equi-spaced around the equator. The ectoaperture is a colpus of length 0.5-0.8 times the surface distance between the poles. It may be parallel-sided or may be narrowly rhombic, but is rarely more than 3 um at its widest. The ends may be acute, blunt, truncate, (rarely) with a short angled beak, or bifurcate (each point ending in any of the preceeding ways). The aperture is closed by a colpus membrane, which may be smooth or granular.

A wide range of endoaperture forms (= ora in Pennington & Styles, 1975, after Erdtman, 1952) are observed, from a circular porus of diameter no greater than the width of the ectoaperture at its centre, through elliptic and rhombic types of various sizes, to elongate oblongs. If one of the non-circular shapes, it can be anything from 0.1-0.6 times the length of the ectoaperture. The long axis of the endoaperture is always perpendicular to that of the ectoaperture (= lalongate, Pennington & Styles, 1975, after

FIG. 3.2

LIGHT-MICROGRAPHS

Photocopy shows all features of original micrographs.

MAGNIFICATION = X 1000

1. H.trijuga (Pennington 7948). 4-colporate grain in equatorial view.
   a. Focus at surface.
   b. Focus at median plane.

2. W.tubulata (Cult.: Oxford). 3-colporate grain.
   a. Oblique view.
   b. Polar view.

3. W.trifoliolata (Haines 1854). 4-colporate grain in equatorial view.
   a. Focus at median plane.
   b. Focus at surface.

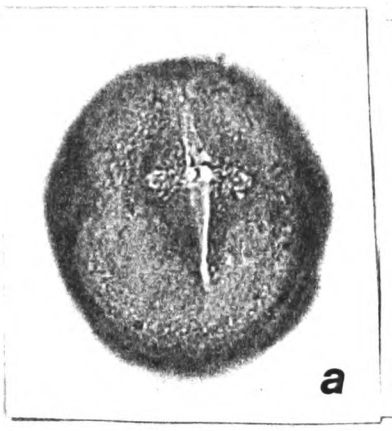
4. W.brachybotrys (Wenzel 295). 4-colporate grain in equatorial view.
   a. Focus at surface.
   b. Focus at median plane.

5. W.trifoliolata (Worthington 2616).
   a. Equatorial view; focus at equator.
   b. Polar view of 4-colporate grain.
   c. Polar view of 5-colporate grain.

6. C.baccifera (Forrest 9884). 4-colporate grain in equatorial view.
   a. Focus at surface.
   b. Focus at median plane.

7. O.venosa (Helms 136).
   a. Equatorial view of 4-colporate grain, in surface focus.
   b. Polar view of 3-colporate grain.
   c. Polar view of 5-colporate grain.

8. T.solitudinis (Berg P18585).
   a. Eqautorial view of 3-colporate grain, in surface focus.
   b. Equatorial view of 4-colporate grain, in median focus.
   c. Polar view of 3-colporate grain.



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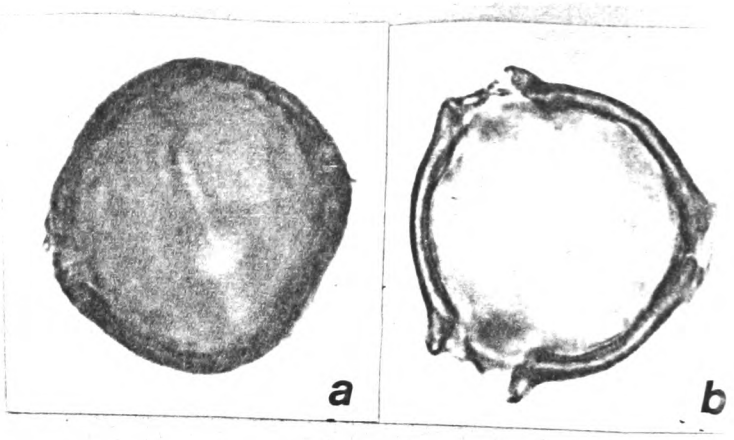

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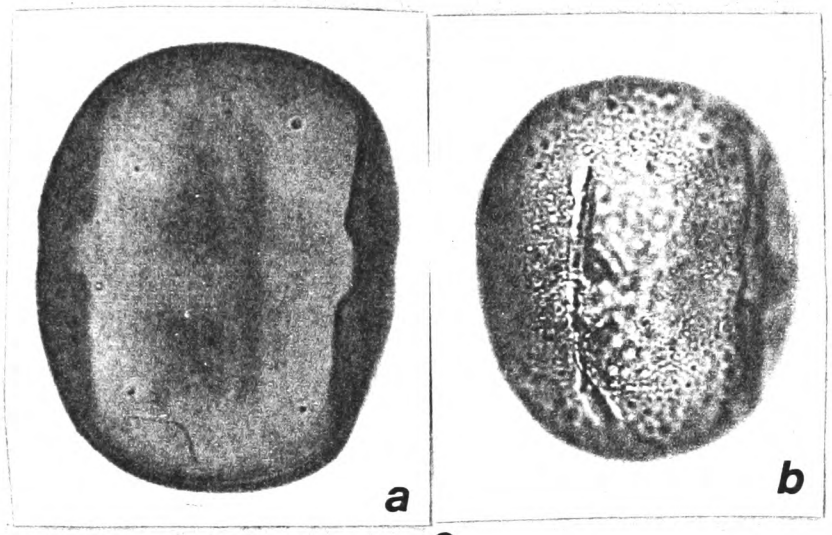

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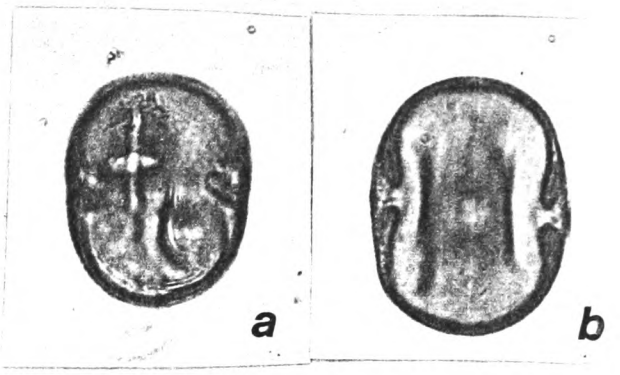

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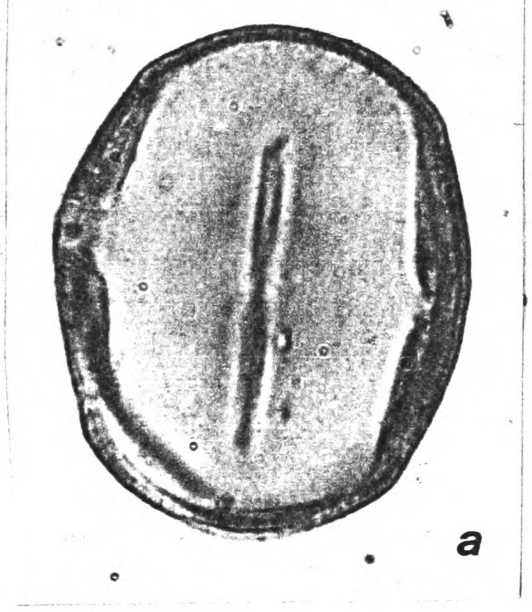

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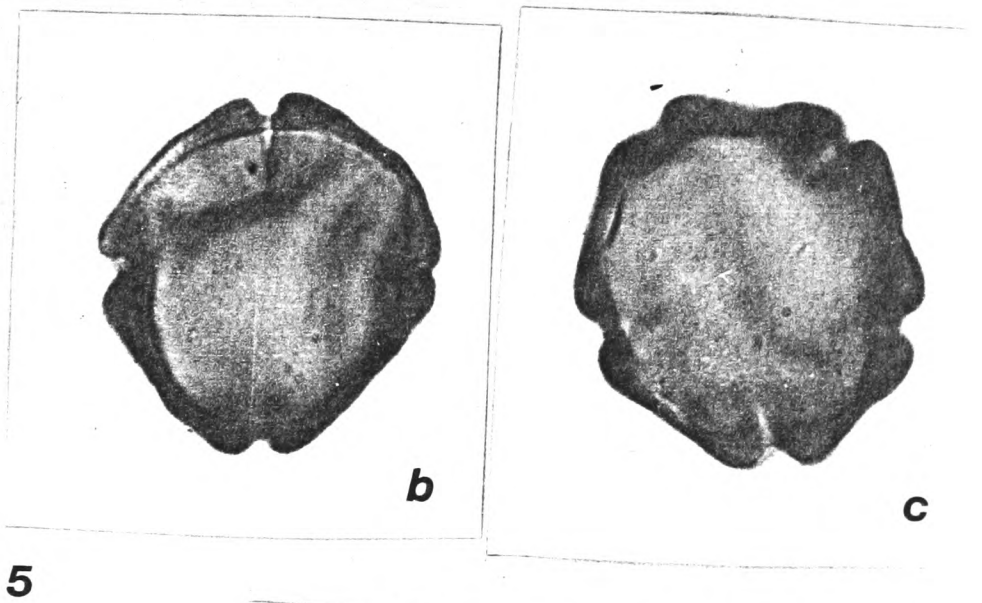

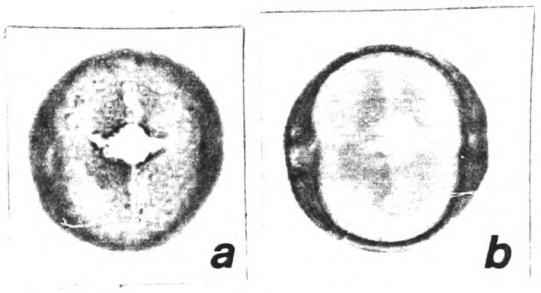

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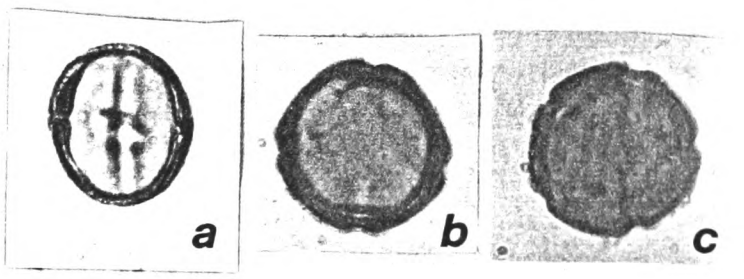

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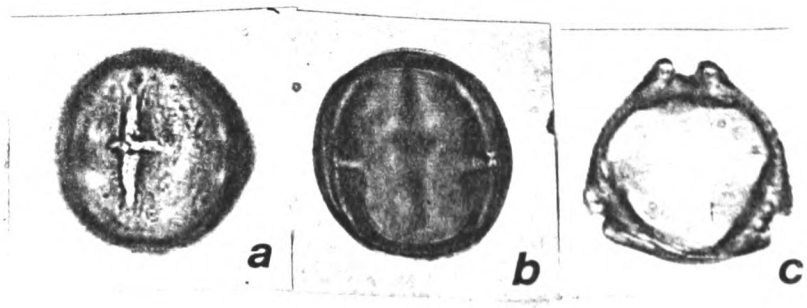


FIG. 3.3

LIGHT-MICROGRAPHS

Photocopy shows all features of original micrographs.

MAGNIFICATION = X 1000

1. T.dregeana (Styles 321).
   a. Equatorial view of 5-colporate grain.
   b. Polar view of 4-colporate grain.

2. T.emetica (Styles 625).
   a. Polar view of 4-colporate grain.
   b. Polar view of 5-colporate grain.

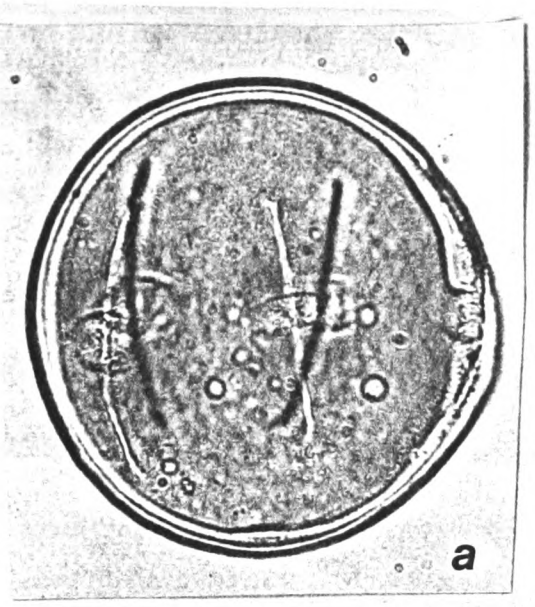
3. T.martiana (Gentle 2732). 4-colporate grains.
   a. Equatorial view in surface focus.
   b. Equatorial view in median focus.
   c. Polar view.

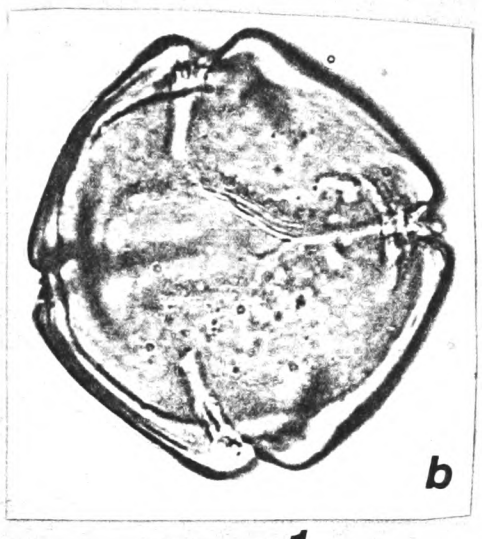
4. E.senegalensis (Collection unknown). 4-colporate grains.
   a. Equatorial view in surface focus.
   b. Polar view.

5. L.volkensii (Eggeling 1678). 4-colporate grain.
   a. Equatorial view in median focus.
   b. Polar view.

6. M.excelsum (Humbert 2494). 4-colporate grain.
   a. Oblique equatorial view.
   b. Polar view.

7. P.mossambicensis (Torre 6328). 4-colporate grain.
   a. Equatorial view in surface focus.
   b. Equatorial view in median focus.





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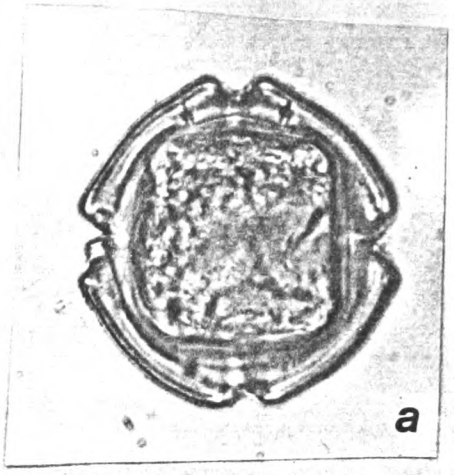

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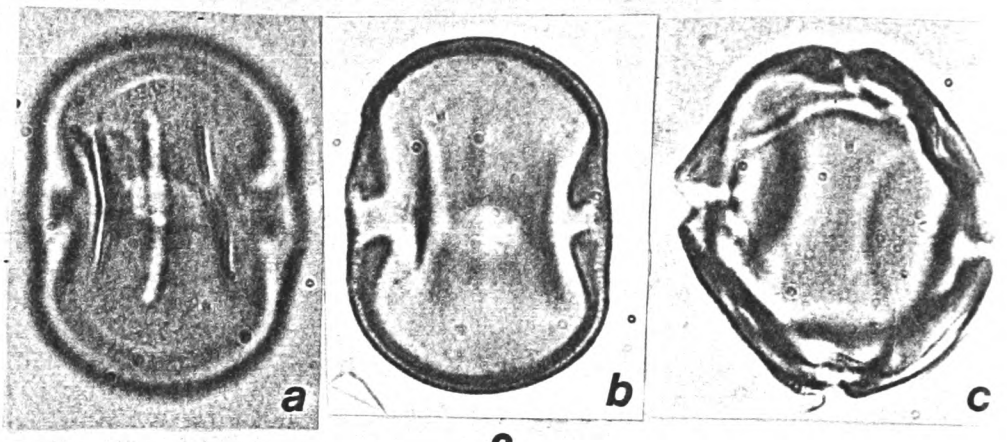

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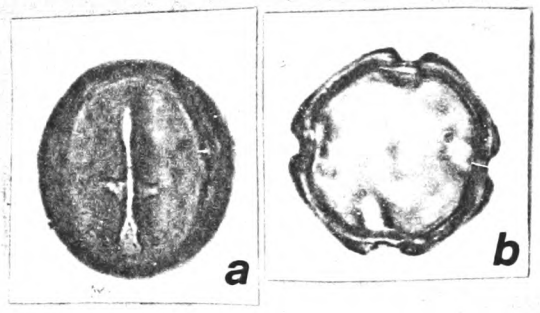

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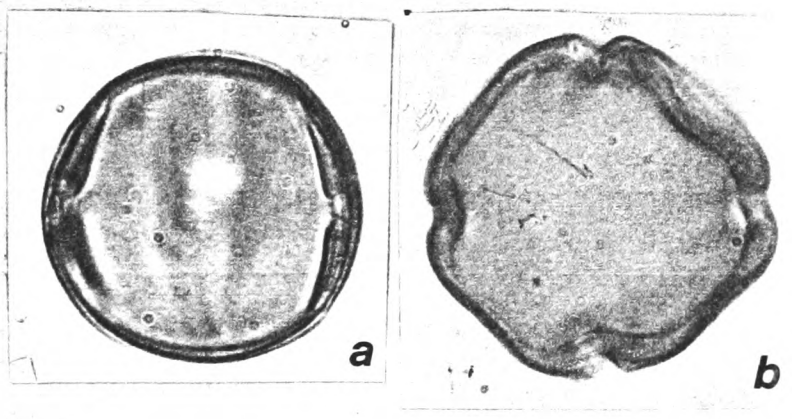

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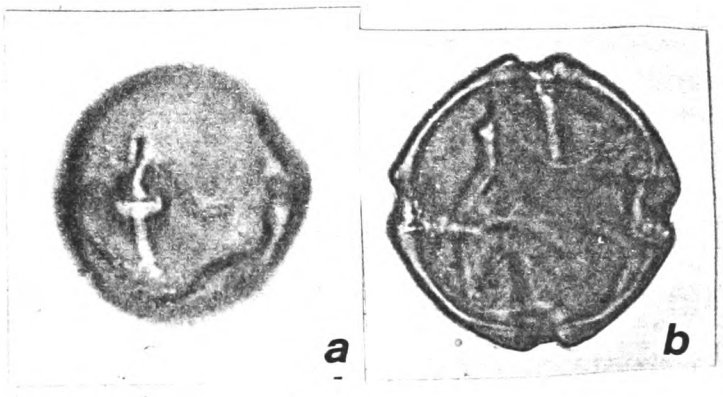

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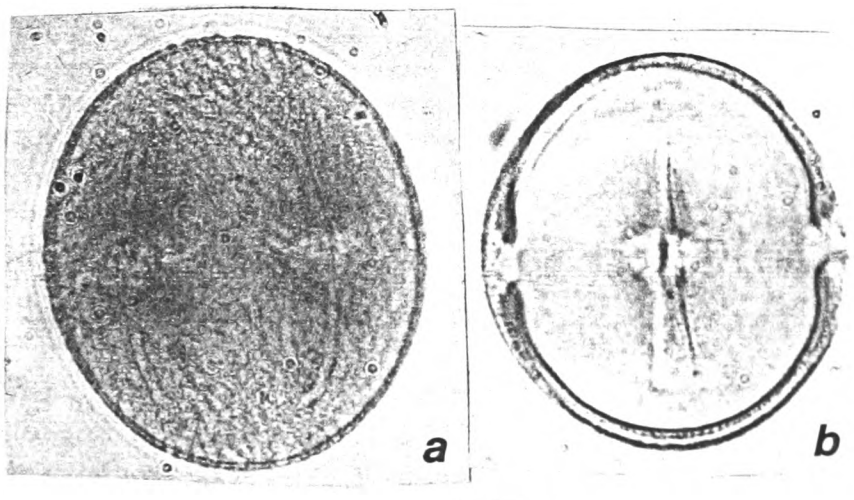


7

Erdtman, 1952) and they always cross centre-to-centre forming a cruciform arrangement. The ends of the endoapertures may take any of the forms described above for the ectoapertures OR may be praemorse.

The ecto-apertures are usually parallel to each other, but in a few species are occasionally set at a slight angle, but are still centred on the equator and perpendicular to the endo-apertures (which are also therefore at a slight angle).

The size and shape of the apertures seems fairly constant in any given species.The number of apertures is also usually constant, but some species exhibit two forms (i.e. 4- & 5- OR 4- & 3- colporate grains) within the same anther. Often however, one form (by far) predominates (usually 4-colporate)and most species in the tribe have only 4-colporate grains anyway.

POLLEN TYPES IN THE TRICHILIEAE

Six distinct types of pollen morphology can be distinguished in the Trichilieae and these are given below along with the taxa which possess each type:

A.

Prolate-spheroidal (to sub-prolate); P>25 um; endoapertures short-rhomboidal with plain ends; micropuncta indistinct.

FIG. 3.4

SCANNING ELECTRON MICROGRAPHS

1. Walsura trichostemon (Bertal 11069).

   Note absence of micropuncta.

2. Walsura tubulata (Cult.: Oxford).

3. Heynea trijuga (Pennington 7948).

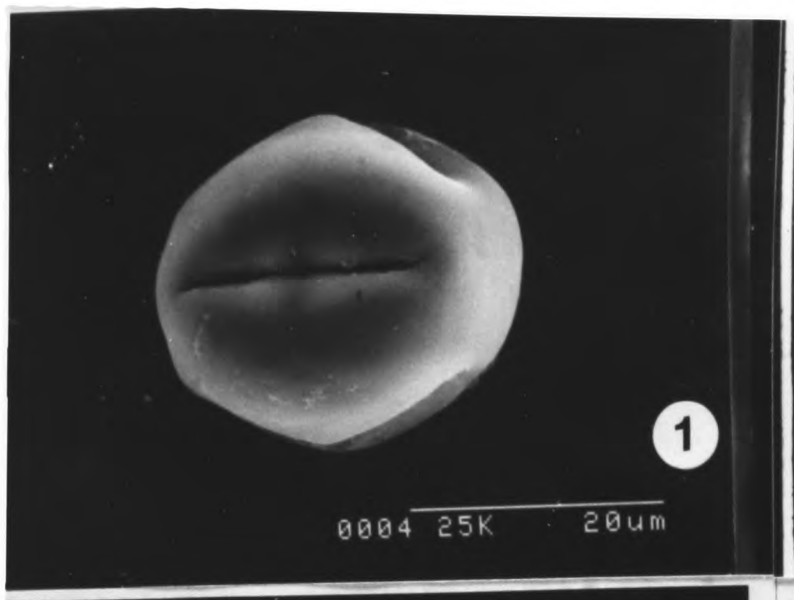
4. " " "

5. " " "

6. Trichilia emetica (Styles 265).

7. Trichilia capitata (Torre 776).

8. " " "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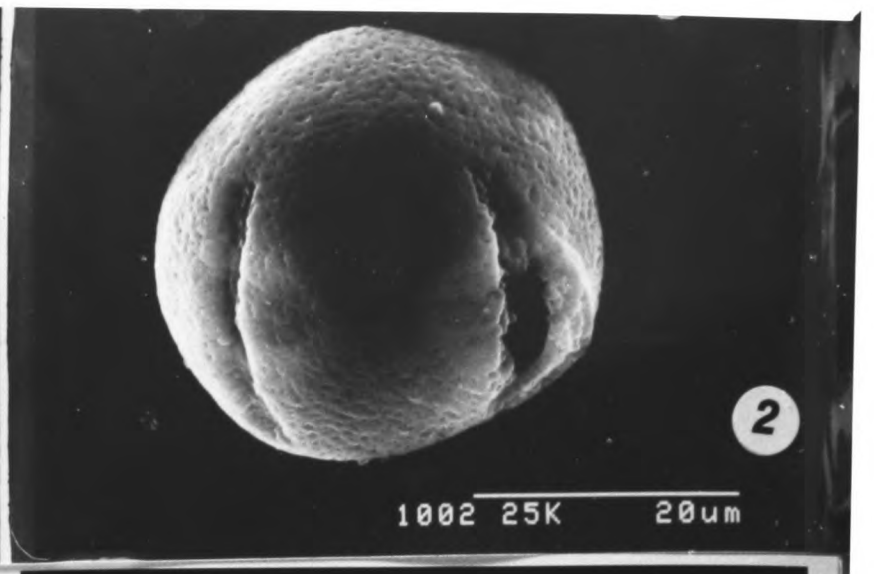
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3
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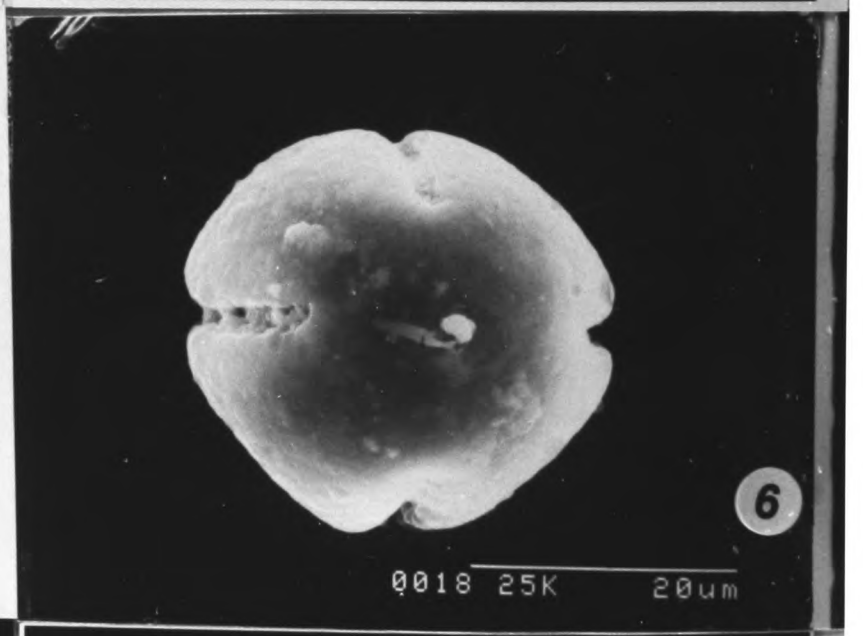
3016 25K 20um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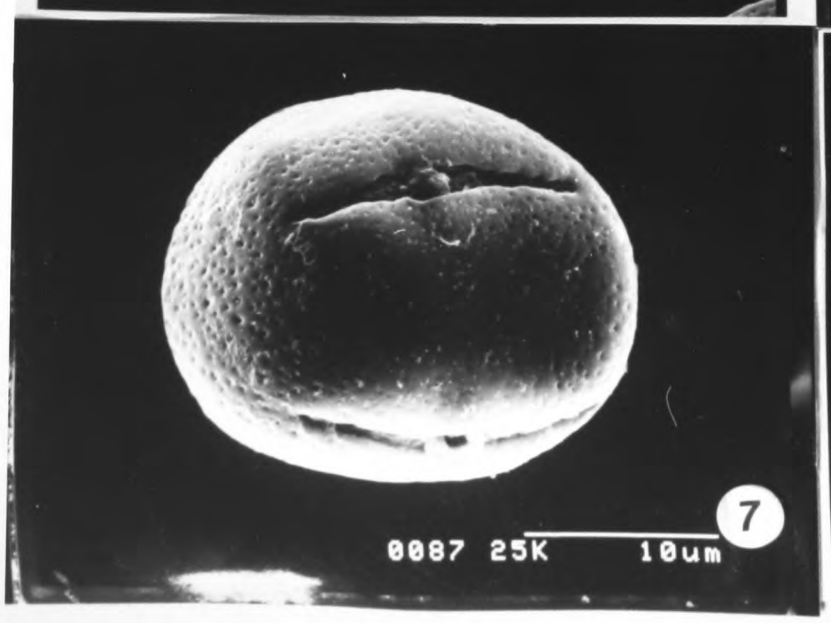
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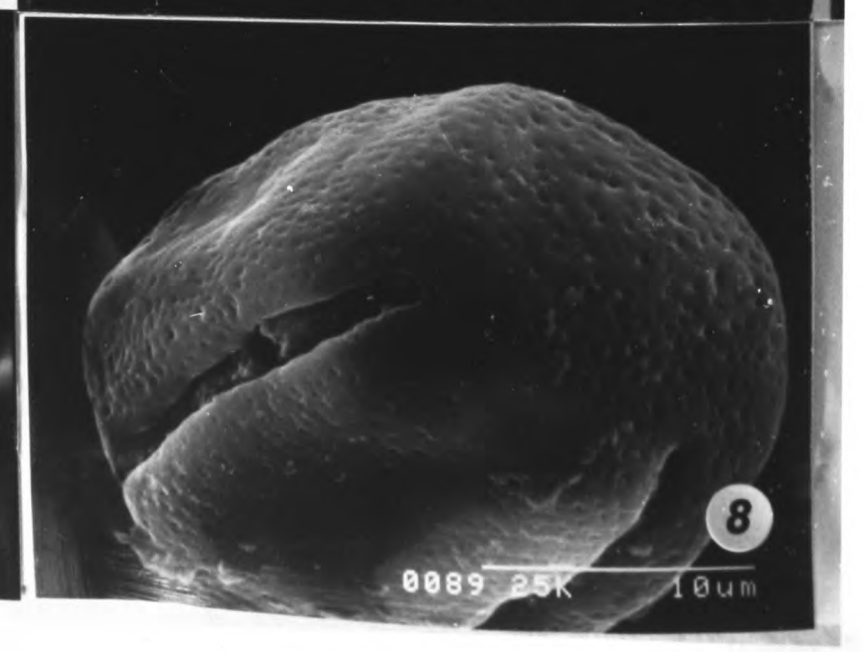
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FIG. 3.5

SCANNING ELECTRON MICROGRAPHS

1. Trichilia quadrijuga (Bahia 60).

2. Trichilia solitudinis (Berg P18585).

3. Astrotrichilia valiandra (Humbert 29663).

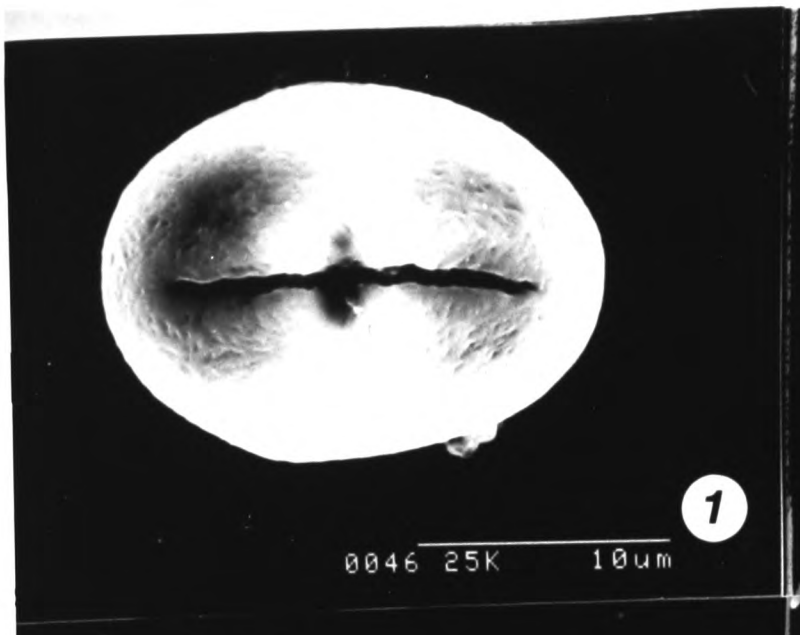
4. Ekebergia senegalensis (Collection unknown).

5. Cipadessa baccifera (Forrest 9884).

6. " " " "

7. Owenia venosa (Helms 136).

8. " " " "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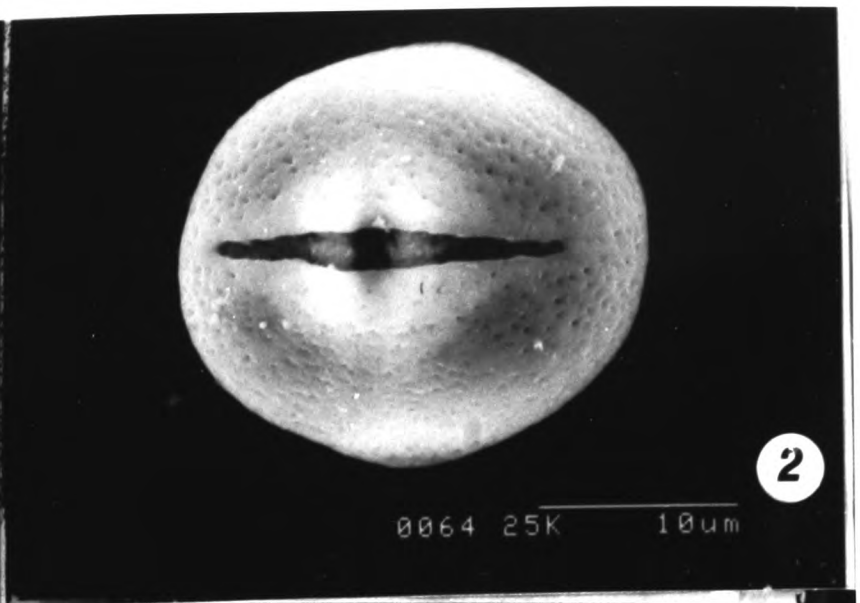
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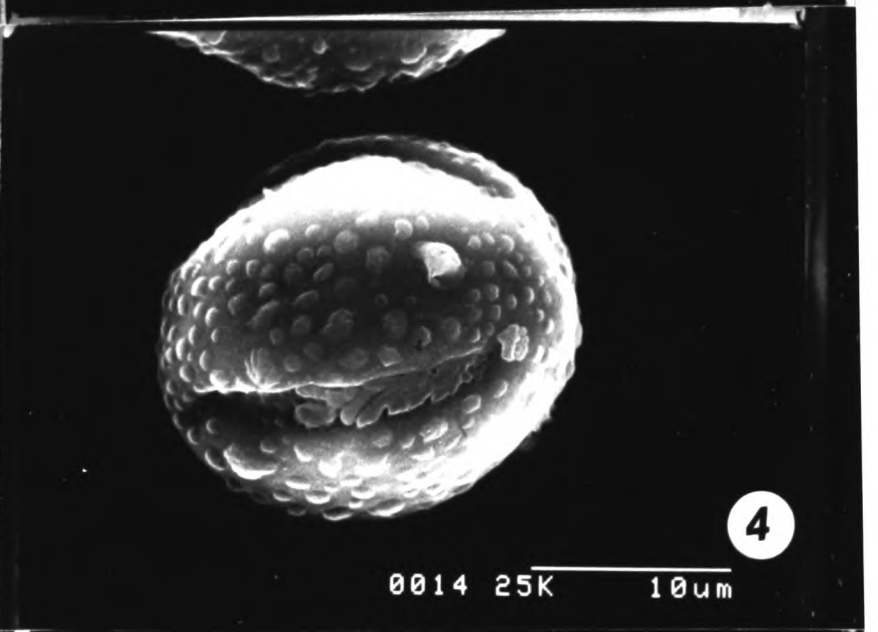
3
1004 25K 20um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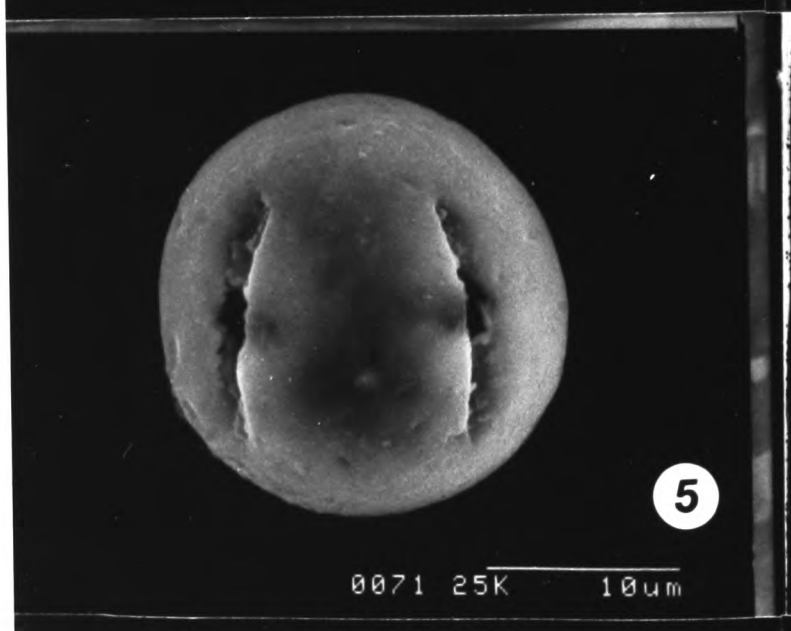
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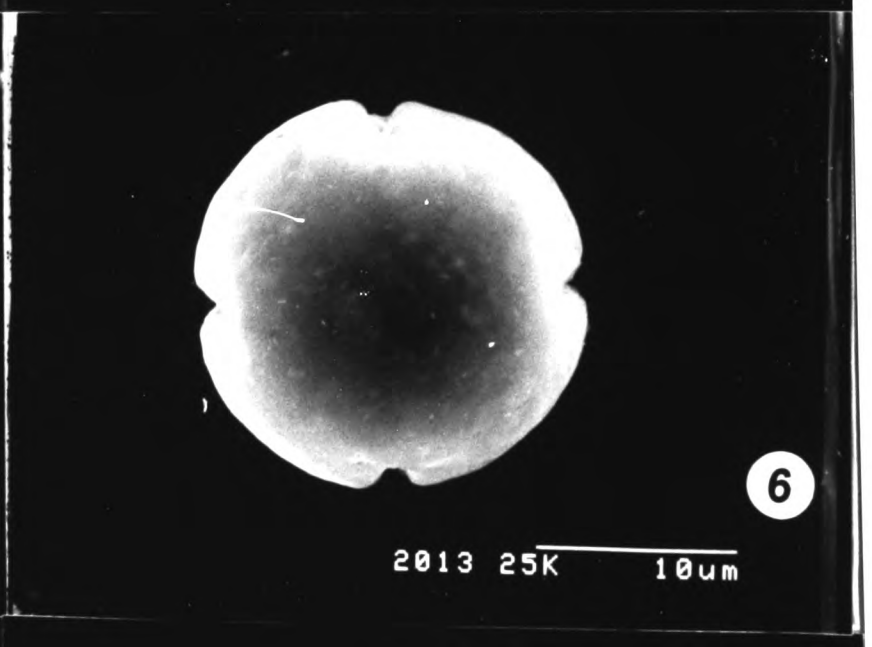
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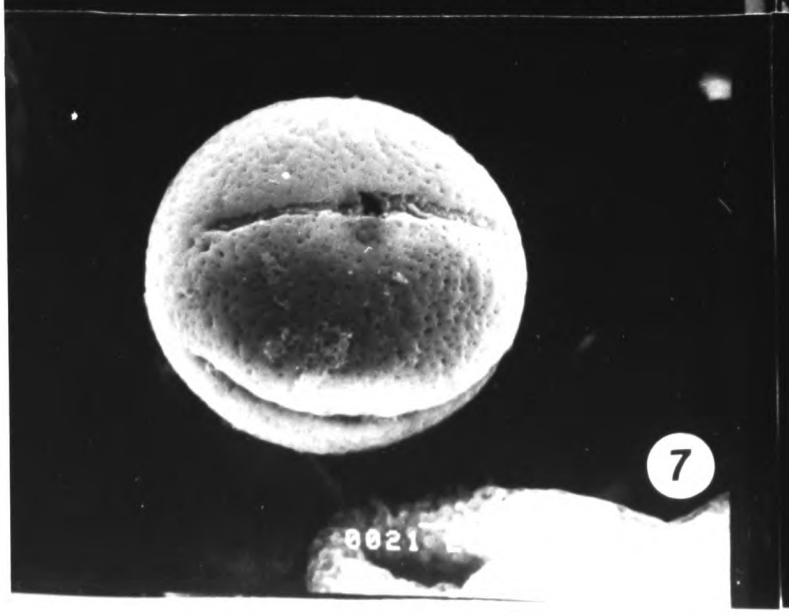
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0021


8
0026 25K 10um

Taxa: Lepidotrichilia; Astrotrichilia (FIG. 3.5/3); Pseudobersama (FIG. 3.3/7); Malleastrum (FIG. 3.3/6); Pterorhachis; Ekebergia (FIGS. 3.3/4; 3.5/4).

B.

Sub-prolate (to prolate-spheroidal); endoapertures narrowly oblong; micro-puncta distinct.

Taxa: Trichilia (FIGS. 3.2/8; 3.3/1/2/3; 3.4/6/7/8; 3.5/1/2); Heynea (FIGS. 3.2/1; 3.4/3/4/5).

C.

Sub-prolate (Walsura spp.) or sub-spheroid (Cipadessa baccifera); P<26 um; endoapertures narrowly rhomboidal or narrowly oblong with beaked, bifid or truncate ends; micropuncta indistinct.

Taxa: W.chrysogyne; W.brachybotrys (FIG. 3.2/4); Cipadessa (FIG. 3.5/5/6)..

D.

Sub-prolate; P>30 um; endoapertures rhomboidal to narrowly oblong (a wide range often exhibited within a single specimen) with simple or occasionally with a curved beak; micropuncta indistinct.

Taxa: W.robusta; W.trichostemon (FIG. 3.4/1).

E.

+/- spheroidal to sub-prolate; P>35 um; endoapertures short-rhomboidal with simple ends; micropuncta distinct.

Taxa: W.trifoliolata (FIG. 3.2/3/5); W.tubulata (FIG. 3.4/2); W.pinnata.

F.

Prolate-spheroidal; P<22 um; endoapertures short and narrowly oblong with acute ends (not rhombic); micropuncta distinct, often in regular patterns (cf. random, as in A-E).

Taxon: Owenia (FIGS. 3.2/7; 3.5/7/8).

DISCUSSION

The general description above is based on light-microscopy and SEM and covers practically every feature of the grain that can be observed with these tools. The logical next step would be to embed and section grains for study under the transmission electron microscope (TEM), to show greater detail of wall structure. Limitations of time and the return of data for time spent precluded this here however. Despite this, the current description provides the most comprehensive description of meliaceous pollen to date.

Compared with other families and tribes (e.g. Vernonieae in the Compositae, Kingham, 1976), the exine in the Trichilieae seems to possess little sculpturing diversity. However, there are trends within the tribe which can be represented in six pollen types. The characters employed for this classification are grain shape (in equatorial view); grain size (P); endoaperture shape and end detail; micro-puncta formation. These characters have to be taken in combination.

It is remarkable that all of the African satellite genera of Trichilia should be accommodated within one fairly homogeneous pollen type. Of this group however, Ekebergia senegalensis is unusual (amongst the species examined) in having (c. 1 um diam.) verrucae over most of the exine. This was not observed in E.capensis, which has the usual 'Type A' smooth exine with indistinct micropuncta only.

Trichilia and Heynea form a distinct group for although within Trichilia there is a wide range of grain sizes (P= 20-56 um) all species have a common shape, endoaperture form and micropuncta state. Walsura falls into three types with W.chrysogyne and W.brachybotrys demonstrating affinities with Cipadessa. The sub-prolate shape, oblong endoapertures and distinct micropuncta place Heynea rather closer to Trichilia than to Walsura.

Pollen type E (Owenia spp) is very distinctive, particularly in its micropuncta patterning. It also has the smallest grains in the tribe (P=21.6 um in O.venosa). There is a great range of grain size within the tribe with T.dregeana producing the largest grains examined (P=56.8 um). The exceptionally large size of its grains might be explained in terms of its exceptionally large chromosome number of 2n= c.360 (Styles & Vosa, 1971), compared with:

SPECIES	2n	AUTHOR
Walsura trifoliolata	28	Ghosh, 1961.
Heynea trijuga	28	Mehra & Sareen, 1969.

Trichilia emetica	50	Styles & Vosa, 1971.
Trichilia rubescens	46	" " "
Pterorhachis zenkeri	28	" " "
Pseudobersama mossambicensis	46	" " "
Lepidotrichilia volkensii	38	" " "
Ekebergia capensis	46	" " "
Cipadessa cinerascens (=C.baccifera)	28/56	" " "

The range of variation exhibited within Walsura then (including the rather distinctive W.chrysogyne & W.brachybotrys or not) is greater than that within nineteen species of Trichilia plus one species of Heynea or within the whole of pollen type A (i.e. six Afro-Malagasy genera). This greater variety may be due to the fact that a larger proportion of species, and more specimens of each, were studied for Walsura, but it has to be pointed out that specimens and species in each of types A & B show remarkable uniformity of pollen morphology. The palynological diversity within Walsura therefore seems to reflect its diversity in other features.

CHAPTER 4

FRUIT ANATOMY AND SEED DISPERSAL

INTRODUCTION

In the introduction to his comprehensive and detailed study of seed anatomy in the subfamily Melioideae, Cheek (1989a) reviewed the relatively small amount of information on seed anatomical features previously published, Corner (1976) making by far the greatest contribution with his study of twenty-seven species in sixteen meliaceous genera. Published data on fruit anatomy seem even more scant. Whilst observations of gross morphology of fruits are recorded in the normal course of taxonomic descriptions (although usually in remarkably little detail), information on tissue and cell types and their distributions are (at least for species of this family) extremely sparse. This is perhaps surprising given that tissue distributions are the basis of gross pericarp structure and thence of the dispersal systems of the species, and also, to quote Corner (Vol. 2, Page 185):

"This is a family in which the variety in fruits and seeds far outweigh in complexity the floral details which are the basis of classification. The neotenic flowers have advanced to a static level but the fruits retain a great many stages in evolution from the fleshy arillate capsule to the dry capsule with alate seeds and the drupe."

Cheek examined species in all of the genera of the Trichilieae but, since he was concentrating on seed anatomy, made only basic observations on pericarp structure.

In this study, the fruit anatomy of species in all genera of the tribe have been investigated, with particular emphasis placed on the species of the Trichilia - Heynea - Walsura complex.

Data on seed-dispersal systems in the Trichilieae species are limited to (i) very occasional comments in collectors' notes accompanying herbarium specimens; a few papers on dispersal which refer to Trichilia species; (ii) a few papers where the authors bring together other workers' observations and may add some thoughts of their own. Since this is principally a taxonomic work, dispersal is dealt with only briefly but results of original field-work have been included and some discussion in relation to fruit anatomy is given.

MATERIALS AND METHODS

Most of the fruits examined were from herbarium spirit material and details of collections and herbaria (FHO, K or SAN) from where they were obtained are given for each. Much of the African and Malagasy material was obtained through the kindness of Dr. Martin Cheek. In order to study a wider range of Trichilia material, it was also necessary to rehydrate dried herbarium

material of some species. By trial and error, it was found that the most effective and least damaging method was to boil the dried fruit in a 50:50 mixture of water and glycerol with a small amount of detergent added. Some deformation of the parenchyma tissues is inevitable but this probably occurs mostly during the initial drying rather than upon rehydration.

Sections were cut in L.S. and T.S., mostly by hand with a razor blade but some (particularly the drupaceous fruits) on a sledge microtome. Fruits with hard/woody components often had to be cut open with a hacksaw or electric jigsaw prior to sectioning. Sections were mounted in glycerol and examined under the light microscope, without staining. Where the presence of tannins was suspected (by brown colouration of tissues) a ferrous sulphate stain was employed for confirmation (it turning tannins black). The surface of the fruits was also examined under the light microscope. Photographs and drawings were made.

DESCRIPTIONS

Each description follows a standard format, commencing with gross morphology and proceeding to exocarp, then mesocarp, then endocarp. Although these layers are very different in different genera, I have maintained the terms throughout since they indicate what I believe to be probably homologous layers, and at least indicate an outer, middle and inner series. I have resisted the temptation to examine the seed outer layers but parts of the seeds inevitably occur in some of the

A.Angus 1028
Northern Zimbabwe

TRICHILIA EMETICA Vahl

T.S. mature fruit at the equator.

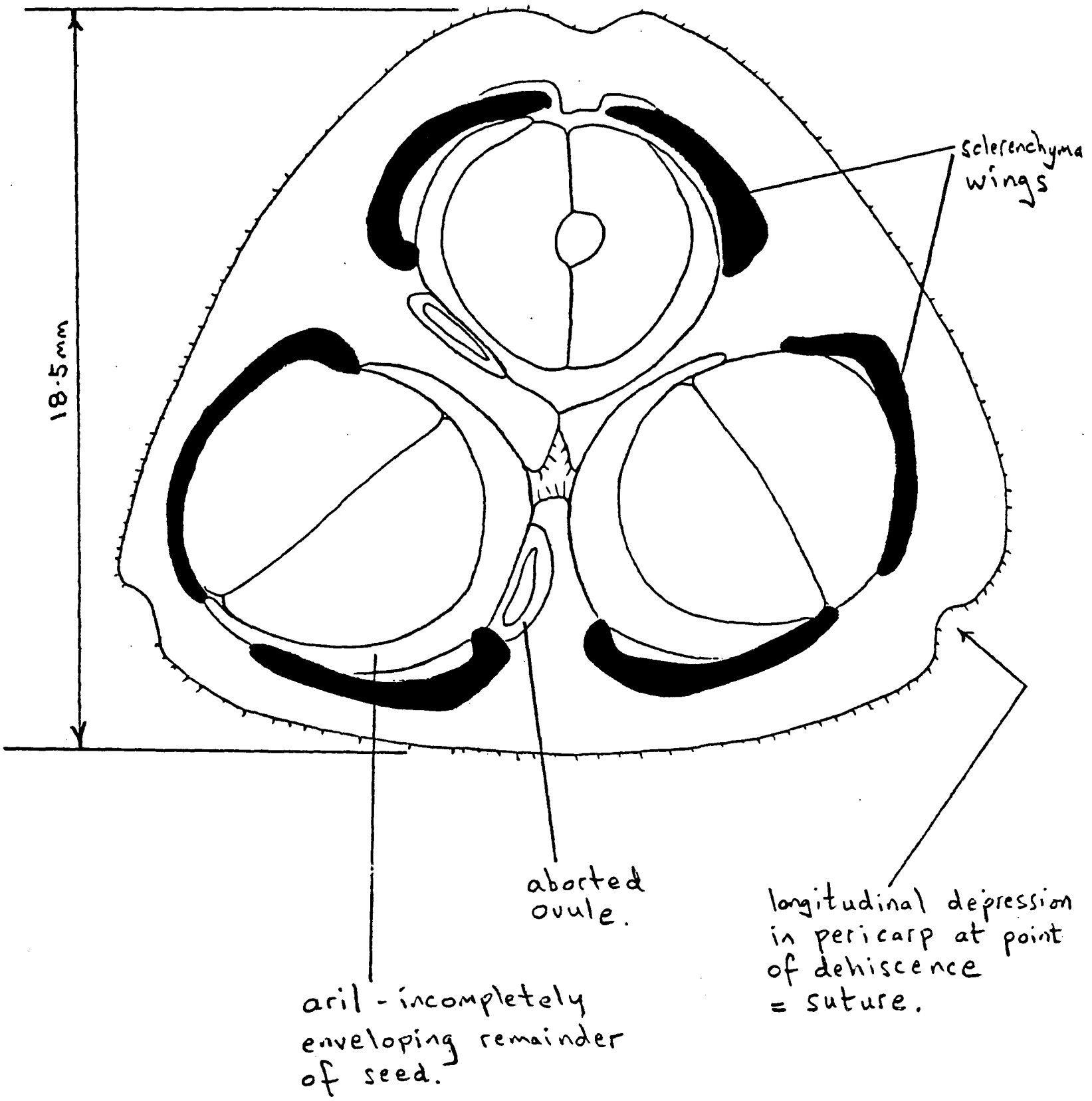


FIG: 4.1 TRICHILIA EMETICA Vahl
Mature three-locular fruit in transverse section.
Plan.

A.Angus 1028
N.Zimbabwe

TRICHILIA EMETICA Vahl

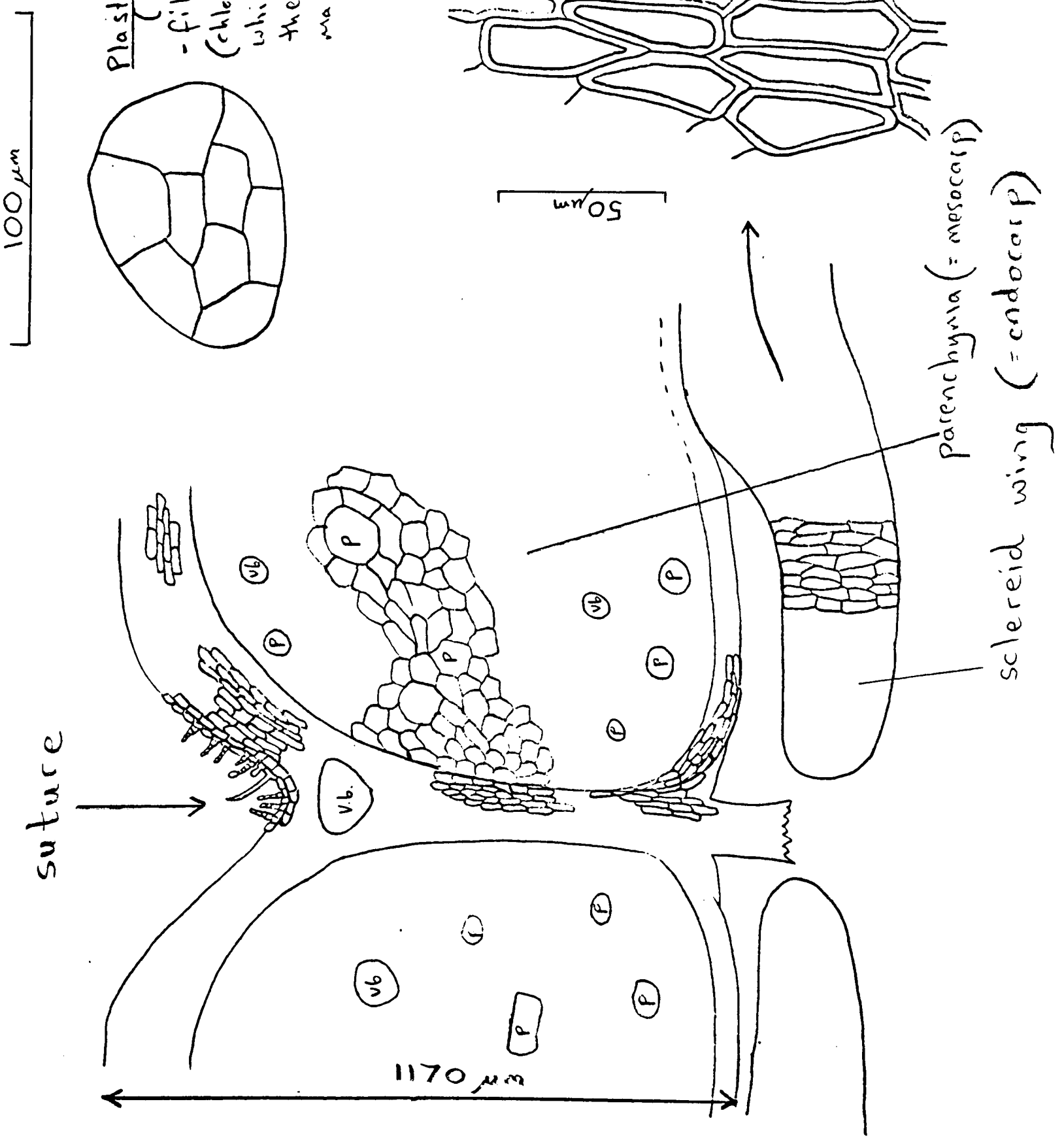


FIG: 4.2 TRICHILIA EMETICA Vahl
Mature fruit in transverse section.
Tissue plan and detail of cells in region of suture.

A.Angus 1028

N.Zimbabwe

The hairs are so dense that there is no well defined epidermis.

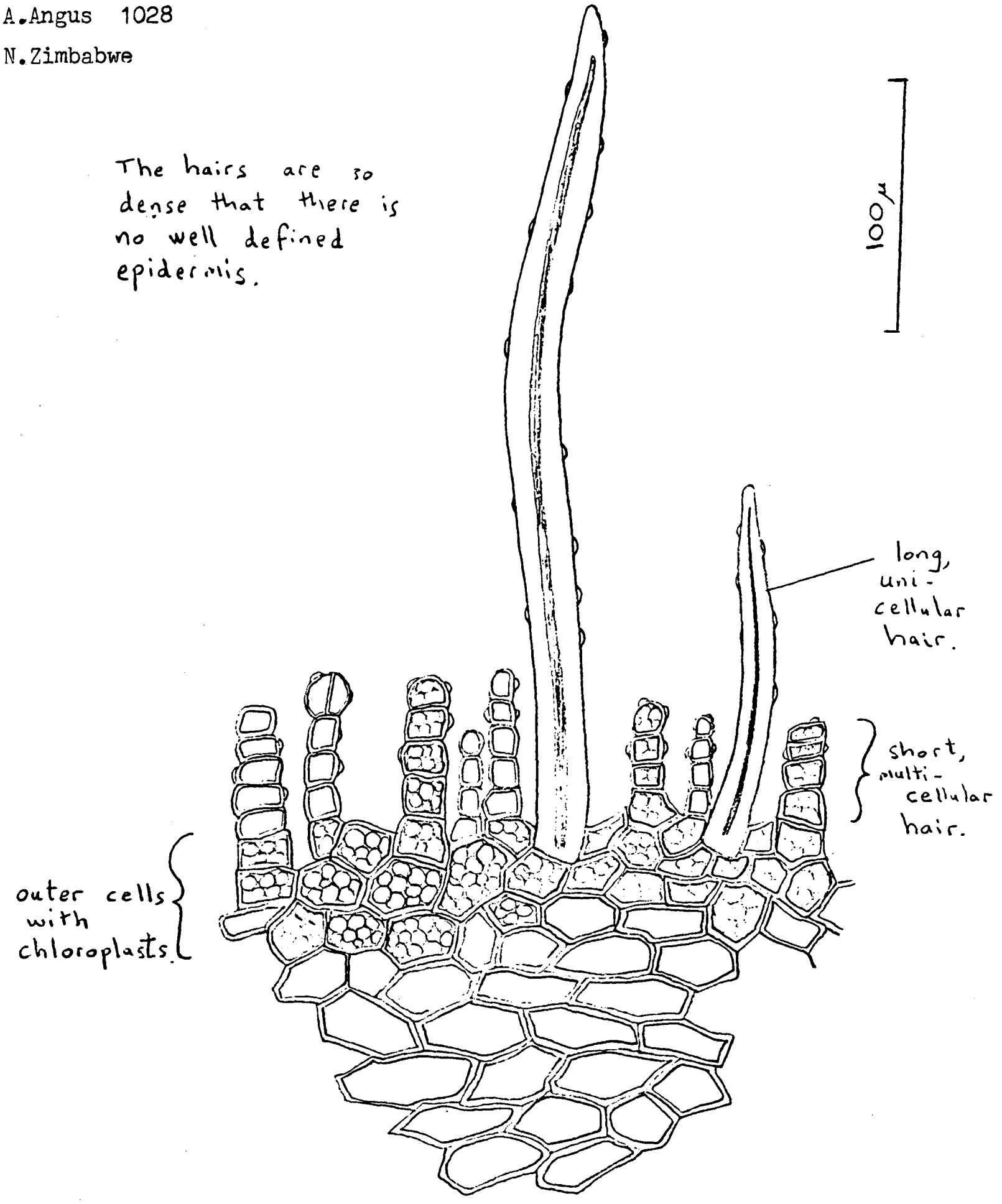


FIG: 4.3 TRICHILIA EMETICA Vahl

Mature fruit in transverse section.

Outer few layers of cells (exocarp) with unicellular hairs.(long) and multicellular hairs (short).

illustrations. When the word 'aril' is used, it is used in the general sense although perhaps 'fleshy seed appendage' would be more appropriate. See Cheek (1989) for a useful discussion of this topic.

The descriptions are based on the specimens named at the beginning of each but in some cases other collections of the same species or genus were also examined. Unless these were significantly different, they are not mentioned except that details of the material are given at the foot of the description. The genera are dealt with in the order in which they are covered in Pennington & Styles (1975) and, in view of the comparatively small number in each genus, the species are in no particular order except in Trichilia where the spirit material is covered first.

Trichilia emetica Vahl (A. Angus 1028; ZAMBIA; FHO)

FIGS. 4.1, 4.2, 4.3

A loculicidally dehiscent 3-valved capsule; pyriform to sub-globose and slightly asymmetric, slightly 3-lobed in T.S.; 1.9-3.0 cm long X 1.6-2.1 cm diam.; surface smooth but minutely velutinous; pericarp coriaceous; prior to dehiscence, each suture is clearly perceptible as a narrow and shallow channel running between the poles of the capsule.

Exocarp with two classes of trichomes: (i) long (up to 400 um) and unicellular, (ii) short (up to 70 um) with 2-8 cells and (?) glandular; the whole surface covered with trichomes, the short form predominating by far.

Mesocarp 1210 (at suture) - 1760 um thick and parenchymatous; larger parenchyma cells scattered throughout the layer each filled with 4-14 plastids (= chloroplasts ?) which are occasionally seen breaking up within the cell; tannins absent; vascular bundles scattered; cells in the area of the suture elongate with their long axes in the radial plane.

Endocarp of wings of sclereid tissue on either side of each suture, each wing running the full length of the suture and terminating abruptly near the suture, with a narrow gap between the two wings and directly below the suture; 440-595 um thick over most of area with slight thickening near wing-tip (edge away from suture), the tip then recurving sharply only a short distance from the tip of a wing from an adjacent pair.

Longitudinal, radial septum originating between adjacent sclereid wing pairs, from the parenchyma (mesocarp) tissue and running the full length of the inside of the pericarp; 3 septa in this 3-valved capsule and each locule with 1 seed attached directly to the mesocarp which comes through the gap between the two sclereid wings; dehiscence occurs at the sutures, the mesocarp and endocarp tearing across a radial plane. The septa do not appear to meet (e.g. at a central column) but terminate abruptly to leave an air-space at the centre of the fruit. The ends of the septa have erect simple trichomes, however, of the sort found on the leaves of this species.

Trichilia pallida Sw. (Prance et al. s.n.; BRAZIL; FHO)

A loculicidally dehiscent 3-valved capsule; ovoid to globose; 0.9-1.2 cm long X 0.6-0.9 cm diam.; surface muricate (minute verrucae) and densely puberulous; pericarp coriaceous; prior to dehiscence, each suture just perceptible as a narrow channel running between the poles of the capsule.

Exocarp trichomes mainly on the minute verrucae, up to 900 um long, non-glandular and multicellular; minute verrucae 160-240 um long.

Mesocarp 340-380 um thick; parenchymatous; tannin in small amounts; vascular bundles scattered.

Endocarp of wings of sclereid tissue on either side of each suture, each wing running the full length of the suture and terminating abruptly near the suture, with a narrow gap between the two wings and directly below the suture; 270-350 um thick over most of the area, tapering abruptly and recurving at wing-tip only a short distance from the tip of a wing of an adjacent pair.

Septum (sometimes incomplete and only present as a low rib) originating between adjacent wing pairs, from the parenchyma (mesocarp) tissue and running the full length of the inside of the pericarp; 3 septa in this 3-valved capsule and each locule with 2 collateral seeds each attached

Pennington + Santos 10168
Brazil

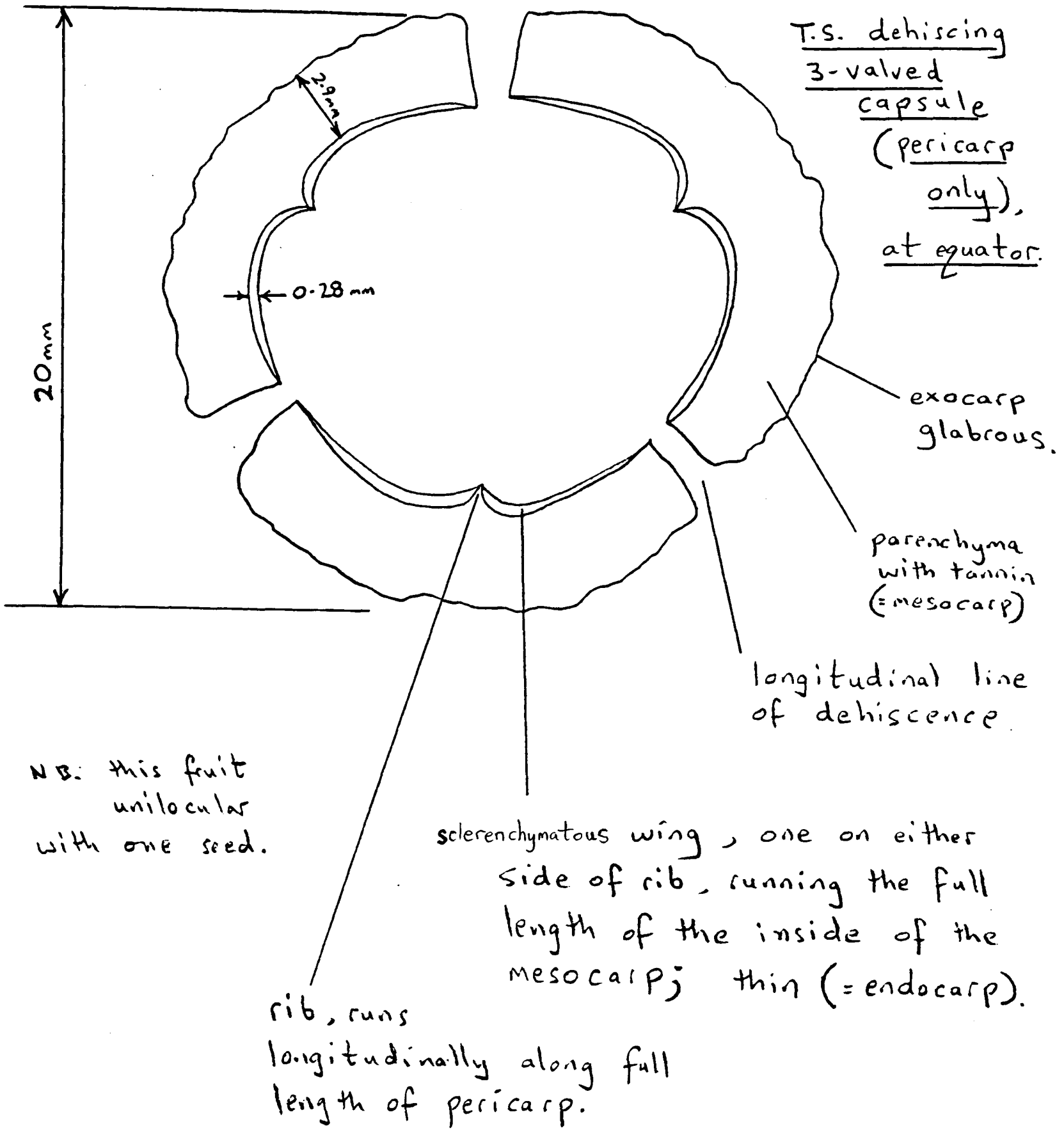


FIG: 4.4 TRICHILIA PLEEANA (Adr.Juss.) C.DC.
Mature one-locular fruit in transverse section.
(Pericarp only shown).
Plan.

directly to the mesocarp which comes through the gap between the two sclereid wings.

Trichilia pleeana (A.Juss.) C.DC. (Pennington & Santos 10168; BRAZIL; K)

FIG. 4.4

A loculicidally dehiscent 3-valved capsule; ovoid; 2.3-2.7 cm long X 1.7-2.0 cm diam.; surface verrucate and glabrous; pericarp coriaceous; prior to dehiscence, each suture is perceptible as a very narrow channel running between the poles of the capsule.

Exocarp lacking trichomes or papillae of any sort.

Mesocarp 2540-3900 um thick; parenchymatous; tannins present, their concentration increasing towards the inside of the layer; vascular bundles scattered.

Endocarp of wings of sclereid tissue on either side of each suture, each wing running the full length of the suture and petering out gradually towards the region of the suture, with a narrow gap between the two wings and directly below the suture; 240-450 um thick over most of its area, petering out abruptly near the wing-tips which recurve sharply only a short distance from the tip of a wing from an adjacent pair.

Septum (sometimes incomplete and only represented by a low rib) originating between adjacent sclereid wing pairs, from the parenchyma (mesocarp) tissue and running the full length of the inside of the pericarp; three incomplete or two complete with one incomplete septum in this 3-valved capsule produce 1 or 2 locules, each locule with 1 seed only attached directly to the mesocarp which comes through the gap in between the two sclereid wings; dehiscence occurs at the sutures, the mesocarp and endocarp tearing across a radial plane.

Trichilia hirta L. (Pennington et al. 10018; MEXICO; K)

A loculicidally dehiscent 3-valved capsule; +/- globose; 1.1-1.3 cm diam.; surface smooth to slightly verrucose and puberulous; pericarp cartilaginous; prior to dehiscence, each suture perceptible as a narrow channel running between the poles of the capsule.

Exocarp trichomes up to 45 um long, each of 2-4 cells and non-glandular.

Mesocarp 570 (at thinnest suture)-720-810 um thick, parenchymatous with tannins, vascular bundles scattered.

Endocarp of wings of sclereid tissue on either side of each suture, each wing running the full length of the suture and petering out gradually

towards the suture, with a narrow gap between the two wings and directly below the suture; <40 um thick over most of area but thickening considerably (up to 450 um) near the wing tips, the tip then recurving sharply only a short distance from the tip of a wing from an adjacent pair.

Septum originating between adjacent sclereid wing pairs, from the parenchyma (mesocarp) tissue and running the full length of the inside of the pericarp; 3 septa in this 3-valved fruit give 3 locules, each locule with 2 collateral seeds.

Rehydrated material

The following notes on Trichilia specimens are from rehydrated material. All exhibit a sclerenchyma arrangement similar to that in the specimens above, i.e. wings of sclerenchyma on either side of the suture, the wing tips recurving and often running a short distance down either side of the septum or rib. In view of this and since it is difficult to estimate how much rehydration gives a deformed picture of the original fruit, measurements and other observations were more limited than with the spirit material.

Trichilia tessmannii Harms UNH 11; NIGERIA; FHO)

Exocarp with short (<100 um long) multi-cellular, possibly glandular trichomes.

Mesocarp parenchymatous with much tannin.

Sclerenchyma wings of fairly uniform thickness, composed of sclereids only.

Trichilia dregeana Sond. (J.H.Ross 1271; SOUTH AFRICA; FHO)

Exocarp with two classes of trichomes: (i) long (up to 240 um) and unicellular, (ii) short (up to 48 um) each of 2-6 cells and some glandular.

Mesocarp 600-1100 um thick.

Wing-tips peter out near suture; sclerenchyma up to 1200 um thick at bend of wing-tip; sclereids only.

Trichilia capitata Klotzsch

(Leach & Rutherford-Smith 10939; MOZAMBIQUE; FHO)

Glabrous.

Mesocarp 485-890 um thick; most cells of the innermost layer of parenchyma (immediately adjacent to the sclerenchyma) have one large cubic to oblong to rhombic crystal inclusion, the frequency of cells possessing this feature increasing to 100% where the layer follows the sclerenchyma down the septum for a short distance.

Wings 100-120 um thick over most of area, but up to 340 um thick at the bend of the wing tip; sclereids towards the outside and fibres towards the inside.

Trichilia rubescens Oliv. (Evrard 5784; CONGO; FHO)

Glabrous.

Mesocarp 220-450 um thick, parenchyma with some tannin; many channels (up to 60 um diam.) running through the layer.

Wings peter out towards suture but are c.200 um thick over most of their span.

Trichilia micrantha Benth. (Maguire et al.-NYBG- 56515; BRAZIL; FHO)

Poor material: few data.....

Glabrous.

Some tannin in outer parenchyma.

Sclereids and fibres present.

Trichilia lepidota Mart. (Steyermark -NYBG- 88275; VENEZUELA; FHO)

ssp. leucastera (Sandw.) Pennington

Exocarp with multicellular stellate hairs (to 280 um long) and muricate (minute verrucae).

Mesocarp 400-650 u thick; tannins; scattered channels.

Sclerenchyma 190-320 um thick over most of area but up to 650 um at the bend in the wing-tip; sclereids and fibres present.

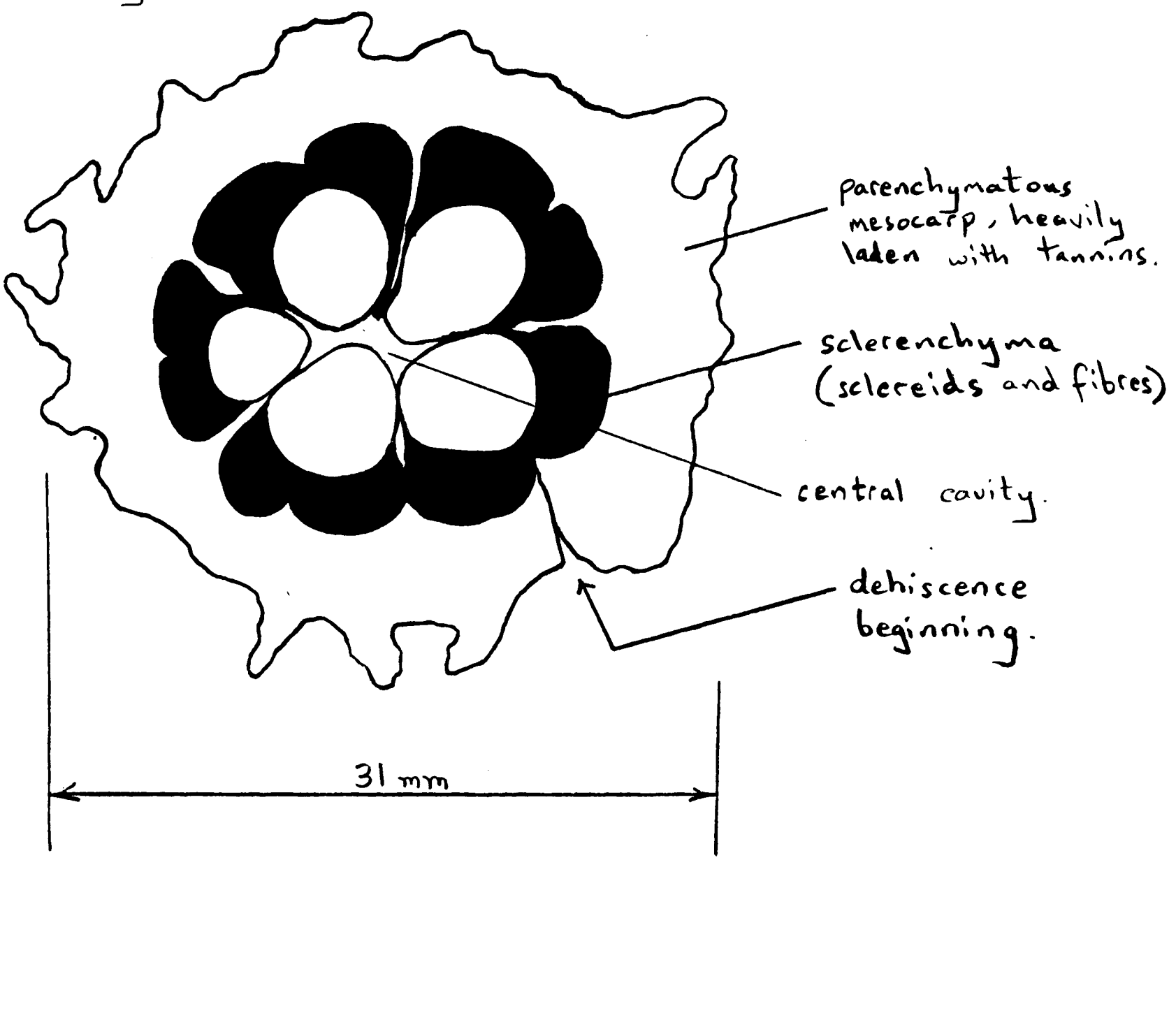
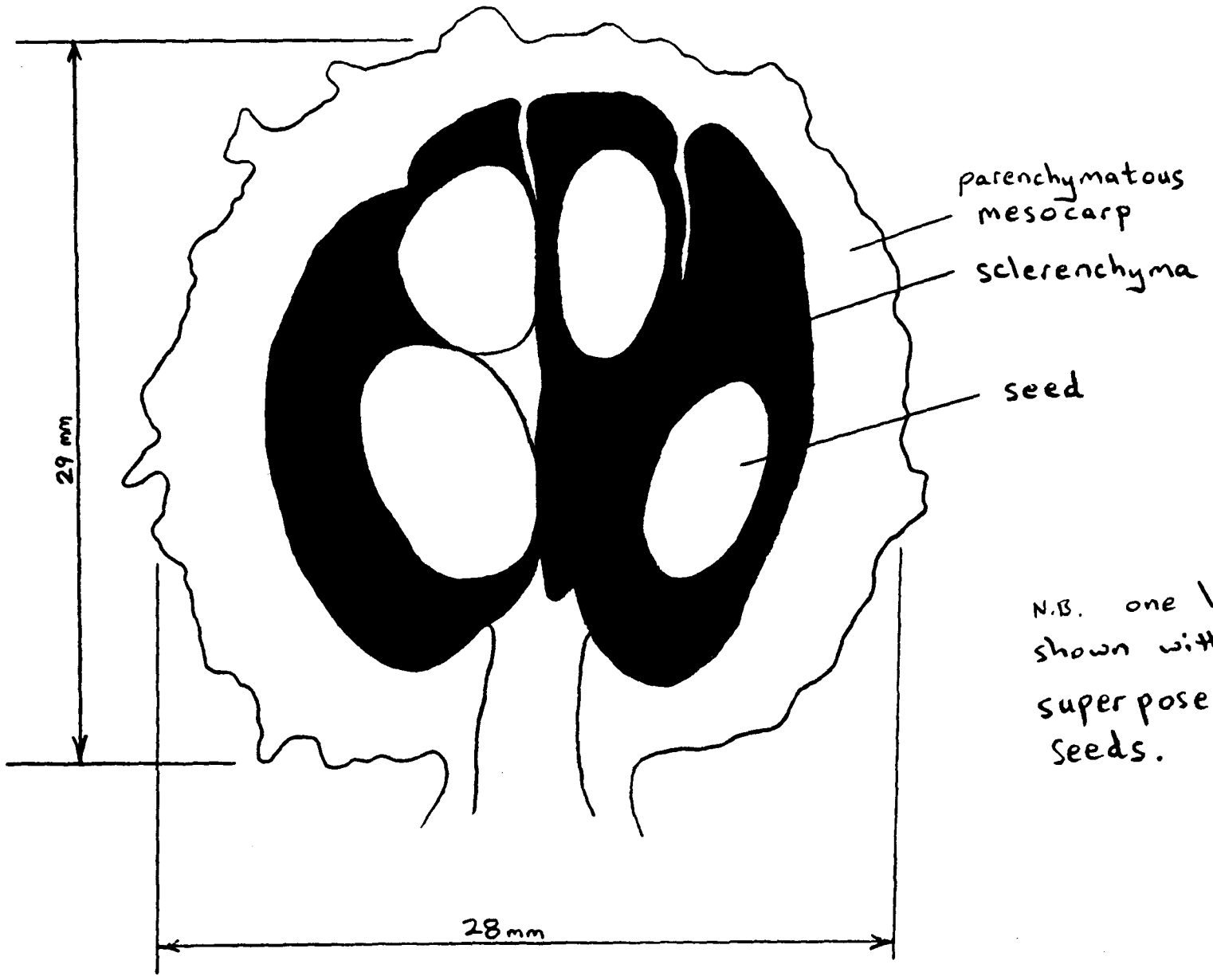


FIG: 4.5 PSEUDOBERSAMA MOSSAMBICENSIS (Sim) Verdcourt
Mature five-locular fruit in transverse section.

cheek et al. 1603.
Kenya



N.B. one locule shown with two superposed seeds.

FIG: 4.6 PSEUDOBERSAMA MOSSAMBICENSIS (Sim) Verdcourt
Mature fruit in longitudinal section (Sub-median plane).
Five-locular fruit.
Plan.

Pseudobersama mossambicensis (Sim) Verdcourt (Cheek et al. 1603; FHO)

FIGS. 4.5, 4.6

A loculicidally dehiscent (4- or) 5-valved capsule; globose to globose-elliptic, each valve covered by irregular lamellar excrescences to 5 mm long; 2.8-3.8 cm long X 3.0-3.5 cm diam.; surface sparsely and minutely puberulous; pericarp woody; sutures perceptible as narrow and very shallow furrows running between the poles of the capsule or (in some fruits) totally obscured by the excrescences; vivid red in vivo.

Exocarp trichomes simple and uni-cellular.

Mesocarp 1.8-4.5 (-8.8, due to excrescences) mm thick; parenchyma heavily laden with tannins; vascular bundles scattered and often poorly defined.

Endocarp of sclerenchyma consists of 2 layers: (i) a 0.29-0.37 mm thick layer of sclereids on the outside and (ii) a 1.4-1.9 mm thick layer of fibres on the inside; the endocarp is broken at each septum which is formed by an invagination of the mesocarp (tannin-parenchyma) with recurved arms of the endocarp (mainly fibres) on either side of it; septa do not meet in the pericarp cavity giving an air space in the middle of the capsule.

Letouzey n.m.
Cameroon.

t.s. mature fruit

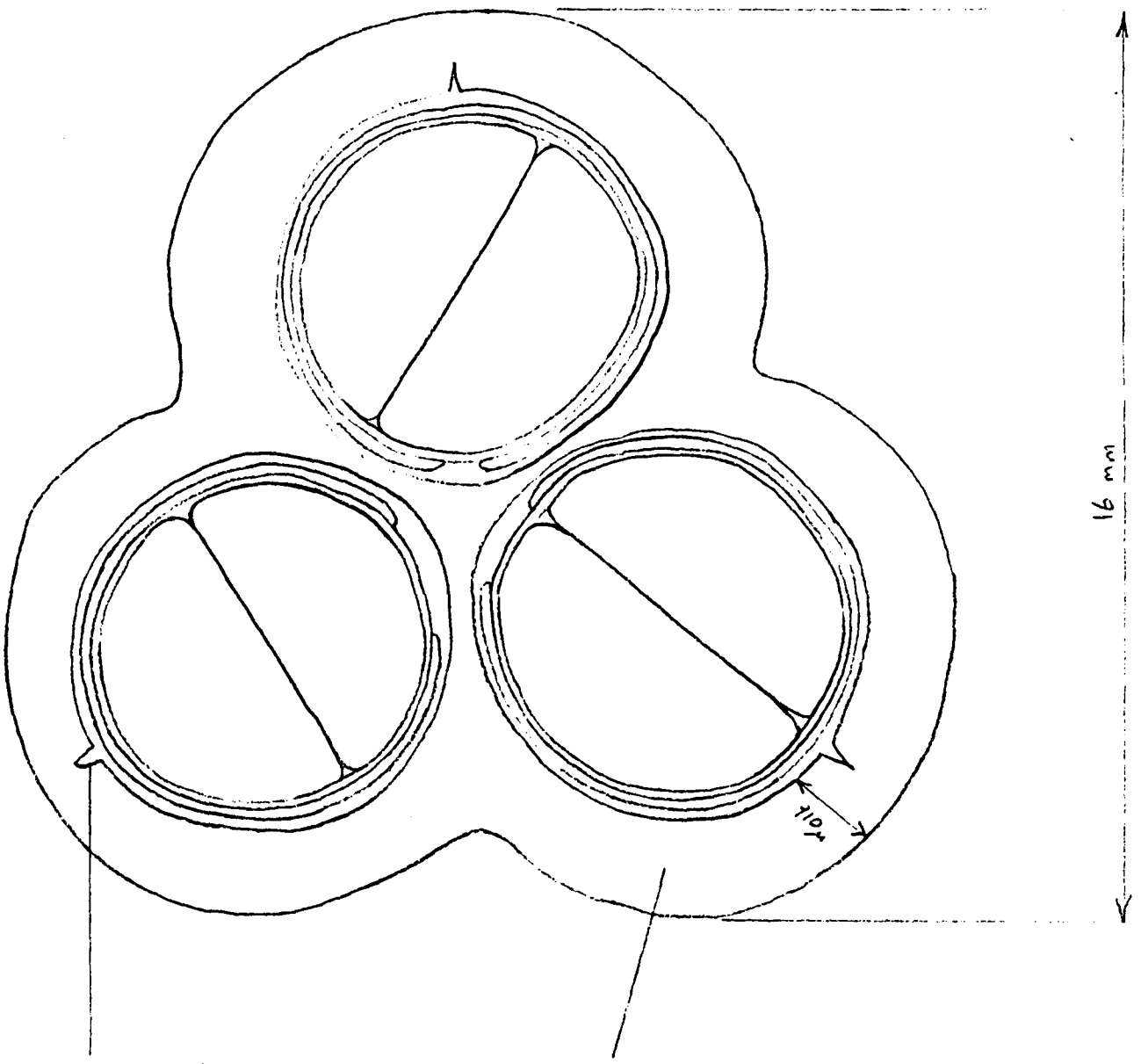


FIG: 4.7 PTERORHACHIS ZENKERI Harms
Mature three-locular fruit in transverse section.
Plan.

Letouzey s.n
Cameroon.

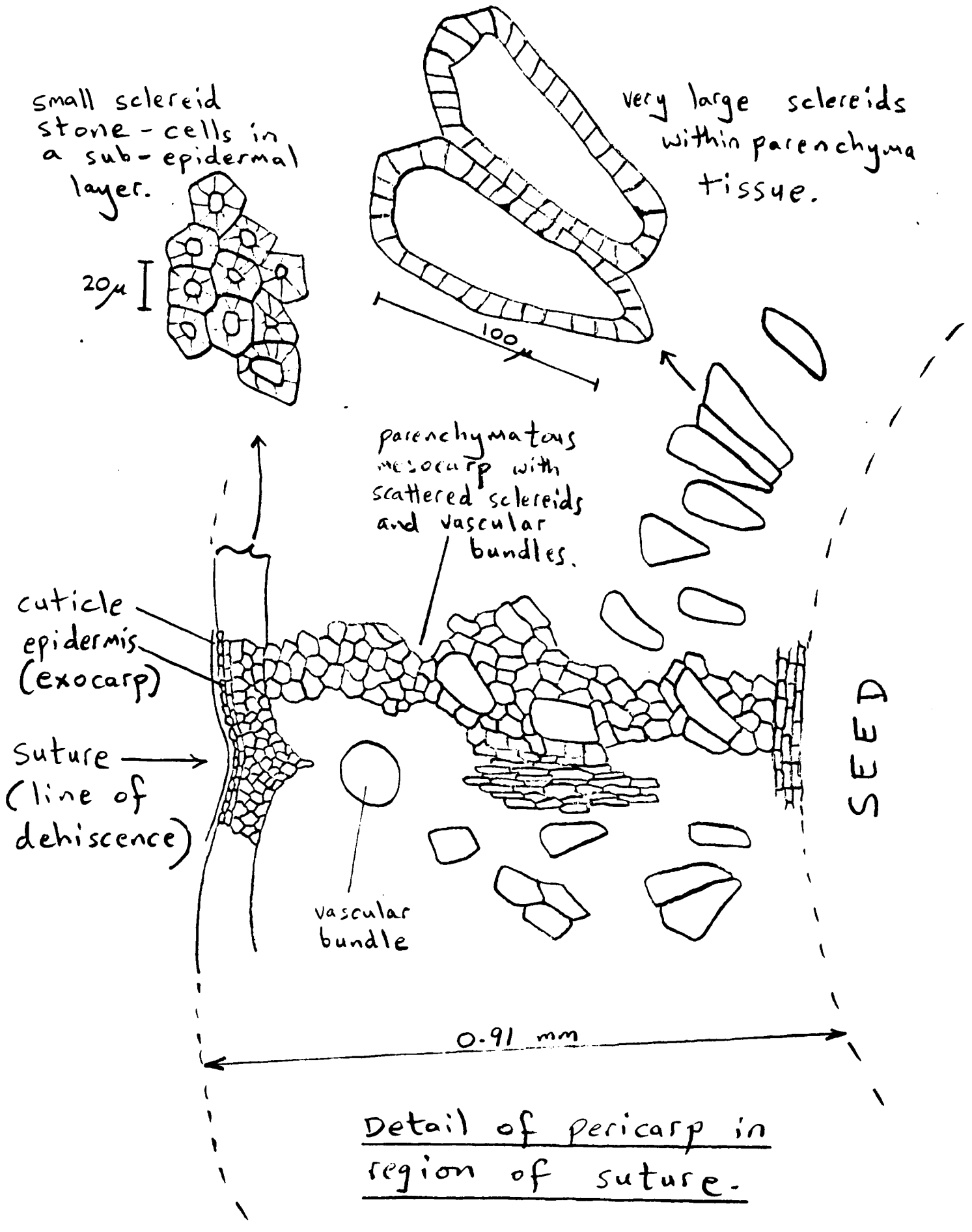


FIG: 4.8 PTERORHACHIS ZENKERI Harms
Mature fruit in transverse section:
detail of pericarp in region of suture.

Dehiscence occurs at the sutures where the mesocarp and exocarp separates along a well-defined radial line above a break in the endocarp.

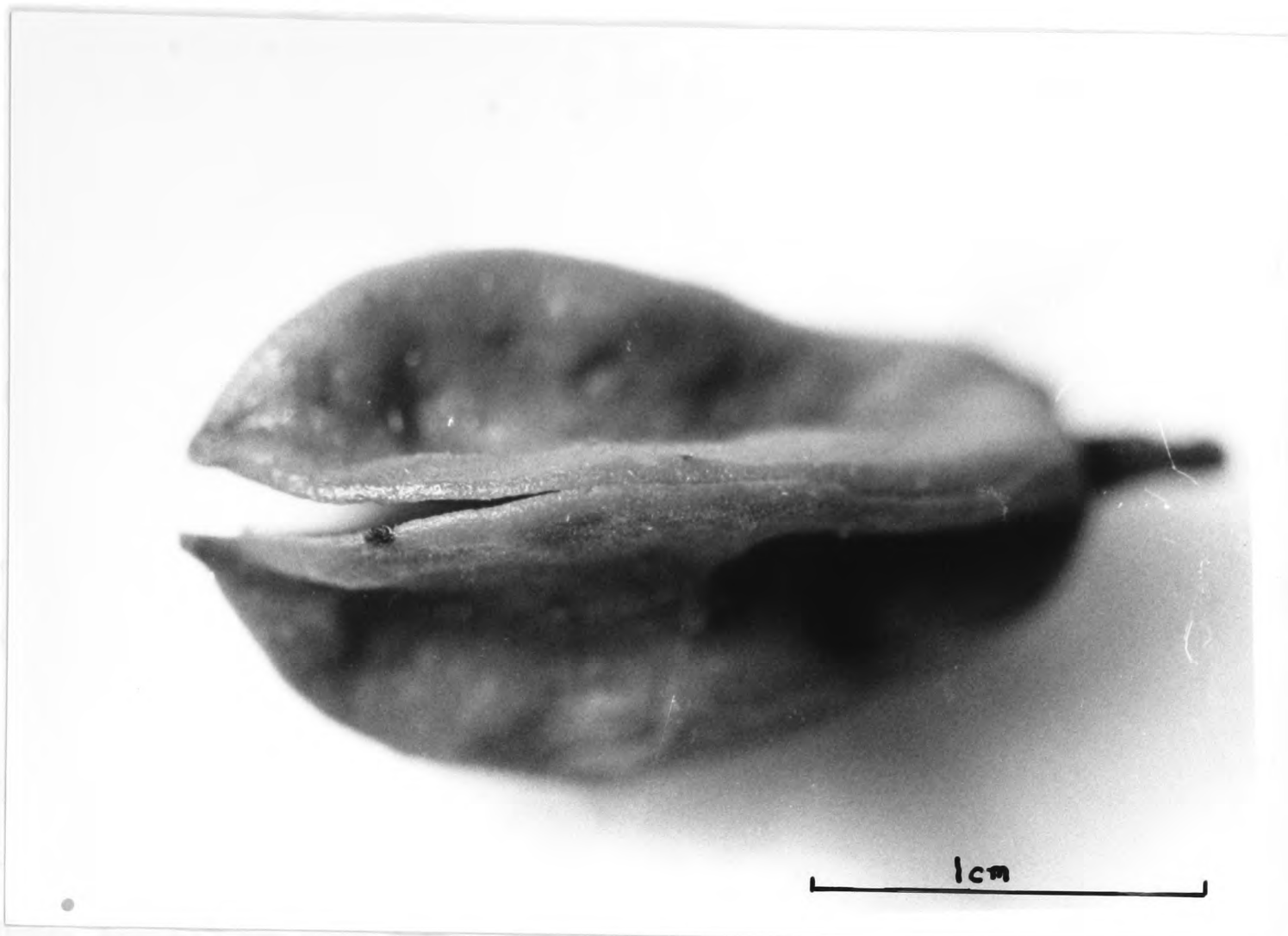
Pterorhachis zenkeri Harms (Letouzey s.n.; CAMEROON; FHO)

FIGS. 4.7, 4.8

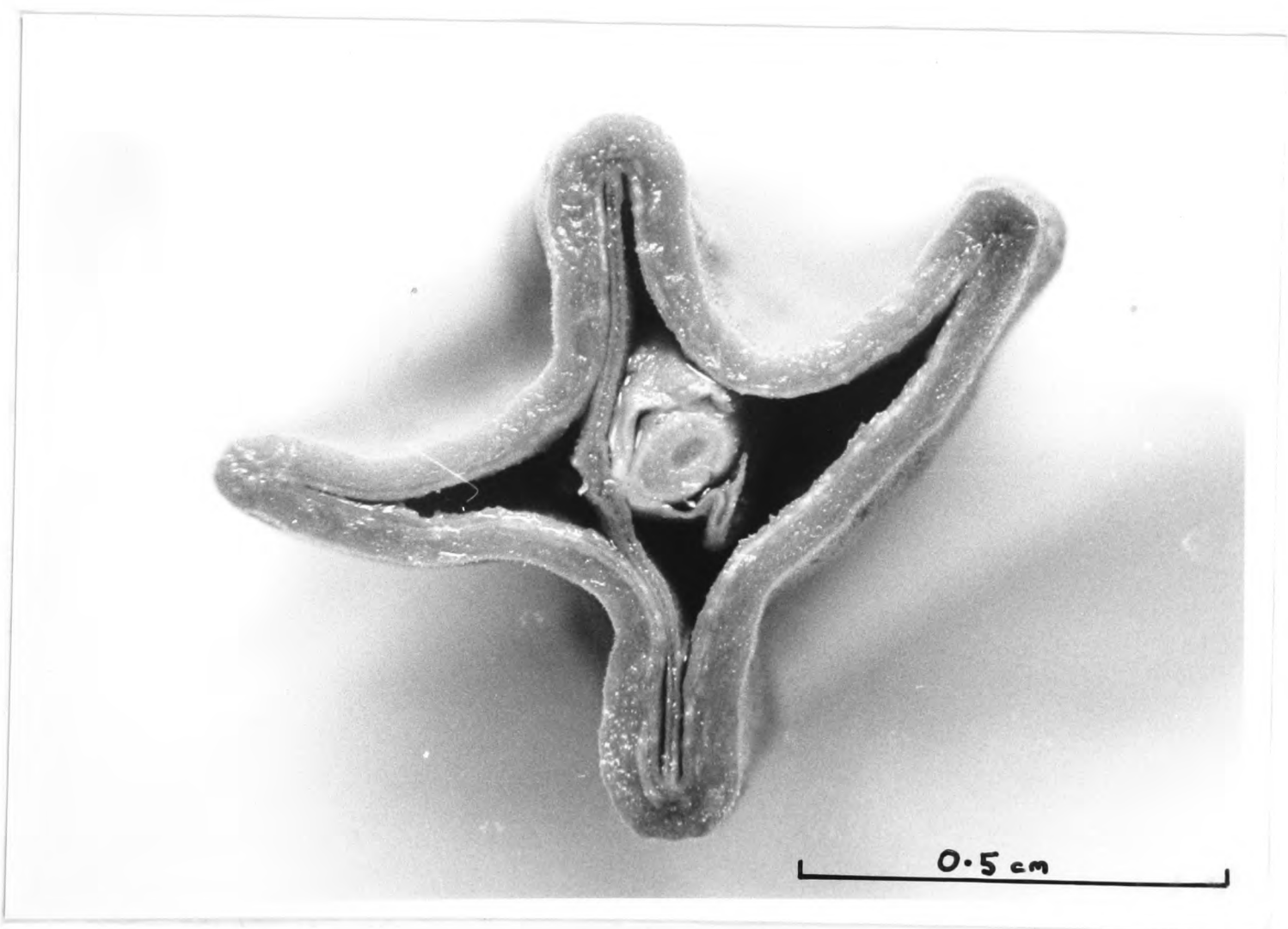
A loculicidally dehiscent 3 (or 4)-valved capsule; strongly 3 (or 4)-lobed with a short apical beak (<2 mm long); 1.5 cm - 1.7 cm long X 1.4-1.7 cm wide; surface slightly rugose and glabrous - sparsely puberulous; pericarp cartilaginous; prior to dehiscence, each suture perceptible as a shallow and very narrow furrow running down one of the lobes between the poles of the capsule.

Exocarp indumentum predominantly stellate but some unicellular simple trichomes also present.

Mesocarp / Endocarp: Below the epidermis is a very thin (2-4 cells thick) layer of small-celled parenchyma and below this a thin (50-80 um) layer of sclereid stone cells (c. 15 um diam. and of the sort found in Pyrus spp. fruits) with the rest of the pericarp (0.83-0.87 mm thick) a ground tissue of parenchyma with scattered very large elongate sclereid cells (85-130 um long); large sclereids occur mostly towards the inside of the layer with their long axes in radial planes, and also along either side of the suture parenchyma; suture parenchyma of small elongate (in the radial plane) cells; vascular bundles are scattered in this parenchymatous tissue.



A. Walsura dehiscens. Sub-mature fruit just beginning to dehisce. Note suture-line which runs the full length of the capsule. T.Clark 79.



B. Walsura dehiscens. Sub-mature fruit sectioned transversely at approx. the median plane. Note septum, running between the two sutured 'wings' of the capsule. T.Clark 79.

FIG. 4.9

Dehiscence occurs at the sutures where the suture parenchyma and the stone-cell and exocarp tissue above it tears.

Walsura dehiscens T.Clark ined. (see below) (T.Clark 79; SARAWAK; FHO)

FIGS. 4.9(A & B), 4.10(A & B), 4.11(A) & 4.12.

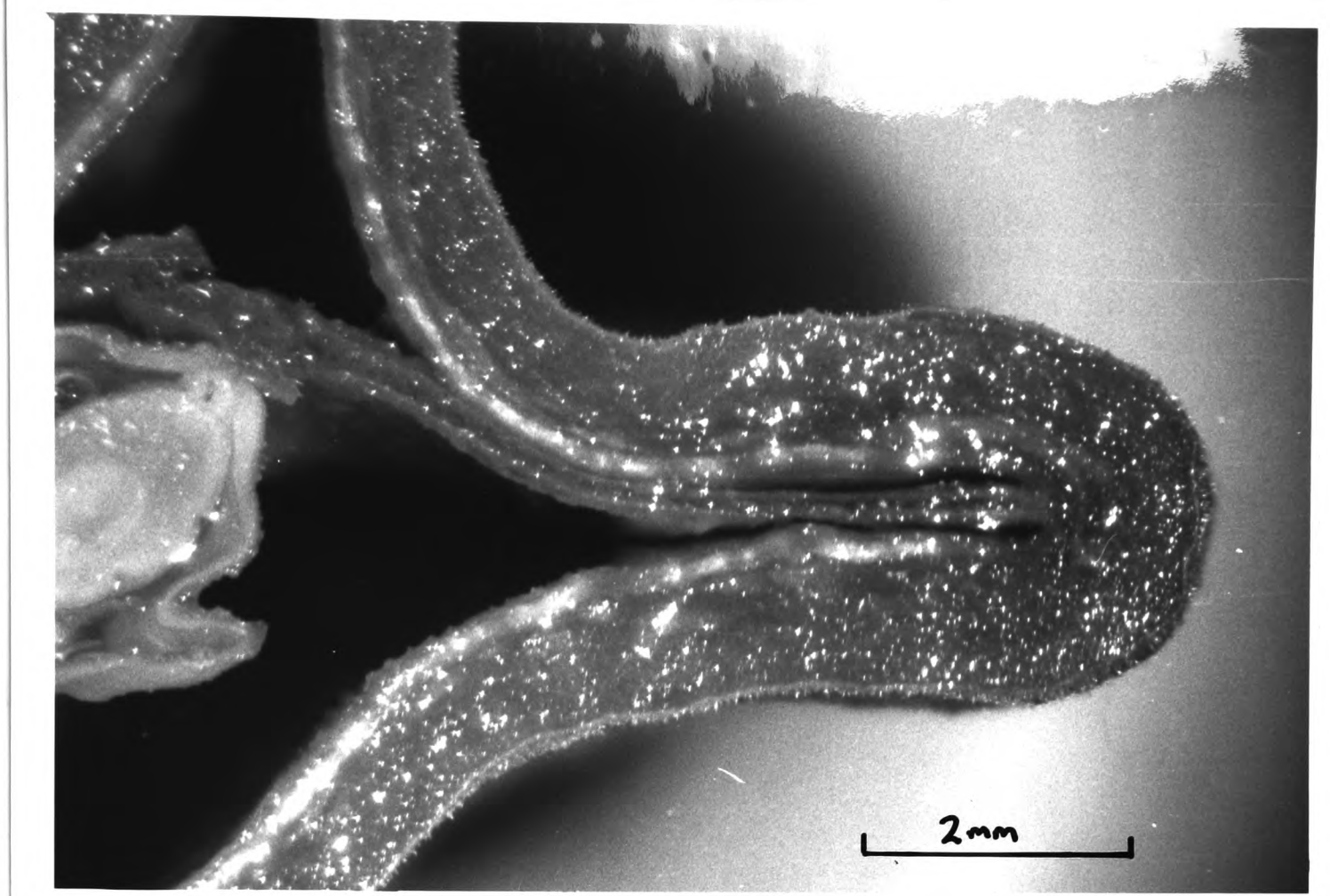
A septicidally/loculicidally weakly-dehiscent 2 (or ? 4)-valved capsule; 4-winged (immature) to rhomboidal (in T.S.) to sub-globose and slightly 4-lobed; 1.7-2.5 cm long X 0.6-0.9 cm diam.; surface slightly rugose, smooth and sparsely puberulous; olive-green (in vivo) or brown (in sicco).

N.B. This fruit is weakly-dehiscent compared with Heynea trijuga or the Trichilia spp. since the valves separate only in the distal half of their length, or (in some fruits) not at all, as the seed(s) expand. For further separation, slight external pressure has to be applied.

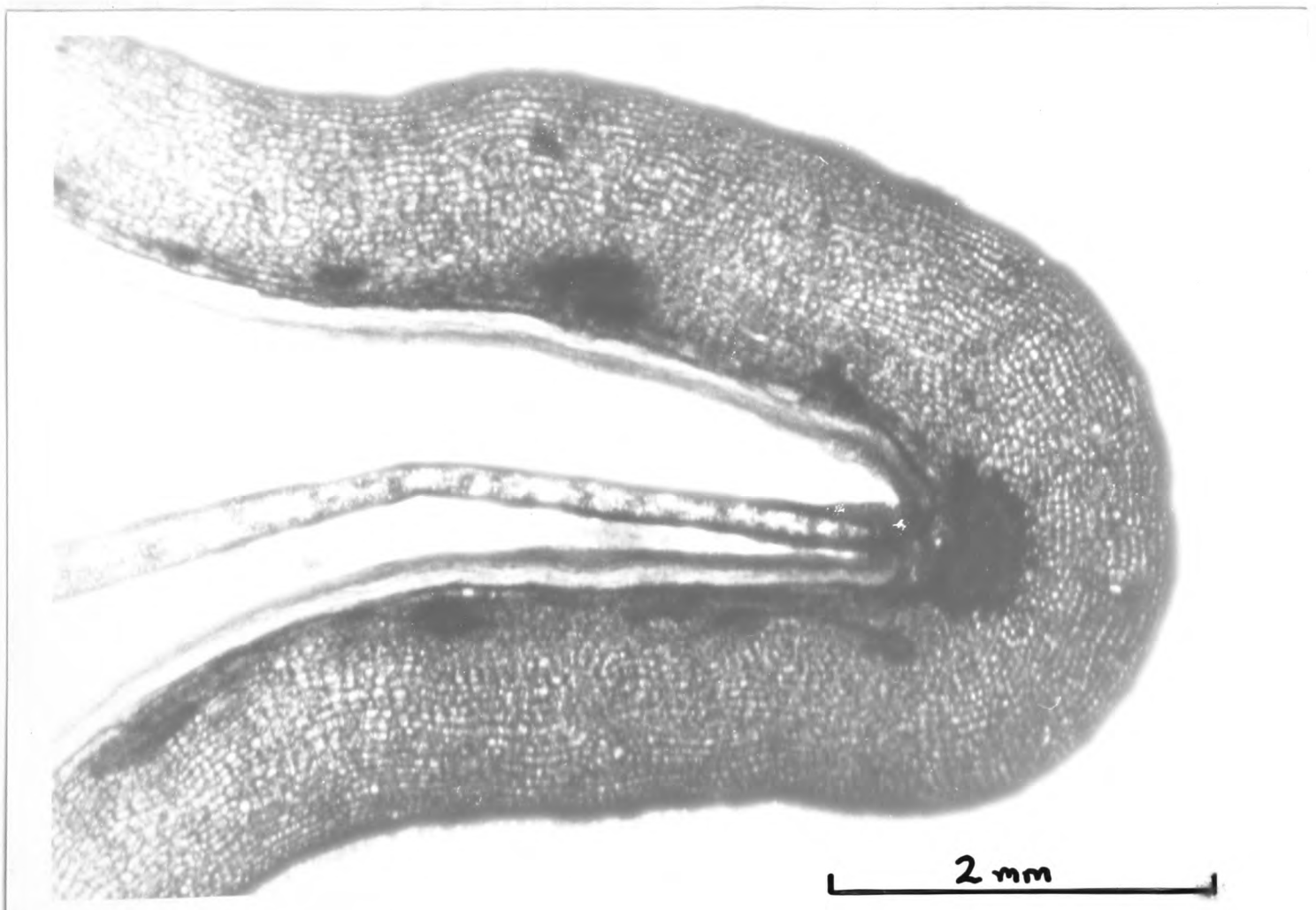
Exocarp trichomes unicellular and up to 100 um long.

Mesocarp 580-810 (-830, at a suture) um thick; parenchyma with tannins; vascular bundles scattered and one particularly large bundle at each suture.

Endocarp completely covering the inside of the mesocarp; consisting of two distinct layers: (i) 70-95 um thick layer of large-celled sclereids, on the

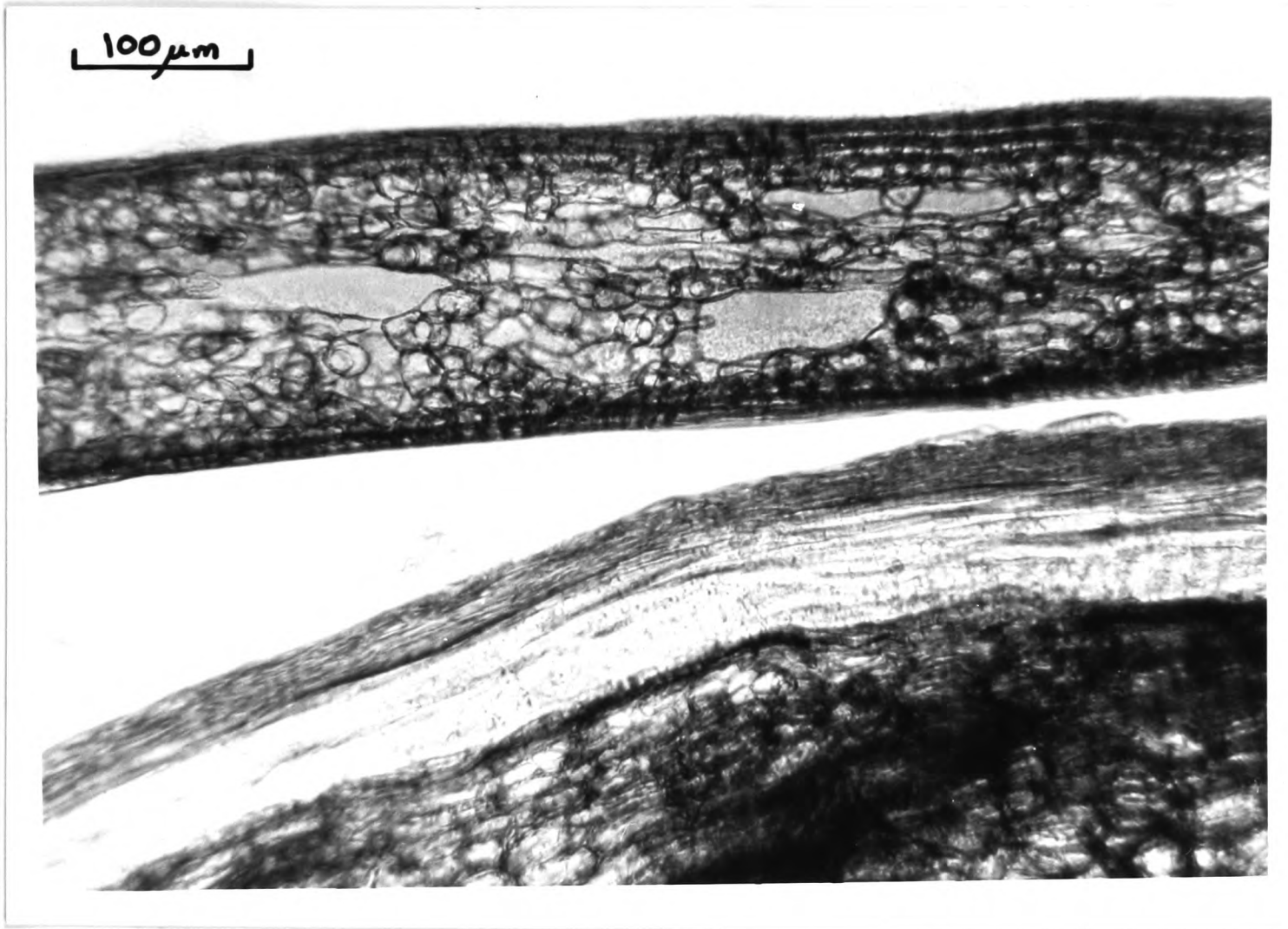


A. Walsura dehiscens. Sub-mature fruit sectioned transversely at approx. the median plane. One edge of septum. T.Clark 79.

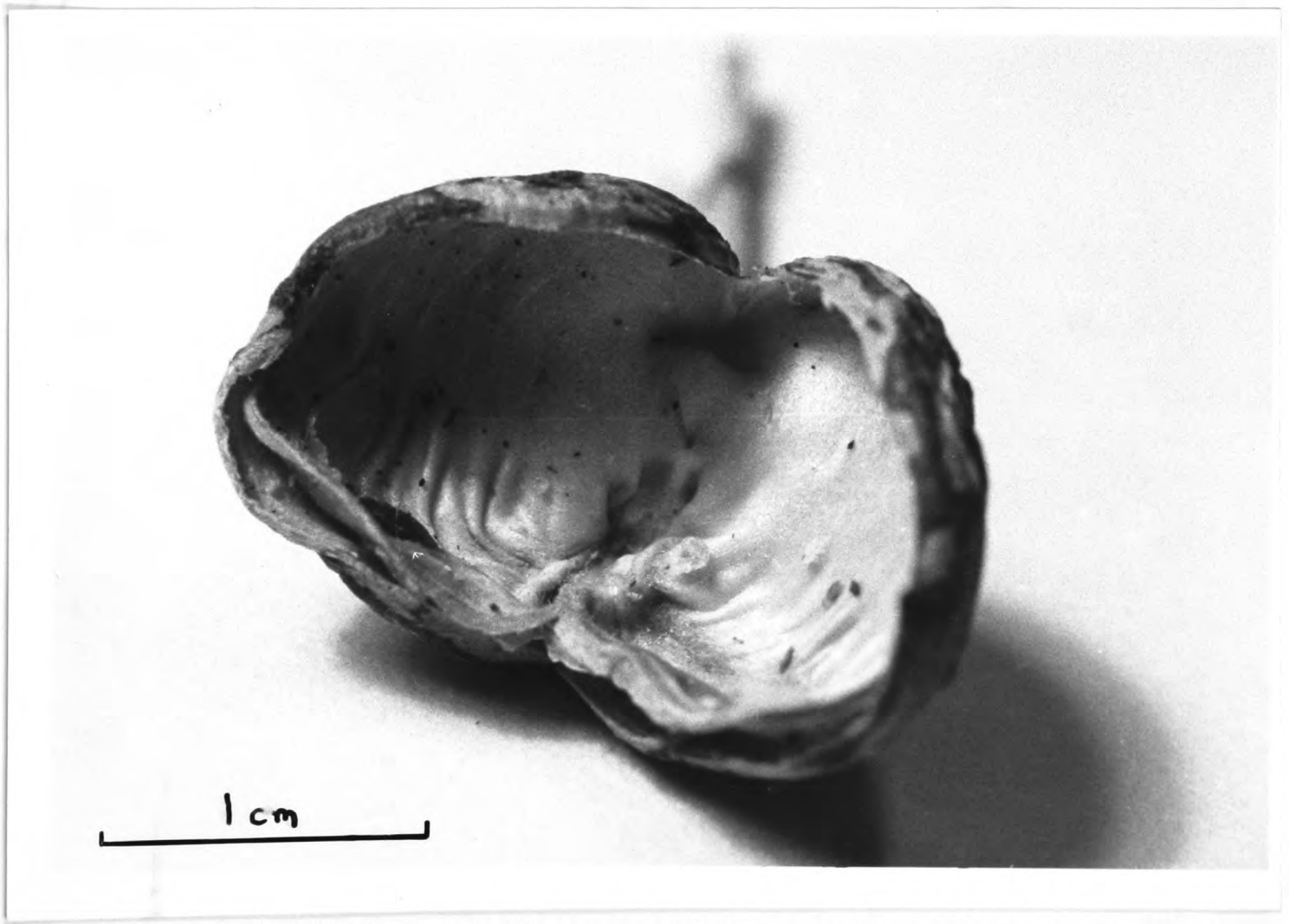


B. Walsura dehiscens. Sub-mature fruit sectioned transversely at approx. the median plane. (Thin section). T.Clark 79.

FIG. 4.10



A. Walsura dehiscens. Sub-mature fruit sectioned transversely. Detail of septum (above) and sclerenchymatous endocarp - parenchymatous mesocarp (below). In the endocarp, note the sclereids on the mesocarp side and the fibres facing the septum. T.Clark 79.



B. Heynea trijuga. A dehisced mature capsule with seed removed. T.Clark 92.

FIG. 4.11

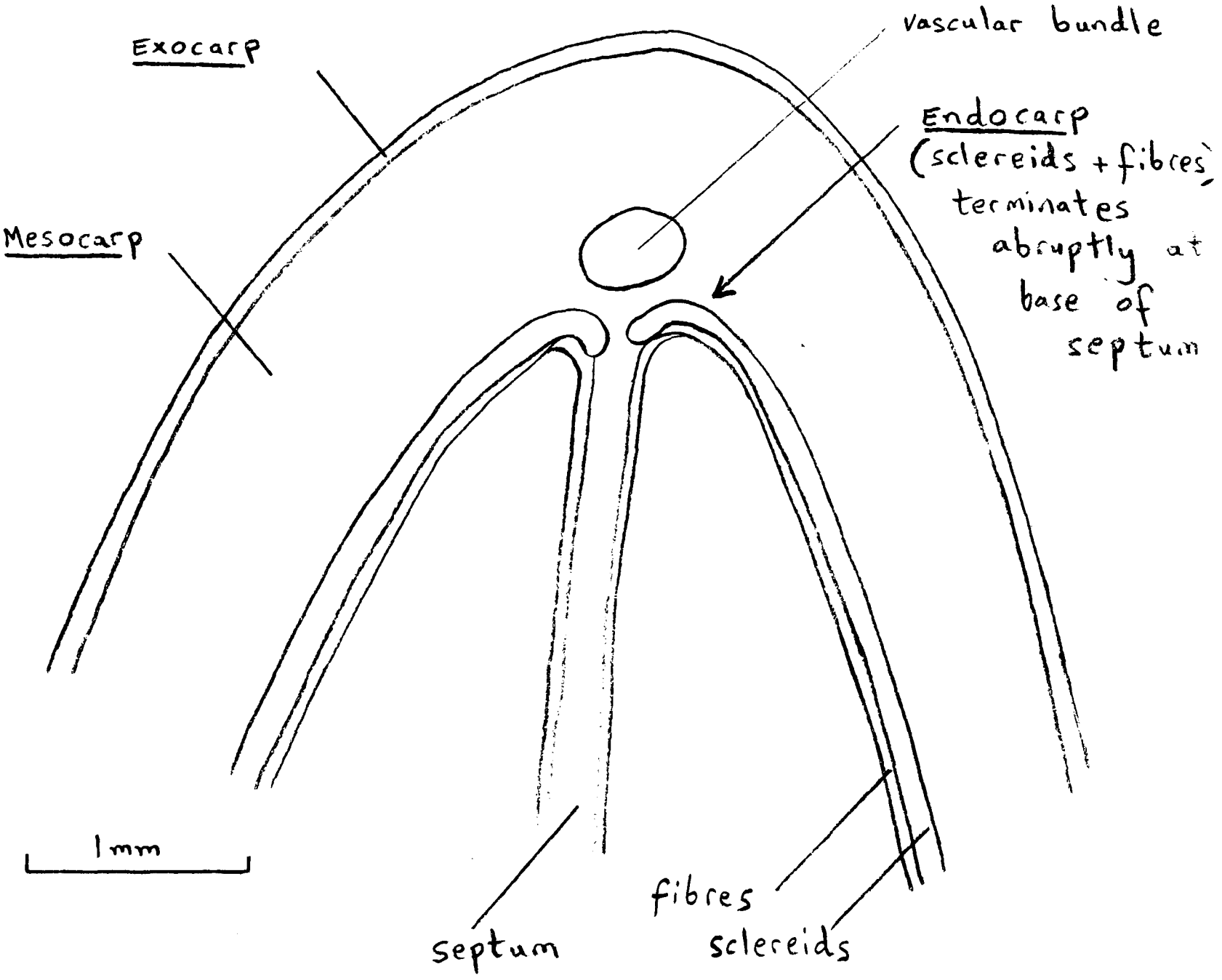


FIG. 4. 12 Walsura dehiscens. Sub-mature fruit sectioned tran sversely. Tissue displacement in the region of point of attachment of septum to pericarp.
T.Clark 79.

outside, (ii) 60-85 um thick layer of fibres on the inside; a septum originates from the fibrous layer at two opposite sutures; at a septate suture the sclereid and fibre layers both terminate abruptly near the septum base; at a non-septate suture the sclereid and fibrous layers continue with little or no change in thickness.

Septum divides the pericarp cavity completely into two locules; it is of uniform thickness (c. 180 um) and consists solely of parenchyma tissue; the outer 1-3 layers of cells are small, closely packed and cubic to rectangular but the cells in the middle (i.e. the bulk of the septum) are 2-3 times larger and have large air-spaces between them; the whole septum readily separates (even in immature fruits) down the middle to give 2 hemi-septa (i.e. separate but complete septa).

Dehiscence normally occurs only at the two sutures connected by the septum i.e. septicidally, but it also seems possibly (unusually) across the other two sutures (i.e. loculicidally), in which case causing haphazard tearing of the septum.

FRI 2016
Taman Negara,
Malaysia.

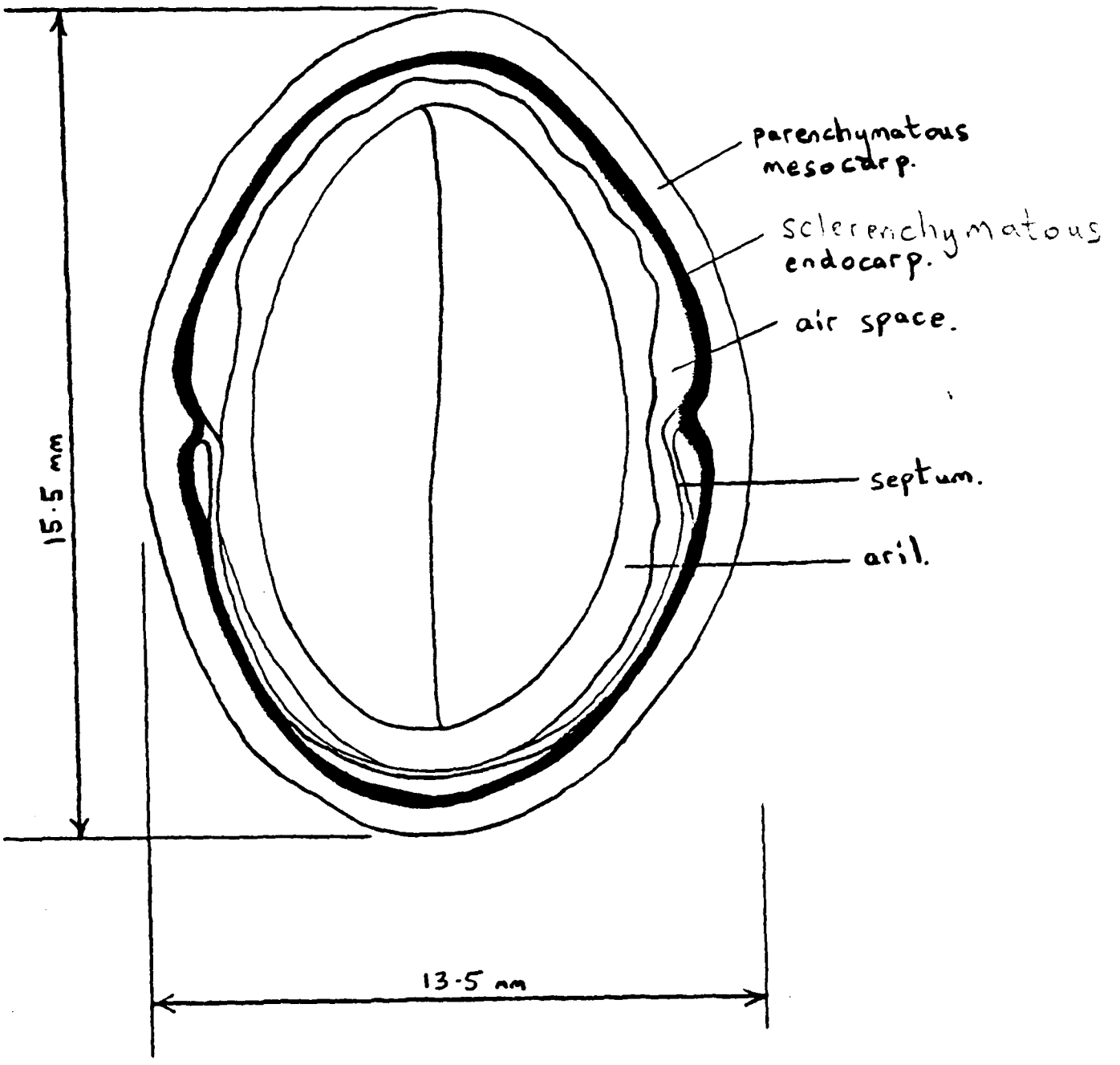


FIG: 4.13 WALSURA ROBUSTA Roxb.
Mature one-seeded fruit in transverse section.
Plan.

FRI 2016
Taman Negara,
Malaysia.

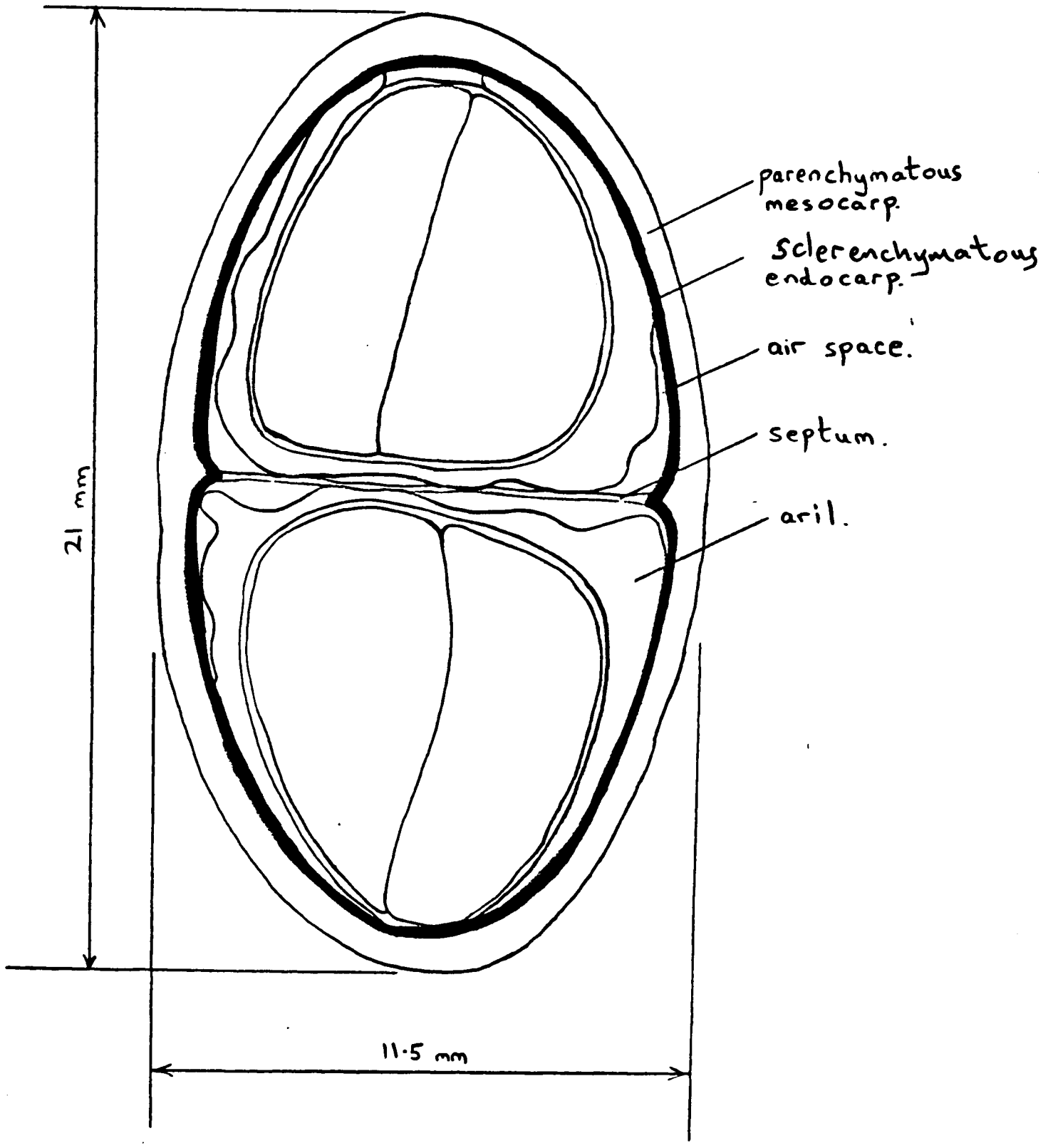


FIG: 4.14 WALSURA ROBUSTA Roxb.
Mature two-seeded fruit in transverse section.
Plan.

Walsura robusta Roxb. (FRI 2016; MALAY PENINSULA; FHO)

FIGS. 4.13, 4.14

A berry; (if 1-seeded:) globose to ellipsoid and 1.5-2.2 cm long X 1.3-1.6 cm diam., (if 2-seeded:) ellipsoid and c.1.7 cm long X 2.1 cm wide X 1.2 cm deep; surface smooth but minutely velutinous; pericarp leathery; olive-green (in vivo) or brown (in sicco).

Exocarp trichomes unicellular and simple, up to 120 um long.

Mesocarp 480-560 um thick; parenchyma with scattered vascular bundles.

Endocarp completely covers inside of mesocarp; consists of two distinct layers: (i) 48-85 um (= 2-3 cells) thick layer of large-celled sclereids, poorly defined (so could be sclereid - parenchyma intermediates), laid down with their long axes perpendicular to the layer, (ii) 55-80 um thick layer of fibres; inner (fibrous) surface sparsely to densely pubescent with prostrate to procumbent simple unicellular trichomes of length up to 385 um.

Septum originates from the fibrous layer, along a line all around the inside of the pericarp; anatomically it is very similar to the septum in W.dehiscens (see above); in 1-seeded fruits it is pushed to one side and pressed against the endocarp and in 2-seeded fruits it divided the pericarp cavity into 2 +/- equal locules.

Singhakumara 304
Sri Lanka

Walsura trifoliolata (Adr. Juss.) Harms ssp. trifoliolata

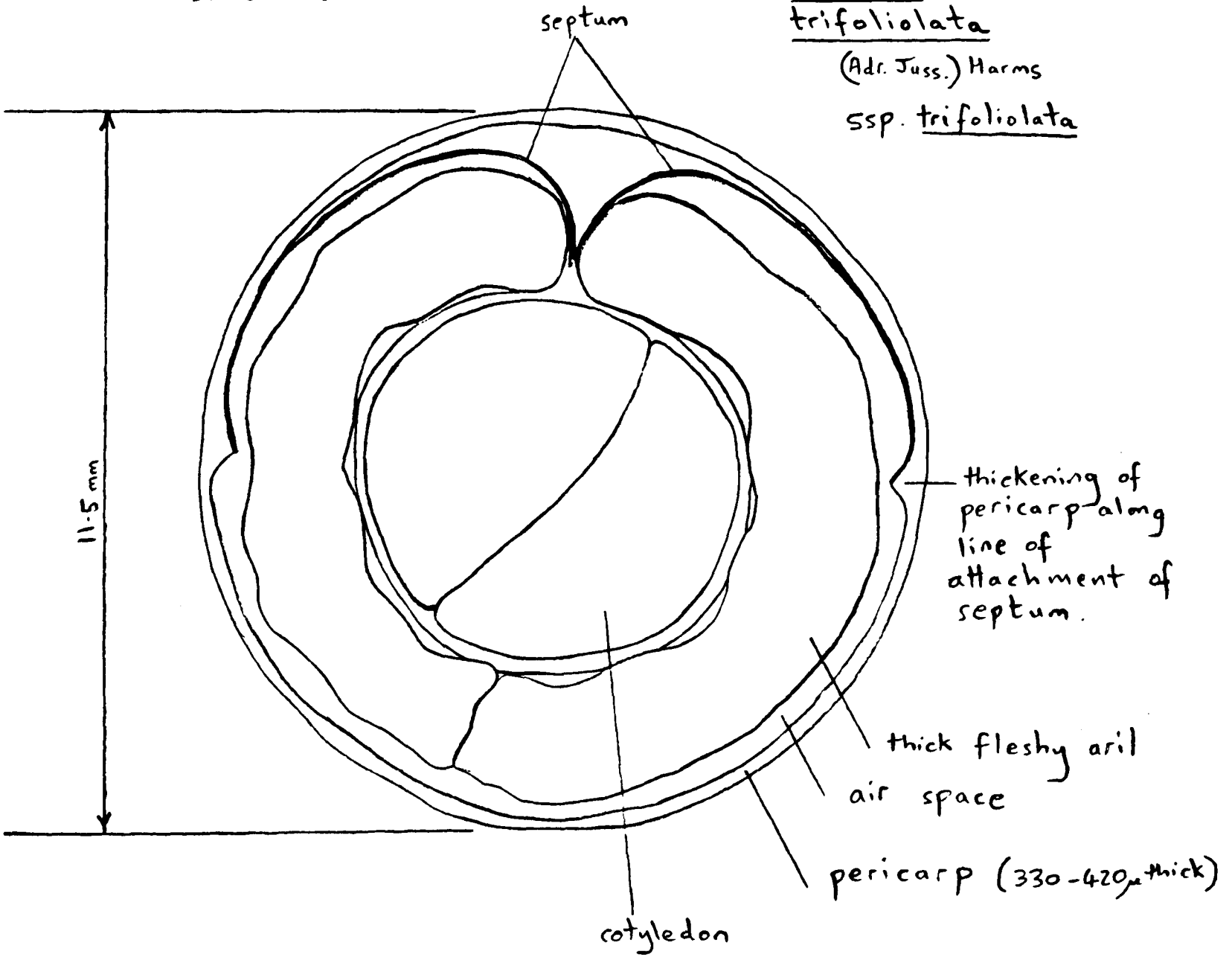


FIG: 4.15 WALSURA TRIFOLIOLATA (Adr. Juss.) Harms
Mature one-seeded fruit in transverse section.
Plan.



(i) Highly immature berry of Walsura tubulata on plant in cultivation at the Oxford Botanic Garden. (Photograph taken June 1988).



(ii) Berry of Walsura pinnata 'villamilii' in longitudinal median section, showing succulent aril around seed. Fresh material from tree at Sepilok, Sabah = T.Clark 81. (Photo. taken August, 1987).

FIG. 4.16

Walsura trifoliolata (Adr.Juss.) Harms (Singhakumara 304; SRI LANKA; FHO)

FIG. 4.15

A berry; globose; 0.9-1.3 cm diam.; surface slightly reticulate and sparsely puberulous; pericarp leathery; light-brown in vivo.

Exocarp trichomes simple and unicellular, up to 100 um long.

Mesocarp 260-380 (-400, at point of attachment of septum) um thick; parenchyma with scattered vascular bundles.

Endocarp intimately associated with the mesocarp and covering the whole inner surface of it; 40-80 um thick; not thickened at point of attachment of septum; composed of sheets of fibres in various orientations.

Septum originates from the fibrous layer along a line all around the inside of the pericarp; anatomically it is very similar to the septum in W.dehiscens (see above); in 1-seeded fruits it is pushed to one side and pressed against the fibrous endocarp and in 2-seeded fruits (rare in this species) divides the pericarp cavity into two +/- equal locules.

(Other material: T.Clark 91, Sri Lanka: FHO: ssp.trifoliolata)

Walsura tubulata Hiern. Cult. Oxford Botanic Gardens

FIG. 4.16(i) = T. Clark 93

Photograph of immature fruit only.

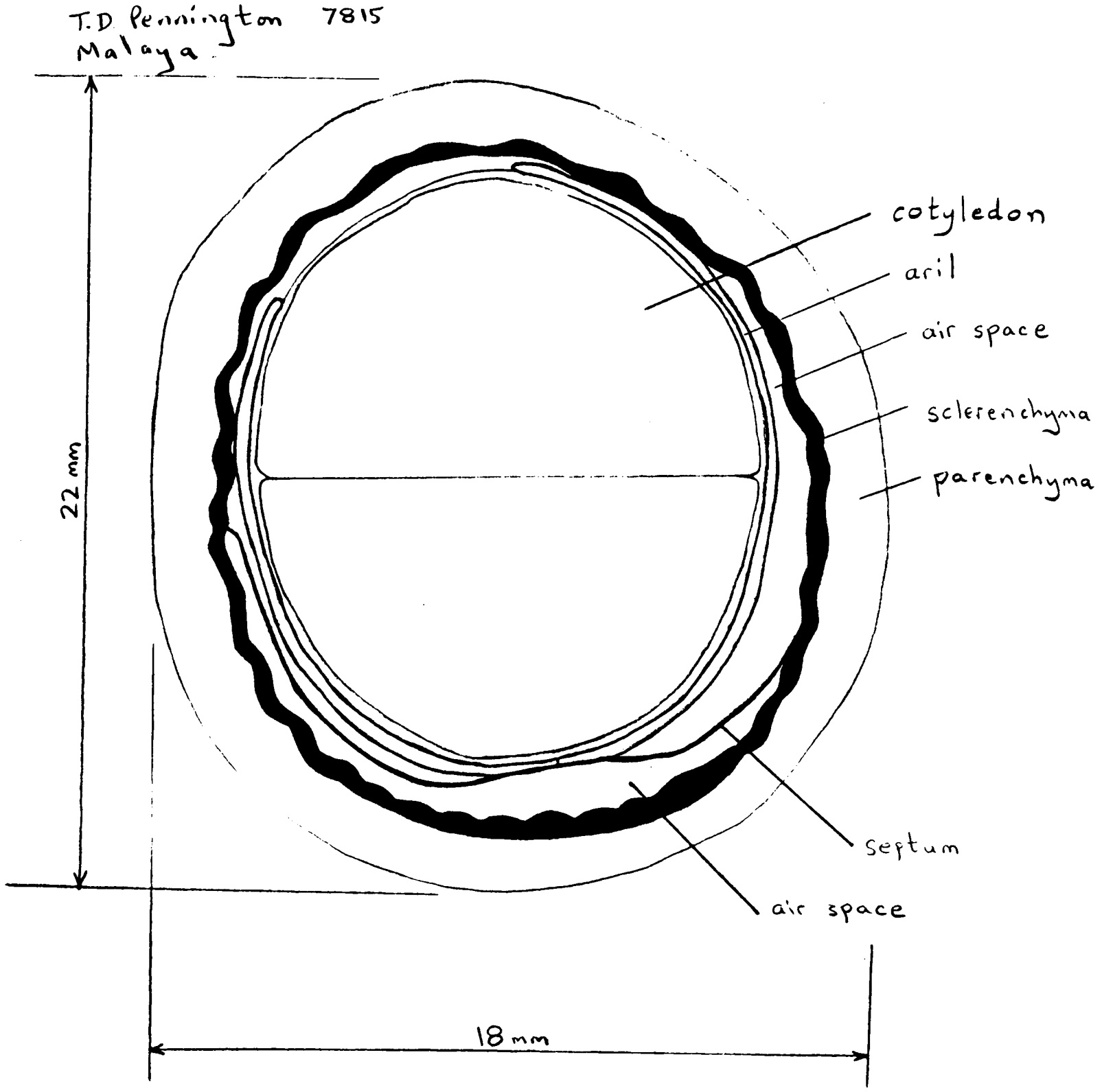


FIG: 4.17 MALSURA PINNATA Hassk.
Mature fruit in transverse section.
Plan.

Walsura pinnata Hassk. (Pennington 7815; MALAY PENINSULA; FHO)

FIG. 4.16(ii), 4.17

A berry; sub-ovoid - ellipsoid; 2.2-3.0 cm long X 1.5-1.9 cm diam.; surface smooth but minutely velutinous; pericarp leathery; pale-green to olive-green in vivo.

Exocarp trichomes simple, unicellular and up to 85 um long.

Mesocarp 1.1-1.7 mm thick; parenchyma with tannins; scattered vascular bundles and scattered bundles of fibres (3-8 cells thick).

Endocarp intimately associated with and completely covering the inside of the mesocarp; 330-660 um.thick; undulating but of even thickness throughout; composed of sheets of fibres in various orientations.

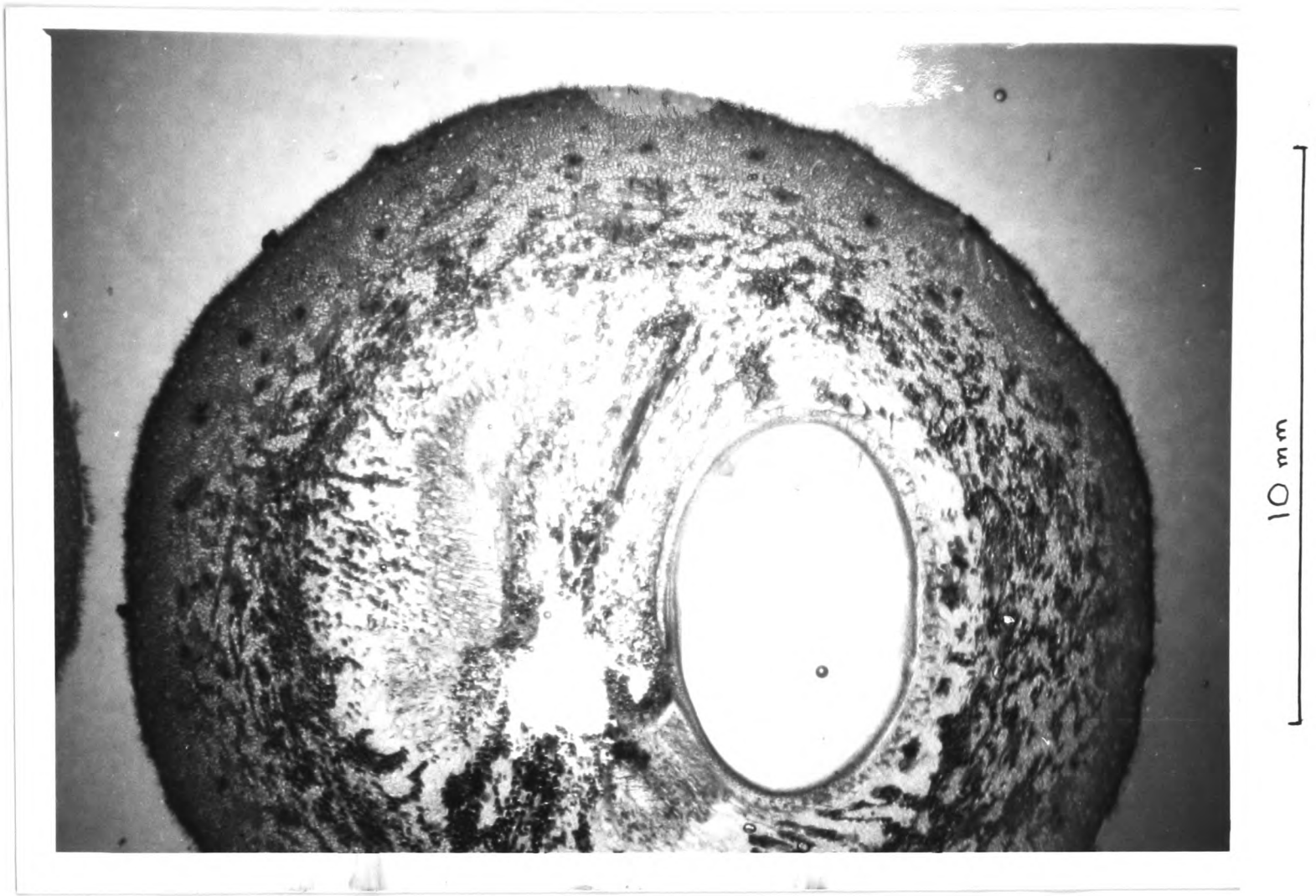
Septum originates from the fibrous endocarp along a line all around the inside of the pericarp; anatomically it is very similar to the septum in W.dehiscens (see above); in 1-seeded fruits it is pushed to one side and pressed against the inside of the endocarp and in 2-seeded fruits it divides the pericarp cavity into 2 +/- equal locules.

(Other material: FRI 891; MALAY PENINSULA; FHO)

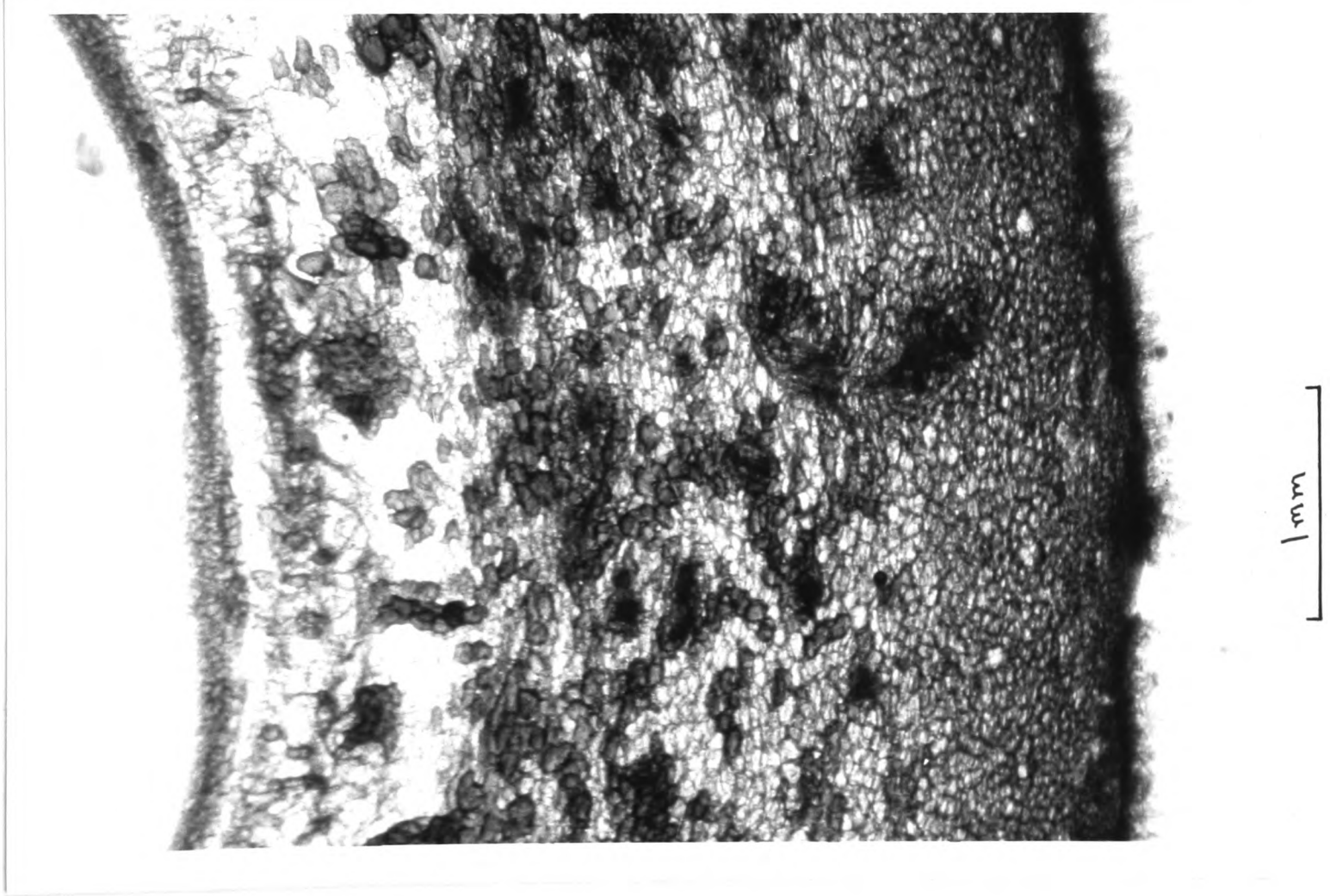


Berries of Walsura species 'A'. Fresh material taken from tree in Semengoh Forest, Sarawak = T.Clark 76. (Photo. taken June 1987).

FIG. 4.18



A. Walsura chrysogyne. Berry in transverse section in approx. the median plane. One ovule aborted, the other developed. Pennington 7831.



B. Walsura chrysogyne. Berry in transverse section to show cellular detail of pericarp. Note that most of the parenchyma cells have tannin (dark coloration). Inner most layer is part of the seed. Pennington 7831.

FIG. 4.19

Walsura sp. A (see below) (T.Clark 76; SARAWAK; FHO)

FIG. 4.18

A berry; (globose to) ellipsoidal; 2.2-2.6 cm long X 1.5-1.8 cm diam.; surface smooth but minutely velutinous; pericarp leathery; olive-green in vivo.

Exocarp trichomes unicellular and simple prostrate and 2-armed prostrate.

Mesocarp, endocarp and septum anatomy very similar to that in W.pinnata.

Walsura chrysogyne (Miq.) Bakh.f. (Pennington 7831; MALAY PENINSULA; FHO)

FIGS. 4.19

A berry; globose and 1.4-1.8 cm diam. with a short mammiform projection (0.5-1.0 mm long) near the distal end, slightly asymmetric; surface smooth but minutely velutinous; pericarp leathery; olive-green in vivo.

Exocarp trichomes simple and unicellular, up to 200 um long.

Mesocarp / endocarp: it is not possible to distinguish two separate layers as the whole is constituted solely of thin-walled parenchyma cells with very high levels of tannins; no sclerenchyma tissue present at all; some poorly defined and randomly scattered vascular tissue, but even this lacking sclerenchyma.



Capsules of Heynea trijuga, just beginning to dehisce. Fresh material taken from tree in Peradeniya Botanic Garden, Sri Lanka = T.Clark 92. (Photo. taken August 1987).

FIG. 4.20

The berry may be 1- or 2-seeded and, in the latter, the two seeds are separated by a continuation of the parenchyma tissue. This extension differs from the rest of the parenchyma only in that it has better defined vascular bundles.

(Variation: SAN 43756; SABAH; SAN)

Heynea trijuga Roxb. ex Sims (T.Clark 92; SRI LANKA; FHO)

FIGS. 4.11(B), 4.20, 4.21, 4.22(A & B)

A loculicidally dehiscent 2-valved capsule; globose (if 1-seeded) or globose to obovoidal (if 2-seeded); 1.7-2.1 cm X 1.1-1.6 cm; surface smooth and glabrous; pericarp leathery; cream to pale-brown in vivo; prior to dehiscence, sutures imperceptible.

Exocarp glabrous.

Mesocarp 880-1100 um thick (but up to 1870 um thick near a 'complex suture' - see below); parenchyma without tannins; many scattered (latex ?) channels; 70% of the cells in the 3 innermost layers (adjacent to the endocarp) have one large cubic or oblong crystal inclusion per cell.

T.D. Pennington 7927
Kinabalu, Sabah.
27-x-1963.

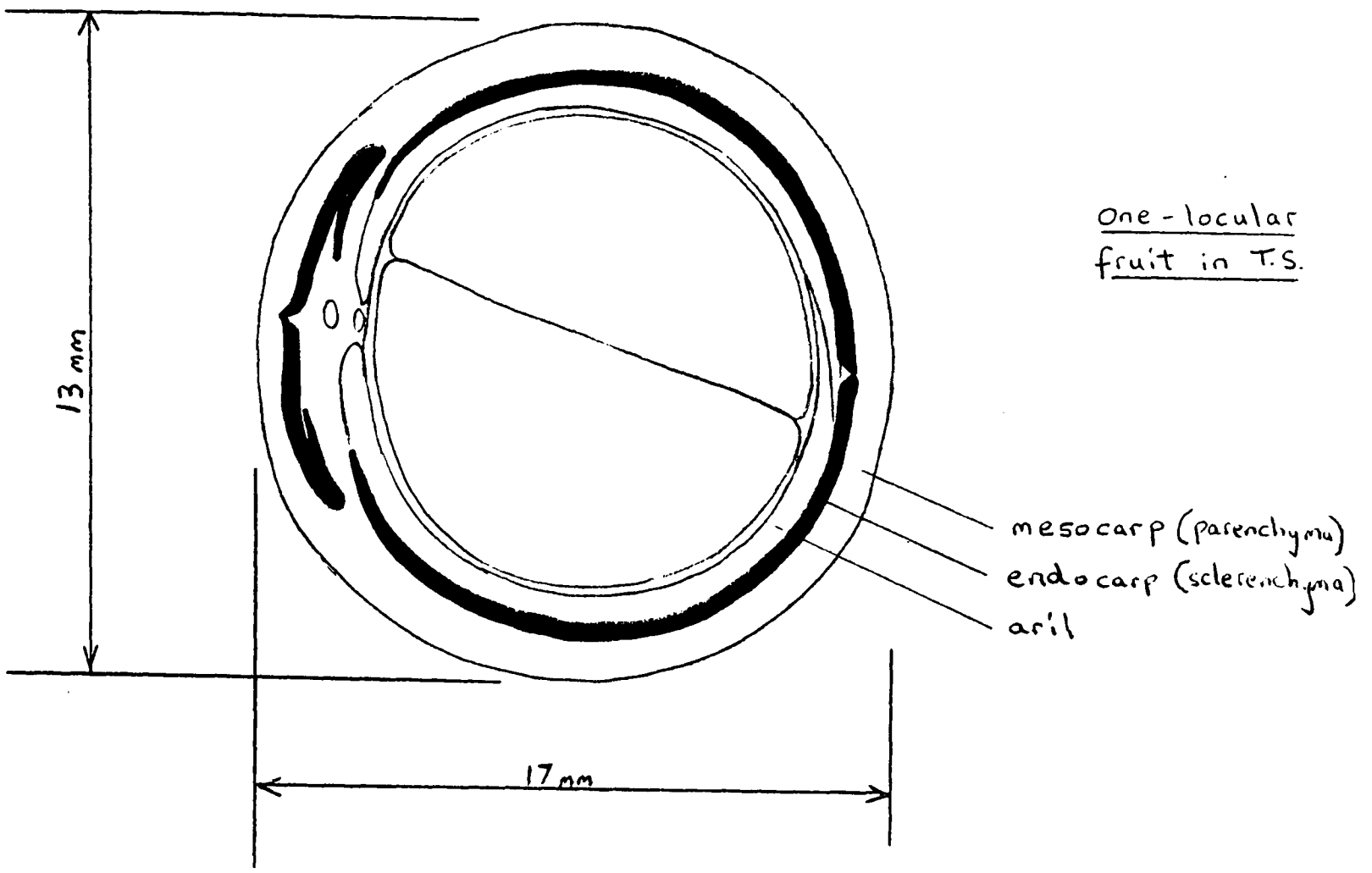
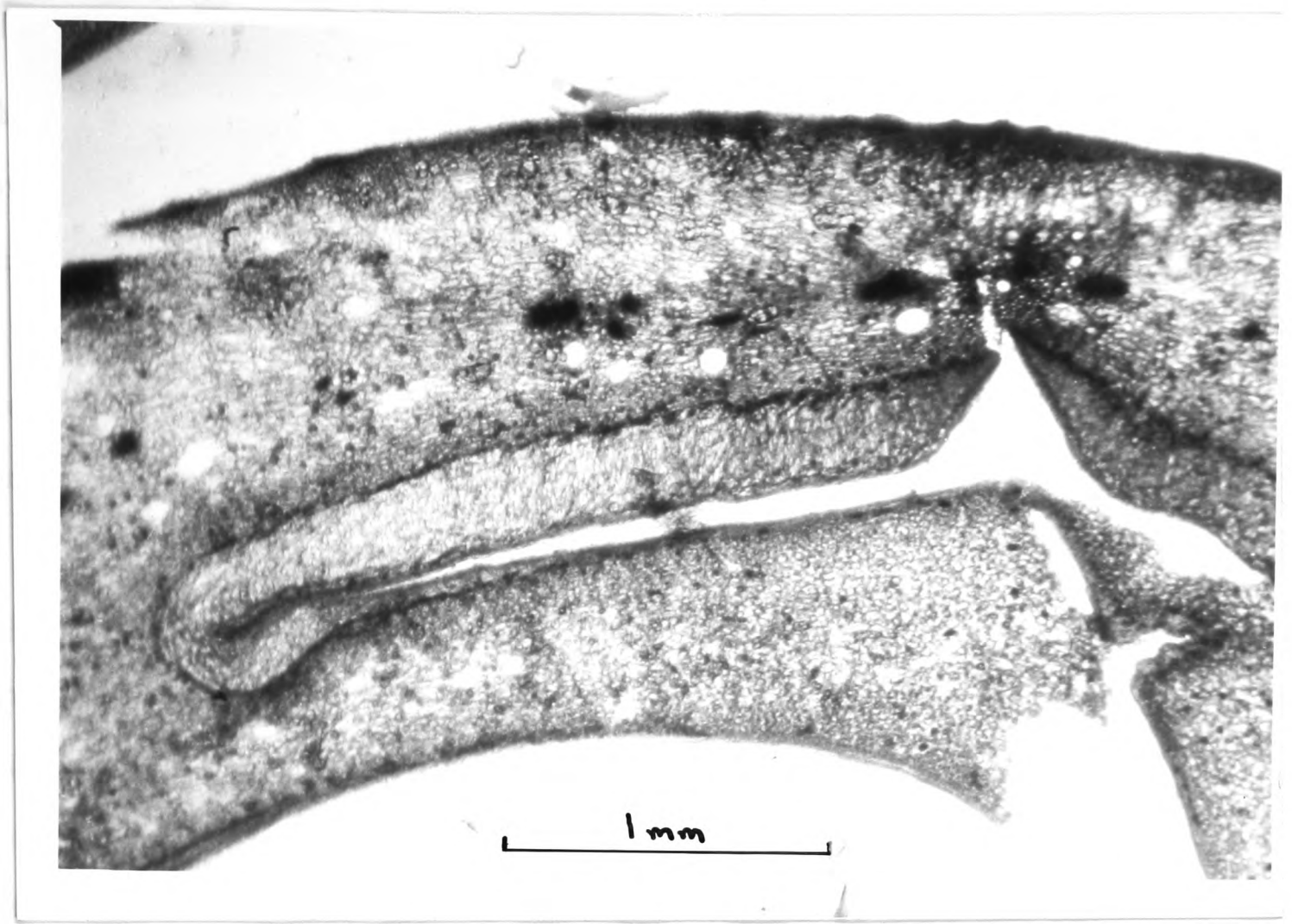
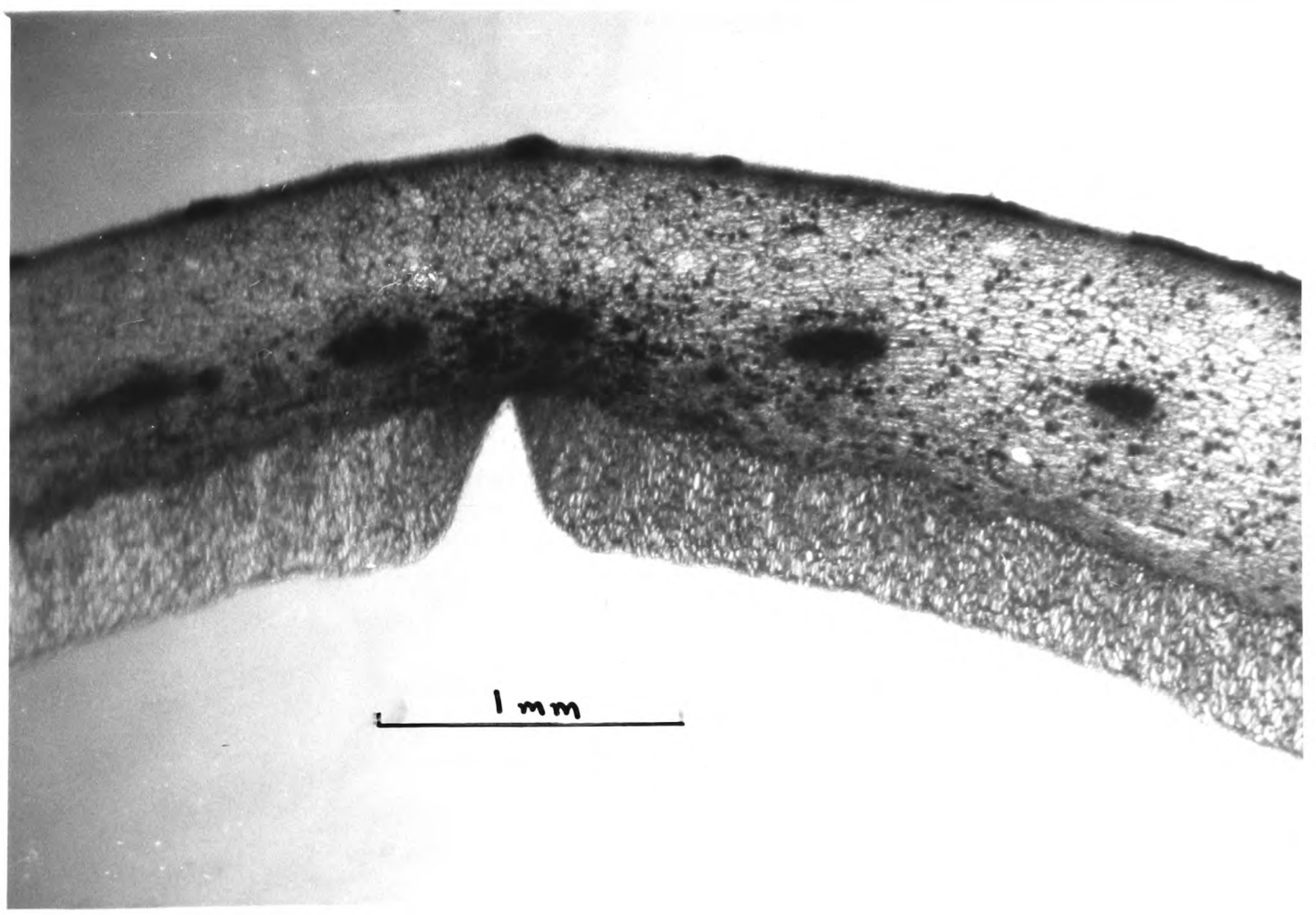


FIG: **4.21** HEYNEA TRIJUGA (Roxb.) Sims
Mature one-locular and two-locular fruits in transverse section.
Tissue plans.



A. Heynea trijuga. Capsule (prior to dehiscence) in transverse section. Detail of one wing of a complex dehiscence apparatus. T.Clark 92.



B. Heynea trijuga. Capsule (prior to dehiscence) in transverse section. Detail of simple dehiscence apparatus.

FIG. 4.22

Endocarp, except for in the regions of the sutures, is a continuous layer of large-celled sclereid tissue, 178-330 um thick and covering the whole inner surface of the mesocarp.

Two different types of dehiscence apparatus are connected with the endocarp:

(i) The 'simple' type consisting of an abrupt thinning or, more often, a break (seen as a V-shaped indentation in T.S.) in the sclereid layer. The thinning or break is narrow but extends the whole length of the pericarp cavity and there is no change in the thickness of the layer in the region of this suture. This type of apparatus occurs at just one suture of a 1-locular fruit, but at both sutures of a 2-locular fruit, in which case it runs down the back of each locule in this loculicidally dehiscent fruit. This apparatus is a slight modification of the sclerenchyma layer.

(ii) The 'complex type' is the second type of apparatus found in unilocular fruits (only). It is +/- diametrically opposite (in T.S.) to the simple apparatus. Here the sclereid layer is broken for 1/7-1/6 of its circumference (as seen in T.S.) and above this break (towards the outside of the fruit) and slightly overlapping (but not touching) the ends on the main layer is a subsidiary layer of sclereid tissue. Down the middle of this layer (along the suture) is a V-shaped indentation (similar to that of the simple apparatus) and the two wings of sclerenchyma on either side recurve sharply near the tips, each tip folding back on itself. The apparatus extends along the whole length of the pericarp cavity.

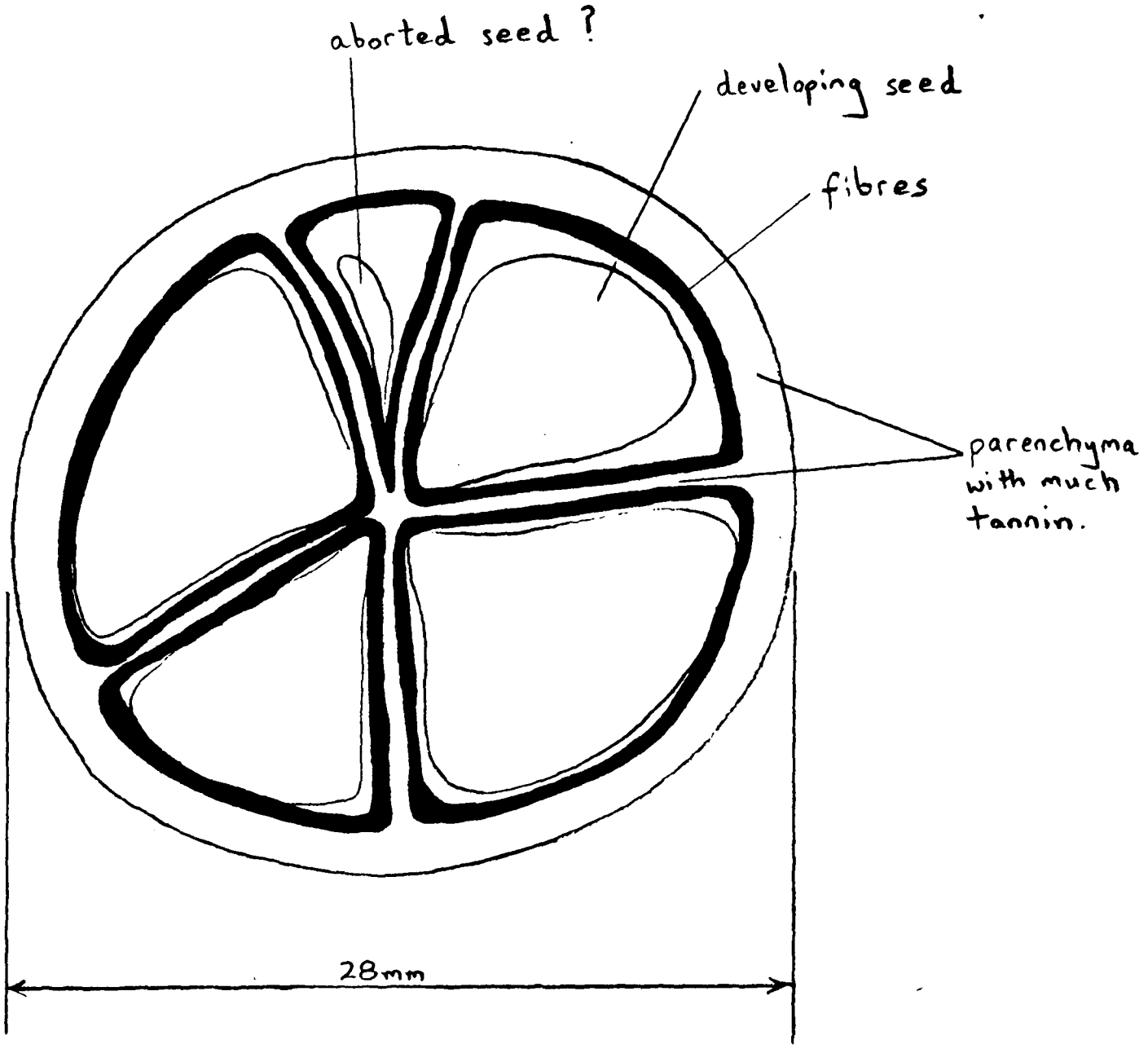


FIG: 4.23 LEPIDOTRICHILIA VOLKENSII (Harms) Leroy
Mature fruit in transverse section.
Plan.

Dehiscence occurs at the sutures, the sclerenchyma parting at the dehiscence apparatus and the mesocarp and exocarp above tearing. In a unilocular fruit it is the simple apparatus which breaks first.

The septum in 2-locular fruits is an extension of both the mesocarp and endocarp and consists of parenchyma (approaching aerenchyma) tissue 55-130 um wide with sclereid tissue on either side, each 250-300 um thick. There are no crystals in the septum parenchyma but (latex ?) channels are sparsely present. In a unilocular fruit, the septum is absent or represented only by the base of the placenta, to which the seed is attached.

(Other materials: Pennington 7877; SABAH; FHO. and Pennington 7927; Sabah; FHO)

Lepidotrichilia volkensii (Harms) J.F.Leroy (Cheek et al. 1675; K)

FIG. 4.23

A drupe; globose-obellipsoid; c. 2.4 cm diam. X c. 2.9 cm diam.; surface rugose and puberulous; pericarp succulent in vivo; yellow in vivo (B.T.Styles 176, collection notes: FHO).

Exocarp trichomes predominantly stellate (up to 160 um high) but simple unicellular trichomes (up to 100 um long) also present.

Cheek et al. 21-6
Madagascar.

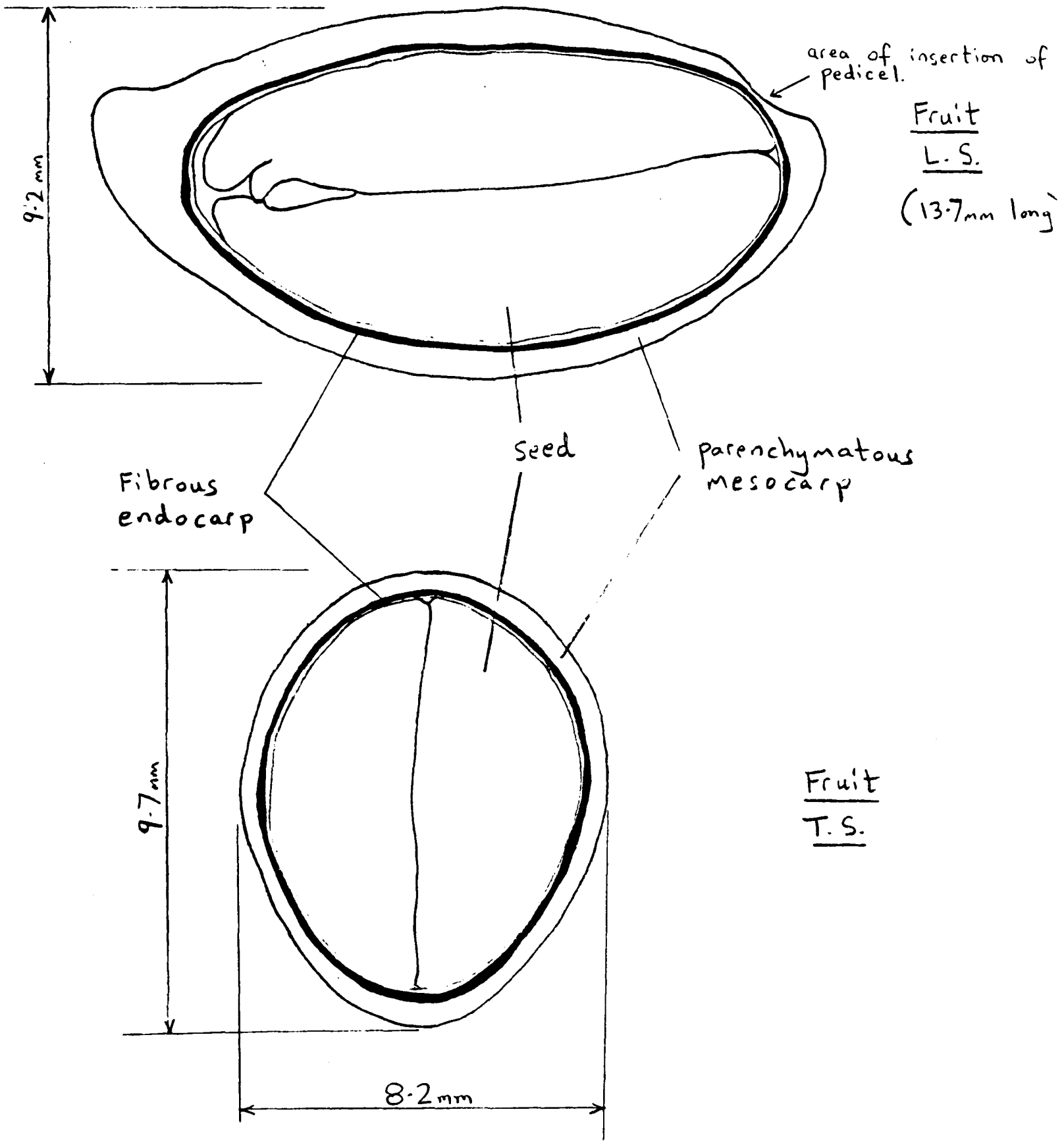


FIG: 4.24 MALLEASTRUM GRACILE Leroy
Mature fruit in transverse section and longitudinal section.
Plans.

cheek et al. 21-6
Madagascar.

Malleastrum
gracile Leroy

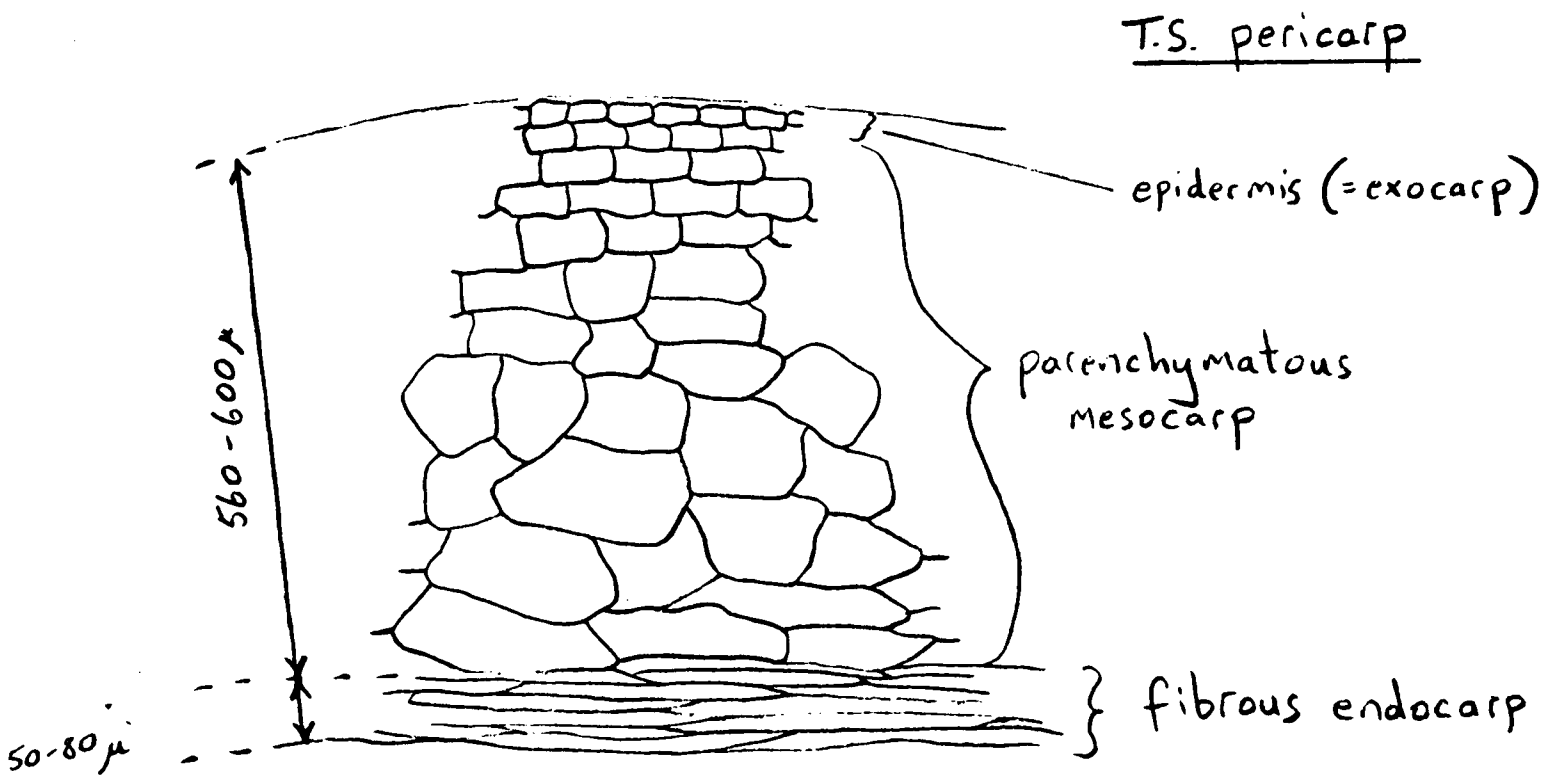


FIG: 4.25 MALEASTRUM GRACILE Leroy
Mature fruit in transverse section.
Cellular detail of pericarp.

Mesocarp parenchymatous; 0.8-1.2 mm thick; heavily laden with tannins; vascular bundles scattered.

Endocarp 350-440 um thick; composed entirely of fibres; broken at each septum and bent down each side of each septum (without change in width) united with that from an adjacent septum near the middle of the fruit; extending the whole length of the pericarp cavity and thus totally enclosing each seed within a hard fibrous layer; in most of the curved (adjacent to the mesocarp) sections of the endocarp, a V-shaped channel (as seen in T.S.) occurs, running down the middle of the section (similar to the 'simple' type dehiscence apparatus in Heynea trijuga but not extending for the whole length of the layer). The layer breaks apart with little applied force along this line.

Septum an extension of the parenchymatous mesocarp; 200-300 um thick; septa meeting at a central parenchymatous column (c. 1 mm diam.).

Malleastrum gracile Leroy (Cheek et al. 21-6; Madagascar; FHO)

FIGS. 4.24, 4.25

A berry; ellipsoidal to ellipsoid-ovoidal with short (<1 mm long) beak near the apex; slightly asymmetric; pedicel inserted obliquely; 1.0-1.4 cm long X 0.7-1.0 cm diam.; surface smooth and glabrous; pericarp thin and coriaceous; pink to cream in vivo.

F. White 1094
Kenya.

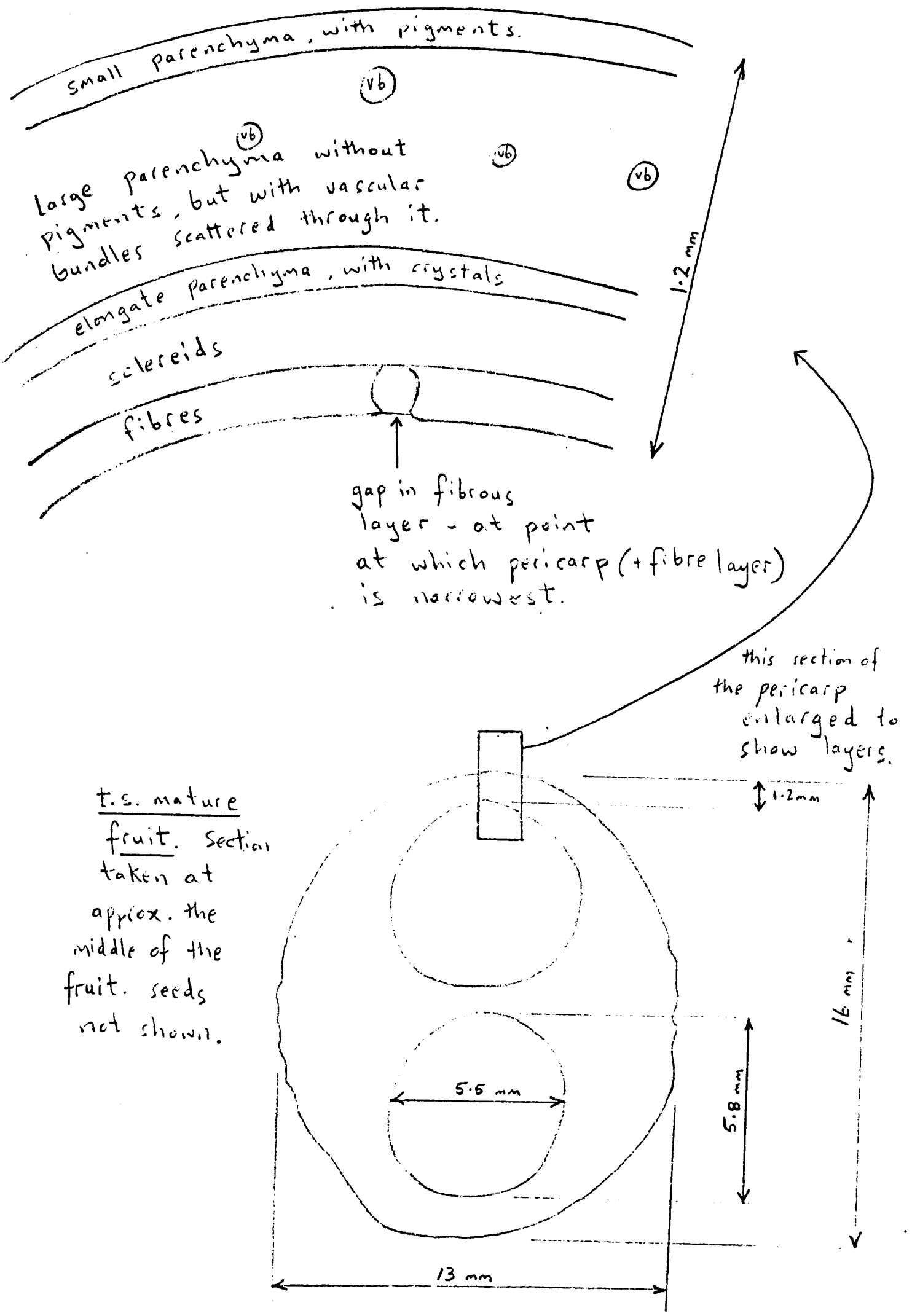


FIG: 4.26 EKEBERGIA CAPENSIS Sparrm.
Mature fruit in transverse section.
Tissue plans.

F. White 1094
Kenya.

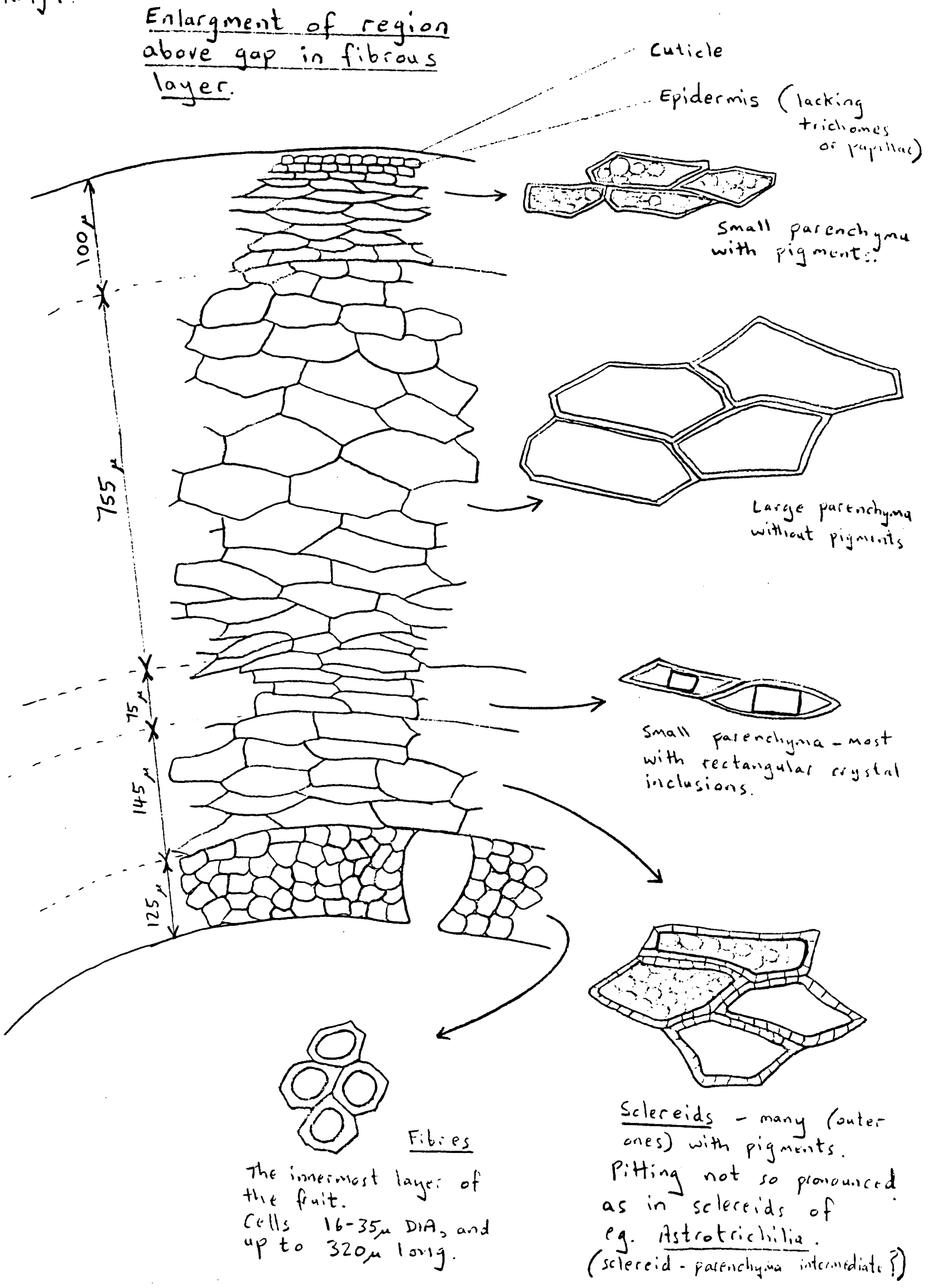


FIG: 4.27 EKEBERGIA CAPENSIS Sparrm.
Mature fruit in transverse section:
detail of region above gap in fibrous layer.

Exocarp glabrous.

Mesocarp thin and *in vivo* succulent like the flesh of a cherry (M.Cheek pers. comm.); parenchymatous; 560-600 um thick, being thickest at the poles.

Endocarp very thin, 50-80 um thick; entirely of fibres; covering the whole inner surface of the mesocarp and intimately associated with it; no sutures.

(Other materials: Cheek 3-26-5, Madagascar: *M.isalense* Leroy)

Ekebergia capensis Sparrm. (F.White 1094; KENYA; FHO)

FIGS. 4.26, 4.27

A fleshy indehiscent drupe; globose or obovoid or ellipsoidal with a short beak (<0.8 mm long) near the distal end; usually slightly asymmetric; surface smooth to slightly rugose, glabrous; orange with brown freckles *in vivo* (collector's notes: M.Cheek 1055: K.).

Exocarp glabrous.

Mesocarp of three distinct layers: (i) uniformly c.80 um thick, immediately below the endocarp; small parenchyma cells with pigment plastids; (ii) 755 um thick at the narrowest point and thickening to extend the mesocarp into

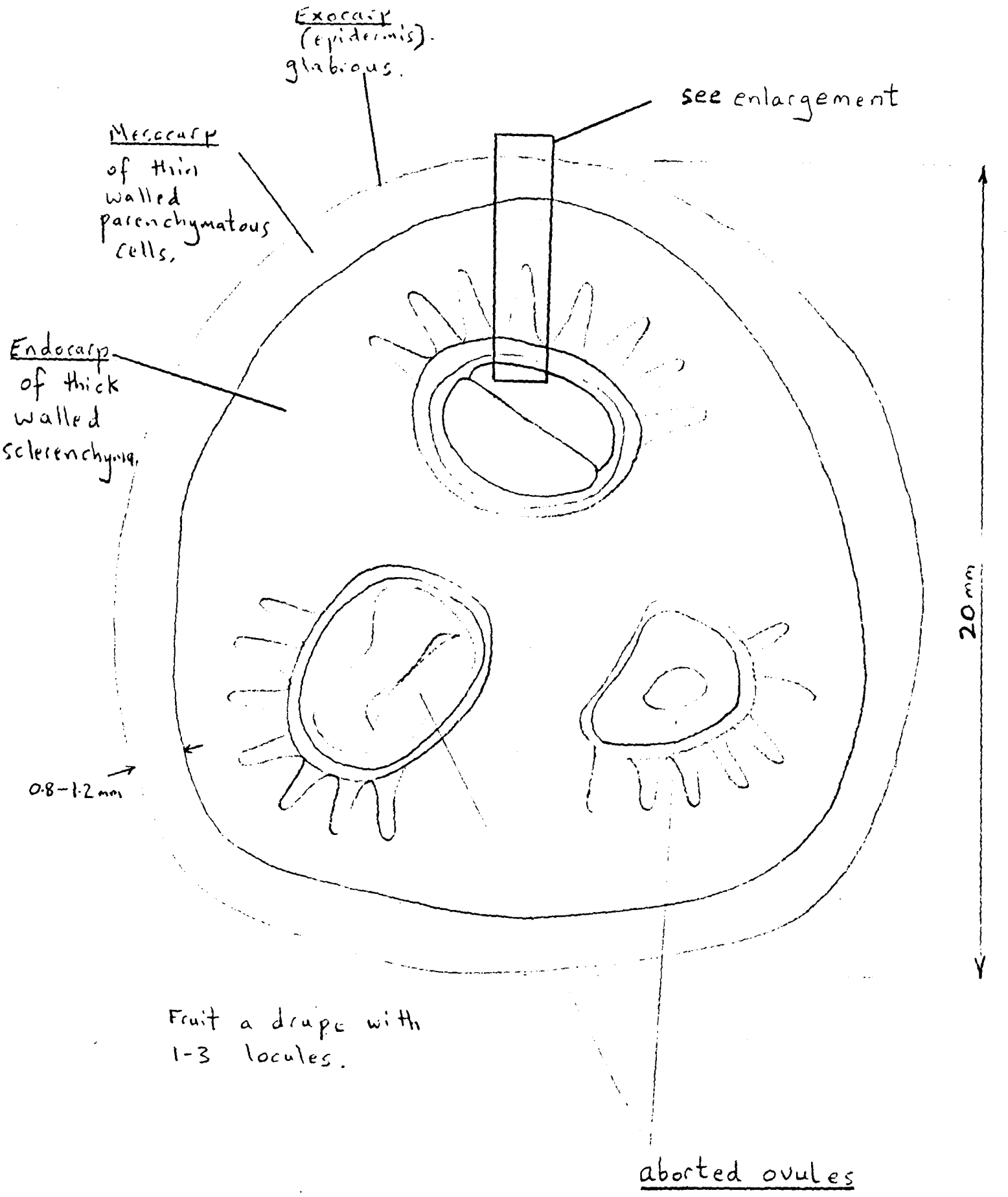
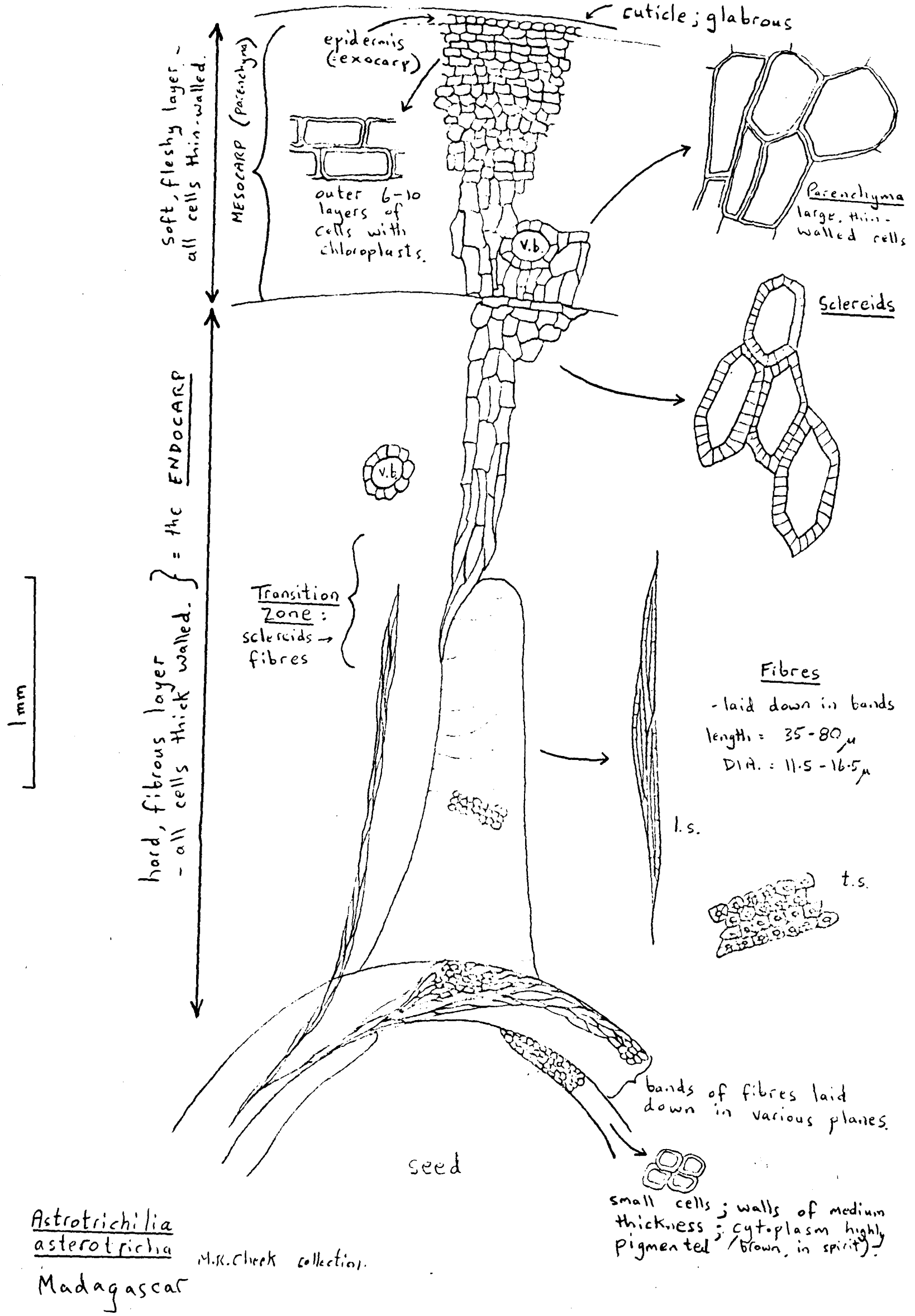


FIG: 4.28 ASTROTRICHILIA ASTEROTRICHA (Rødlk.) Cheek
Mature fruit in transverse section.
Plan.



Astrotrichilia asterotricha

Madagascar

M.S. Cheek collection.

FIG: 4.29 ASTROTRICHILIA ASTEROTRICHA (Radlk.) Cheek
Mature fruit in transverse section.
Cellular detail of pericarp

the 'septum' separating the seeds; large parenchyma cells without pigment plastids; (iii) uniformly c.75 um thick, immediately above the endocarp; small parenchyma cells, most with single oblong crystal inclusions.

Endocarp of two distinct layers: (i) c. 145 um thick; large sclereid cells with (? pigment) plastid inclusions; (ii) c. 125 um thick; fibres. The endocarp extends over the whole inner surface of the mesocarp and totally encloses the seeds. There is a very narrow (c. 100 um) longitudinal gap in the fibrous layer, however, running the full length of the fruit wall at the narrowest points in the pericarp, i.e. one gap associated with each seed in this 2-locular fruit. No other evidence of a suture exists.

The fruits of this specimen had two 'locules', each locule with one seed, but often one of the ovules / seeds seems to have aborted.

Astrotrichilia asterotricha (Radlk.) Cheek (Cheek 2-25-2; MADAGASCAR, FHO)

FIGS. 4.28, 4.29

A drupe; ellipsoid to globose with very short (< 1.5 mm) nipple at distal end; symmetric; 1.6-1.8 cm long X 1.8-2.1 cm diam.; surface smooth and glabrous; green, turning yellow (collector's note).

Endocarp glabrous.

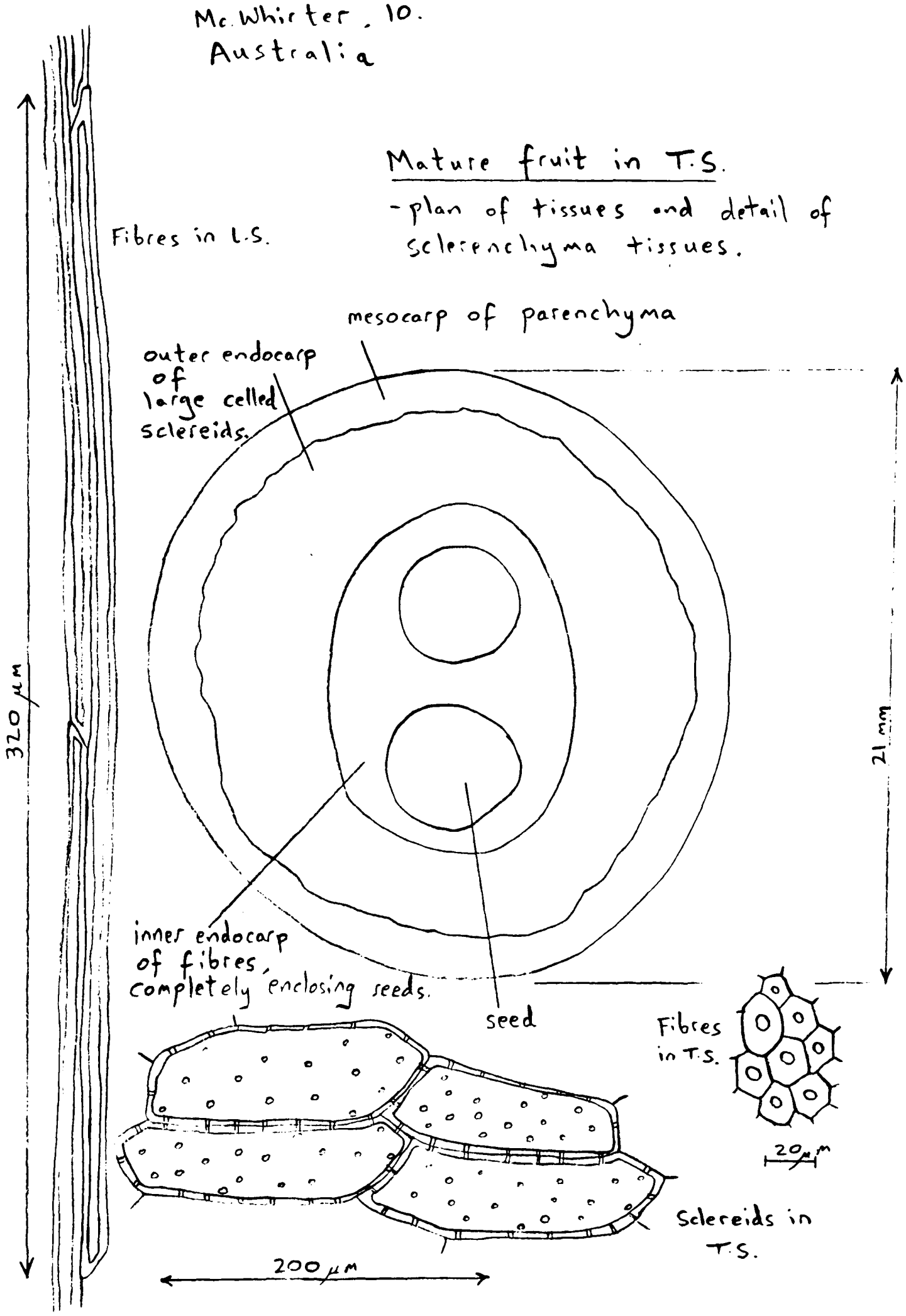


FIG: 4.30 OMENIA ACIDULA F.Muell.
Mature fruit in transverse section .
Tissue plan and detail of sclerenchyma cells.

Mesocarp 0.8-1.2 mm thick; fleshy; thin-walled parenchyma with tannins; vascular bundles scattered; outer cells with (?) chloroplasts.

Endocarp thick and making up the largest part of the fruit volume; very hard; of two layers of approximately equal thickness, merging across a narrow transition zone: (i) an outer layer of large-celled sclereid tissue; (ii) an inner layer of fibres, most of those fibres running longitudinally being in discrete radially projecting wings, reaching as far out as the transition zone, each wing running the whole (longitudinal) length of the seed with which it is associated.

Locules are arranged radially around a central columella of sclereid, fibre and intermediate cells.

N.B. Cheek (1989a) refers not to a multi-layered endocarp in this species but to a "high concentration of sclereids in the thick mesocarp." Since the 'middle' layer here is a clearly defined layer of parenchyma tissue, homologous (at least in the mature fruit) with the mesocarp of other genera, I propose to maintain my terminology here.

Owenia acidula F.Muell. (McWhirter 10; AUSTRALIA; FHO)

FIG. 4.30

A drupe; globose; 2.0-2.6 cm diam.; surface smooth and glabrous; red in vivo (collector's note).

Oxford Botanic Garden Cult.
20-viii-1975.

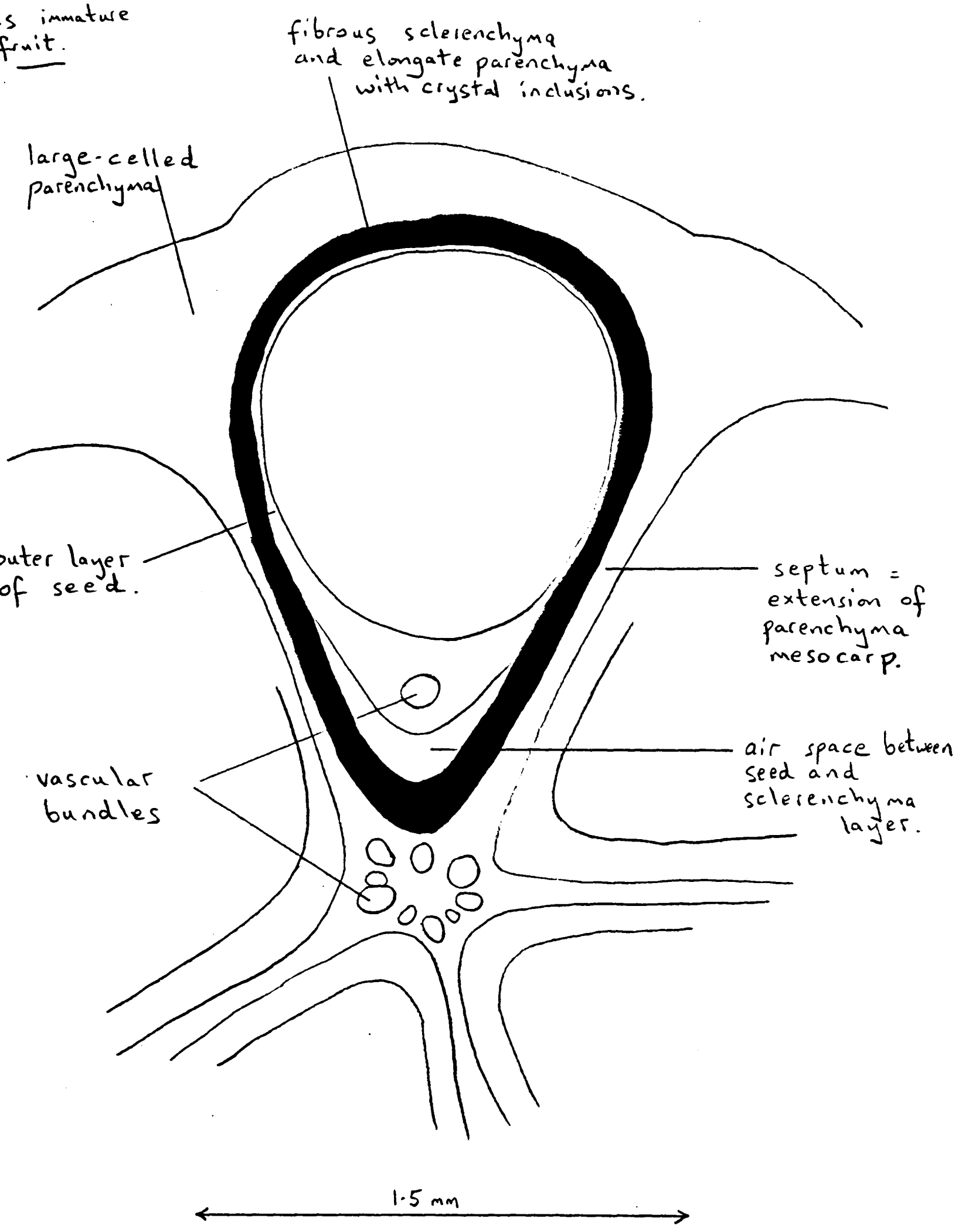


FIG: 4.31 CIPADESSA BACCIFERA (Roth) Miq.
Sub-mature fruit in transverse section.
Plan of one (of five) locule.

Oxford B.G.
20 - viii - 1975.

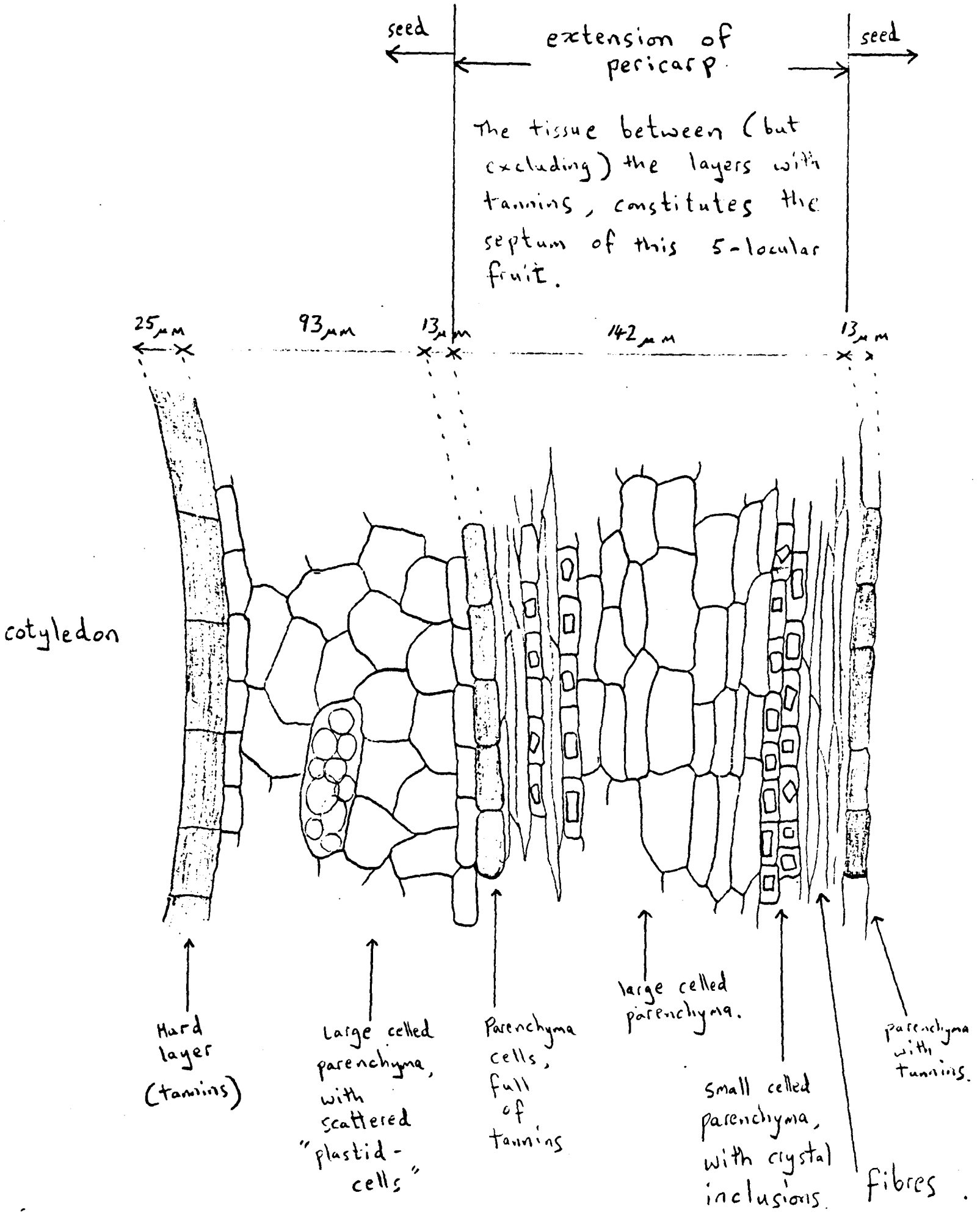


FIG: 4.32 CIPADESSA BACCIFERA (Roth) Miq.
Sub-mature fruit in transverse section.
Cellular detail of septum and sclerenchyma layers.

Exocarp glabrous.

Mesocarp fleshy; 1.0-2.5 mm thick; parenchymatous with scattered vascular bundles.

Endocarp thick and very hard; of two distinct layers: (i) an outer layer (1.9-2.8 mm thick) of sclereids; (ii) an inner layer (3.0-5.3 mm thick), totally surrounding the seed(s), of fibres laid down in various planes.

Cipadessa baccifera (Roth) Miq. (Cult. Oxford Bot. Garden.; FHO)

FIGS. 4.31, 4.32

(N.B. Fruit slightly immature)

A drupe; +/- globose, slightly 5-lobed, with a very short (<1 mm) nipple at or near the distal end; surface smooth and glabrous.

Exocarp glabrous.

Mesocarp parenchymatous, leathery, 330-420 um thick (between a seed and the exocarp); with scattered vascular bundles and small diameter (<40 um) channels running longitudinally.

Endocarp 40-70 um thick; a mixture of layers of fibres and layers of small but elongate parenchyma cells, most of the latter with single oblong

crystal inclusions; this hard fibrous layer totally surrounds the seed and seems to have no weak point or suture.

Septum is an extension of the mesocarp parenchyma down between the seeds, where it is c. 60 um thick, with the fibre and crystal-parenchyma of the endocarp on either side of it; each septum meeting at the core which is parenchymatous and heavily vascularised.

The fruit is 5-locular.

FIELD OBSERVATIONS OF DISPERSAL IN WALSURA

(i) Introduction

In fifteen weeks' field work, only one Walsura tree was encountered which feasibly offered the opportunity for a dispersal study. It was a tree of W.sp. A (aff. W.pinnata Hassk.) in primary dipterocarp forest at Semengoh, c. 30 km north of Kuching, Sarawak, Malaysia. It was 35 m tall and was fruiting profusely. The object of the study was to determine the fate of the fruits, as far as was possible with a time limit of four days.

(ii) Methods

For four days, I was based at the Wildlife Rehabilitation Centre in the middle of the Semengoh reserve, about 20 minutes' walk from the tree under

study. Each day, I visited the tree for periods of three hours at different intervals, from dawn (6.00 a.m.) to sun-set (6.30 p.m.). I positioned myself beneath the tree, camouflaged as much as practicable, without obscuring my view of the crowns of the Walsura or adjacent trees, and observed the crown through binoculars. I also regularly examined the area of forest floor beneath and around the tree.

(iii) Observations

Many small birds were observed to land in the crown but usually departed within ten seconds, none of them making any attempt to eat the fruits.

At various times through the day, but particularly between 7a.m. and 11a.m., one, two and sometimes three squirrels were seen in the crown, taking the fruits. They were not identifiable to species at that range. The debris falling to the ground was considerable and it appeared that the squirrels were removing and discarding pericarp, stripping off and eating the succulent aril (which adheres to the testa) and discarding the rest of the seed. Most of the seeds which fell to the floor were intact (except for the aril), and were probably then still viable. The number of seeds dropped beneath the crown after a fifteen minute feeding session by one squirrel could be as many as thirty. If the site was left for more than a few hours, and certainly over-night, all of these seeds would have disappeared however.

It was not until 11 a.m. on the fourth day, when preparations were being made to put a rope up the tree, that a Bornean Gibbon (Hylobates muelleri)



FIG. 4·33 A Bornean Gibbon (Hylobates muelleri) in Semengoh Forest, Sarawak.
Photograph taken June, 1987.

(FIG. 4.33) was observed in the crown. It was eating the whole fruits in great quantity and remained there for five minutes, seemingly unperturbed by the arrival of four people at the base of the tree, only moving off through the crown as a tree-climber commenced his ascent of the trunk.

(iv) Discussion

The dull-green berries of this species do not seem to attract birds particularly, besides which it would take a large bird (e.g. a Hornbill) to manipulate and swallow all or part of a 2.6 cm X 1.8 cm fruit, and no such birds were seen visiting this tree. Some mammals, however, have apparently learned that the fruit is good to eat, in part or whole. The squirrels only took the aril but perhaps might take the seed also if food in the forest was scarce. The discarded seeds, even though still viable, are obviously being taken by some terrestrial animal(s). The Lesser Mouse-Deer (Tragulus javanicus), which is known to take fallen fruits (Payne et al. 1985), was seen in the area but it is thought more likely that rats and/or mice (of which there are many species in Semengoh Forest) were responsible. Rodents may eat the seeds on site, in which case probably destroying them as viable propagules, or carry them away for storage for later consumption, where they may be forgotten and allowed to germinate. Of the animals observed however, the gibbon, seems to be the most promising vehicle of dispersal, for certainly all of the seed was eaten. The question remaining is whether the seed survives the masticatory (which is perhaps slight given the quantity of fruit ingested) and digestive processes.

DISCUSSION

(i) Taxonomy

Compared with other large tribes in the Meliaceae (e.g. Guareeae with eleven genera and Swietenieae with nine genera) the Trichilieae with eleven genera exhibit an exceptionally wide range of fruit structures, from the fleshy berry of Walsura spp. (one of which lacks sclerenchyma completely) to the drupe of Owenia spp. to the woody capsule of Pseudobersama mossambicensis. If fruit characters were taken in isolation, the tribe would not hold together and they can certainly provide us with excellent characters for the identification of genera and (in some cases, e.g. within Walsura) of species. However, anatomical features of the genera do overlap and similarities may demonstrate relationships. Exocarp and mesocarp features are relatively constant between genera and their tissues are parenchymatous (or collenchymatous in the endocarp) with scattered vascular bundles and, in some, tannins in varying amounts. Latex and crystal cellular-inclusions may also be present. It is the sclerenchymatous endocarp which varies greatly however and this is the basis of much of the phylogenetic speculation here. Sclerenchyma is also important functionally -which probably explains its diversity- in seed protection and (in those species which possess it) dehiscence, but this will be discussed below.

W.chrysogyne, which lacks sclerenchyma of any sort, is therefore difficult to place. Its sub-exocarp pericarp is entirely parenchymatous albeit heavily laden with tannins (more so than any other fleshy fruit investigated here) which seems to be the the basis of its physical

strength. On fruit characters, the species must therefore be placed a little removed from all other members of the tribe.

The Trichilia species seem to be characterised by capsules with wings of sclerenchyma on either side of the suture, each wing tip folded back on itself or folded inwards and along the parenchyma core of a septum. The tissue can consist either entirely of large elongate sclereid cells or a mixture of sclereids towards the outside and fibres towards the inside, but of the ten species examined only T.capitata from Africa and T.micrantha from South America had the latter state. Heynea trijuga also has this type of (sclereid only) winged suture (which is remarkably similar to that of the African Trichilia spp.) but also possesses a thin layer of sclereid tissue which almost completely covers the seed, being broken only just below the sclereid wings and diametrically opposite at the 'simple' dehiscence apparatus.

A thin layer of sclereid tissue occurs in Walsura dehiscens, W.robusta and W.trifoliolata also, except here it is completely unbroken and overlays a thin layer of fibrous sclerenchyma. W.dehiscens has breaks in the sclereid layer at two opposite sutures which makes the fruit weakly bivalved. The breaks tend to occur (most frequently) however along the lines of insertion of the septum (i.e. septicidally) and not along the back of the locules (i.e. loculicidally) as in Heynea and Trichilia species. This (along with possession of the characteristic Walsura-type septum - see also below) might suggest that this species, far from being a possible intermediate between Walsura and Heynea, is in fact a product of parallel evolution and only remotely related to Heynea. If this is so then it clearly demonstrates

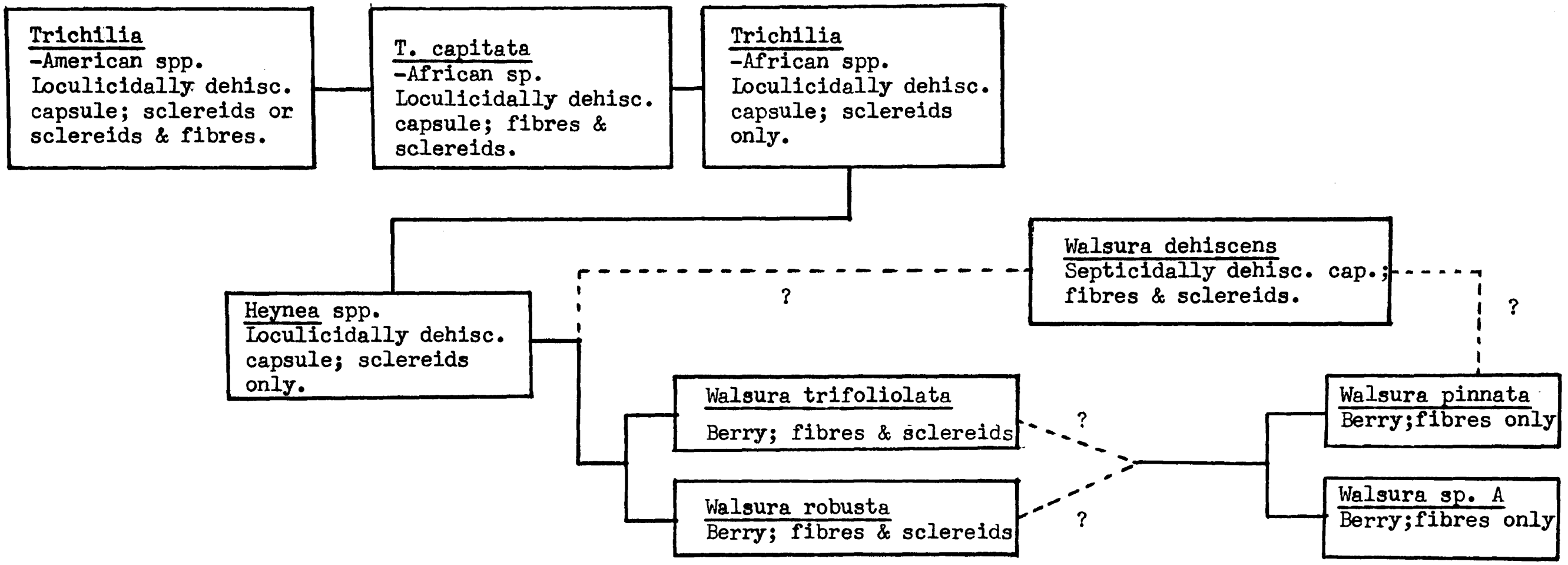


FIG. 4.34 Relationships within the Trichilia - Heynea - Walsura complex suggested by fruit anatomy.

the dangers of considering only superficial features (e.g. dehiscence) when constructing phylogenies. A knowledge of the anatomical (and developmental if possible) basis of features is most important.

W.robusta is unique within the genus, and as far as is known within the family, in having trichomes on the inside of the endocarp and this could be seen as a remnant of a dehiscent state. In T.emetica the trichomes occur at the ends of the parenchymatous septa. W.sp. A is the only species examined that has two-armed trichomes on the exocarp. W.trifoliolata, W.pinnata and W.sp.A differ from the other species of the genus examined in having an endocarp composed solely of fibres but where the endocarp is an extremely thin layer in the first species (and in W.dehiscens and W.robusta, which also have sclereid tissue) it is very thick in W.pinnata and W.sp.A.

The attachment of the seed to the pericarp differs in these three genera also. In Trichilia and 1-locular Heynea fruits it is attached at a placenta arising directly from the parenchymatous mesocarp but in 2-locular Heynea fruits and all Walsura fruits the seed is attached to the septum and via that to the endocarp or mesocarp, even though, in a 1-seeded Walsura fruit, the septum may be pressed against the endocarp by the expanding seed.

The species so far discussed can therefore be arranged in a series (FIG. 4.34) with the Trichilia species at one extreme and W.pinnata at the other. Without anatomical investigation of a large proportion of the c. 90 Trichilia species it is premature to speculate too much on the trends within Trichilia but it is interesting to note that fibres have only been observed in an American species and in T.capitata, the African species most

similar to those of the New World (de Wilde, 1968; Pennington & Styles, 1981; Cheek, 1989).

Owenia and Astrotrichilia have a very similar drupaceous fruit structure, which accords with the conclusions of Pennington & Styles (1975) about the closeness of their relationship. Pseudobersama and Ekebergia differ from these two in that each seed or locule is surrounded by its own individual layer of endocarp. The endocarp consists of a layer of fibres (immediately around the seed/locule) overlaid by a layer of sclereids. Between each of these sclerenchyma-covered seeds/locules is an extension of the mesophyll (hard and woody in Pseudobersama, leathery in Ekebergia) which meet at a central core of the same tissue. Ekebergia is therefore a drupe in the broad sense of the term, its centre being not entirely hard. Whilst these two genera are similar in basic tissue displacement, they differ in the relative thicknesses of the layers and the state of the mesocarp (not to mention the arrangement of the seeds in the locules). Also, whereas in Pseudobersama the whole thickness of the endocarp is broken at the sutures, in Ekebergia there is a slender break in the fibrous layer only. There is one of these semi-sutures associated with each seed and since the fruit is indehiscent, the feature is very interesting in evolutionary terms. Nothing like it has been observed in any other indehiscent fruit in the tribe.

Pterorhachis is unique in the tribe with a layer of very small (Pyrus-type) sclereid cells just below the exocarp and very large thick-walled sclereids towards the inside of the pericarp and across the suture. Neither cell type has been seen in fruits in other members of the tribe and the

absence of a continuous sclerenchyma layer -or at least suture-wings- seems also to be unique.

Ignoring the septum of Walsura, the structure in Malleastrum gracile is similar to that of W. pinnata and W.sp. A., it being a simple berry with a fleshy mesocarp and a thin, fibrous endocarp. A bilocular fruit of a Malleastrum specimen has not yet been investigated but it would be most interesting to see if the septum is merely an extension of the mesocarp (as in e.g. Cipadessa and Trichilia species) or a rather specialized thin septum of the Walsura type.

Cipadessa and Lepidotrichilia fruits have certain affinities with one another. Each has a parenchymatous mesocarp which extends down between the seeds/locules to a central parenchyma core and each has its seeds/locules individually surrounded by a thin layer of fibres. Both have tannins in the parenchyma, at least in the latter stages of development. The presence of small crystal-parenchyma cells amongst the sclerenchyma has not been encountered outside Cipadessa.

Certain affinities within the tribe have been pointed out, but it is still difficult, with the notable exception of the Heynea - Walsura series, to see how the smaller genera tie in with Trichilia.

The various characters mentioned can be used in the identification of genera and species and some of the more useful ones are utilised below in a synoptic key.

(ii) Seed dispersal

All of the capsular fruits in the tribe dehisce because of gaps between sheets (i.e. breaks in the layer or gaps between the wings) of sclerenchyma. When the parenchyma and collenchyma above it dries and contracts, the thick-walled sclerenchyma retains its shape and size and the tissues split along the line of least resistance (i.e. the suture above the gap in the sclerenchyma). The two types of dehiscence apparatus in Heynea fruits assure rapid dehiscence by causing the simple one to break first, since it has larger sheets of sclerenchyma on either side of it. If both apparatus were the same then forces to pull the pericarp apart would be split evenly and dehiscence would be slow. Also, the placenta and point of attachment of the brightly coloured aril is on the complex apparatus side and so if dehiscence occured here first, the aril might not be clearly visible by dispersal agents, or it might even break or become detached. In a bilocular fruit with two simple apparatus , there is a septum and much more tissue between the two sutures and so they tend not to interfere with each other.

The seeds of the capsular species of the tribe are probably dispersed principally by birds (Pannell & White, 1985). A loculicidally dehiscent capsule with an arillate seed, the aril often brightly coloured (e.g. orange-red in Heynea species), seems to be more appealing to a bird than to a mammal. Frost (1980) reports eight species of birds taking seeds of Trichilia emetica in Natal, and Leck (1969) observed thirteen species taking seeds of T.martiana in Costa Rica. The orange-red aril of T.cuneata

from Central America is 59.7 % lipid and 15.1 % protein, making it one of the most nutritious fleshy seed appendages of all bird-dispersed tropical species, and birds pluck and swallow the seed & aril digesting the latter and either regurgitating the seeds or passing them through their gut undigested (Foster & McDiarmid, 1983). Dispersal by fish may also play a small part. Seeds of T. emetica falling into the water are reported to be eaten by barbel in South Africa (Palmer & Pitman, 1973, pp.1052-1077), and seeds of T.dregeana are used as fish bait at Mt.Kilimanjaro (White & Styles, 1963). Pannell & White (1985) believe P.mossambicensis to be probably bird dispersed, even though its resources seem to be put much more into seed protection than disperser attraction.

Fleshy fruits, whether drupes or berries, might be taken by mammals or birds. The berries of Walsura species are probably taken mainly by mammals, but as we have seen (above) the story may be far from straightforward with some animals taking only the aril and discarding the rest of the seed on site. Birds, baboons, monkeys and bush-pigs eat the drupes of Ekebergia capensis in South Africa (Phillips, 1927), and emus eat those of Owenia species in Australia (Harms, 1940).

Whatever ingests the fruits however, in almost all cases we can only speculate that the seeds survive the digestive system and that the animal has been a disperser rather than a destroyer of the propagule. Very little work has been done on this (crucial) part of the system. On the other hand, it may be that some fruits require a digestive treatment in order to germinate. It is difficult to imagine the sclerenchyma-encased seeds of

Owenia or Astrotrichilia germinating if the fruits were subjected merely to weathering processes.

SYNOPTIC KEY TO THE GENERA OF THE TRICHILIEAE BASED ON FRUIT CHARACTERS.

N.B. More than one character-state may occur within a genus or species group and where this is so, the genus/species is asterisked.

Genus / species codes:

1 Trichilia; 2 Pseudobersama; 3 Pterorhachis; 4 Walsura dehiscens; 5 Walsura robusta, W. trifoliolata, W. pinnata & W. sp. A; 6 Walsura chrysogyne; 7 Heynea; 8 Lepidotrichilia; 9 Malleastrum; 10 Ekebergia; 11 Astrotrichilia; 12 Owenia; 13 Cipadessa.

1. Fruit:	a) a drupe	8, 10, 11, 12, 13.
	b) a berry	5, 6, 9.
	c) a septicidially dehiscent capsule	4.
	d) a loculicidially dehiscent capsule	1, 2, 3, 7.
2. Exocarp:	a) glabrous	1*, 7, 9, 10, 11, 12, 13.
	b) with simple trichomes only	1*, 2, 4, 5*, 6.
	c) with 2-armed trichomes	5*.
	d) with stellate trichomes	3, 8.

3. Outer tissue of fruit: a) fleshy 8, 9, 10, 11, 12.

b) leathery 1, 3, 4, 5, 6, 7, 13.

c) woody 2.

4. Sclerenchyma tissue: a) absent 6.

b) sclereids only 1*, 7.

c) fibres only 5*, 8, 9, 13.

d) sclereids & fibres 1*, 2, 3, 4, 5*, 10, 11, 12.

5. Sclerenchymatous endocarp thickness as percentage of total pericarp thickness: a) <25% 1*, 4, 5*, 7*, 9, 10, 13.

b) 25-50% 1*, 5*, 7*, 8.

c) >50 % 2, 11, 12.

d) N.A. 3, 6.

6. 2+ locular capsules and berries with:

a) a longitudinal central cavity (i.e. septa not meeting) 1, 2.

b) a continuous septum, dividing the fruit interior longitudinally 3, 4, 5, 7.

c) N.A. 6, 8-13.

CHAPTER 5

ISOENZYMES

INTRODUCTION

Erdtman (1963) and Harborne (1984) discuss the great potential of biochemical analysis for the elucidation of phylogeny where conventional taxonomic characters (i.e. morphology or, to a lesser extent, anatomy) are of little use. Taxa (or populations or individual plants) which, appear, superficially, very similar can often be demonstrated to be the products of convergent evolution rather than of close phylogenetic proximity when biochemical data are additionally considered. There are several arguments for and against the use of chemical characters compared with traditional ones (see: Davis & Heywood, 1973, pp. 232-258; Harborne & Turner, 1984) and some of these will be mentioned below. However, where one is faced with a taxonomic complex such as Trichilia - Heynea - Walsura, the additional data which chemical studies can provide are most welcome.

It was decided to make a study of a range of isoenzyme systems from leaf material since the necessary fresh material, the required laboratory facilities and the electrophoresis expertise (Linda Lockhart) were available in the Department of Plant Sciences at Oxford. Brewer (1970) discusses the various definitions of an isoenzyme in the literature and recommends the operational one: "...multiple molecular forms of enzymes....seen after separation procedures such as

electrophoresis....sharing a catalytic activity." The multiple molecular forms are due to their being coded for at more than one gene locus. Because of this, they tend to have slightly different electrical charges (a function of the relative numbers of amino acids with positive and negative charges on their surfaces) which cause differential migration in a semi-porous medium (such as polyacrylamide gel) when subjected to an electrical potential difference (i.e. electrophoresis). Migration is also affected by molecule size and configuration. The implication of all this is that, following electrophoresis, an isoenzyme will produce a series of bands which is visualised by a stain reaction specific to that enzyme. Since amino acid sequences of polypeptides are colinear to the nucleotide sequence of its coding structural gene locus, and in the absence of full genetic analysis, it was assumed for this study that zones of staining after electrophoresis correspond to individual loci and bands within the zones to their alleles.

Electrophoresis of proteins (particularly in seeds) is widely employed for taxonomic purposes today (e.g. Vaughan & Waite, 1967; Lockhart, 1988; Triest et al., 1989) but no reference can be found to its application to taxonomic problems in the Meliaceae.

For taxonomic purposes, the study of electrophoretic banding patterns of isoenzymes would seem to have two major advantages over morphological characters:

(i) Colinearity of amino-acids and nucleotides allows banding patterns to be equated directly to gene positions (loci) and gene forms (alleles). Convergent evolution may produce similar enzymes in different taxa but it

is extremely unlikely that they will be coded for by the same nucleotide sequences, since they are products of different transformation series (evolutionary lines).

(ii) Isoenzymes are little influenced by the environment. Except for those switched on and off developmentally, enzymes are always present in the respiring tissue. As well as being greatly influenced by the environment, many morphological characters are the product of several genes and expression of any one of these can be influenced environmentally, giving a phenotype which is very difficult to analyse in genotypic terms.

The disadvantages of isoenzyme work seem less significant but the following two are suggested:

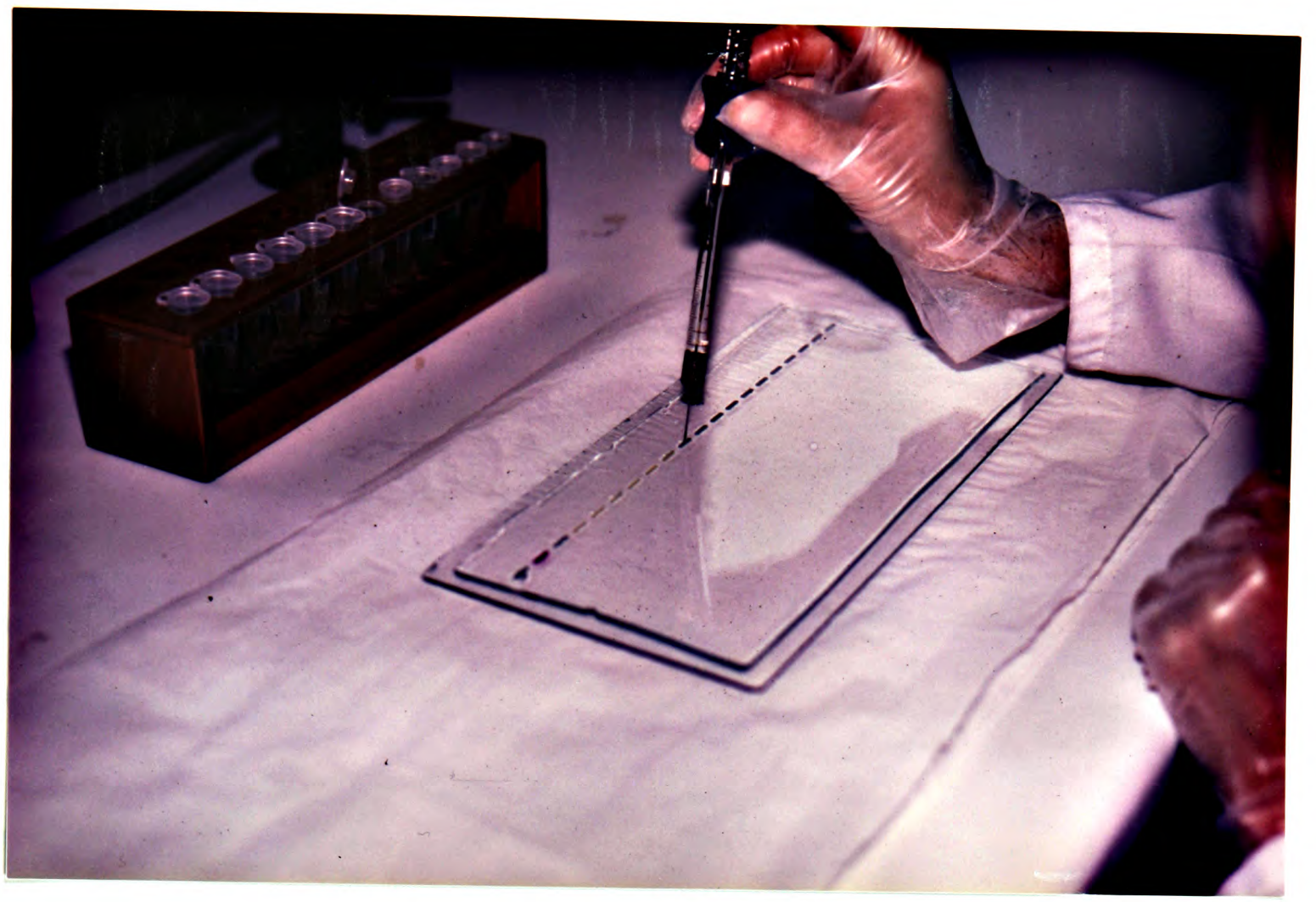
(i) Not all electrophoretic allelic variants are picked up since changes in amino-acid sequences may not alter the electrical and configurational properties of the enzyme forms sufficiently to give bands with different mobility. The full range of genetic variability may not therefore be expressed in the banding patterns.

(ii) Since infraspecific variation seems to be commonly encountered when dealing with isoenzymes (Harborne & Turner, 1984; and indeed they are frequently studied taxonomically at infra-specific levels, e.g. Comas et al., 1979; El Kassaby & Sziklai, 1982; Lockhart, 1988), it is important to sample as much material as possible of each species under study from across its geographical range.

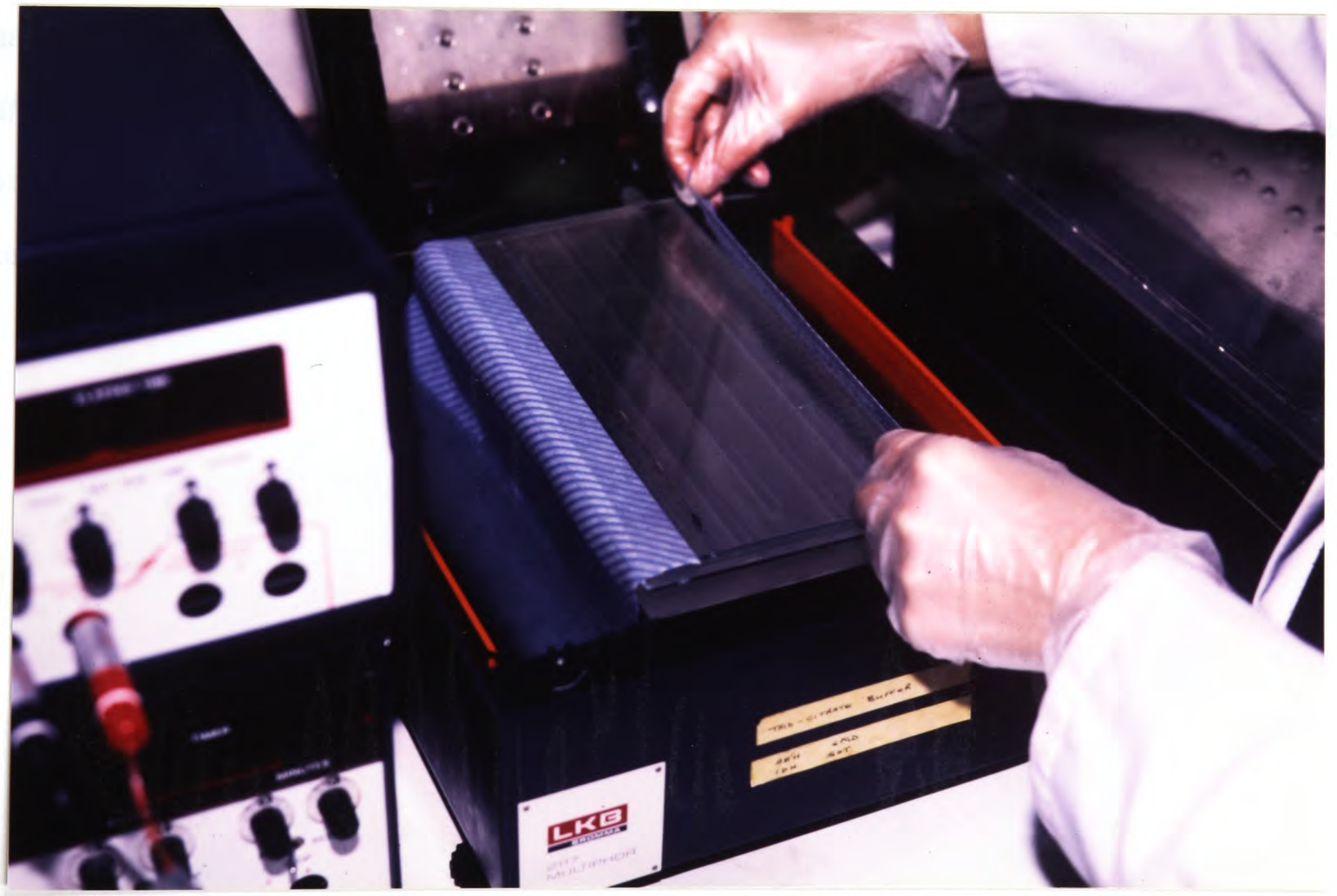
MATERIALS AND METHODS

Leaf material was collected from plants of *Trichilia dregeana*, *Trichilia emetica*, *Heynea trijuga* and *Walsura tubulata*. The first three species were available as about 12-year-old plants grown at the University field station at Wytham and the *Walsura* was about 4 years old and had been grown at the University Botanic Garden. All plants were maintained in stable conditions of temperature and humidity in the three months prior to material collection. Two plants of both *T.dregeana* and *H.trijuga* were available (but probably from the same seed batch) and one of each of the others. For each plant, two fresh-looking but fully expanded leaves were taken and material with insects or other foreign bodies was avoided. Although only small quantities (<1 g of each) of tissue were required, the whole leaves were collected undamaged and kept at c. 5°C (to slow down oxidation of proteins by phenolic compounds).

Leaflets from near the end of the (imparipinnate) leaves were used and 200 mg of lamina tissue from the middle region of the leaflet was taken. This was ground in a 'Tris' extraction buffer, which included a small amount of mercaptoethanol to arrest all metabolic reactions, centrifuged and the supernatant refrigerated. Polyacrylamide gels were made up and allowed to polymerise (i.e. set). These could be made days in advance and stored in the refrigerator. Each one consisted of a c.3 mm thick oblong of gel supported on a glass plate with a line of twenty reservoir slots c. 2 cm from the top. Each slot was loaded with an identical amount of a different



a. Loading the reservoirs in the polyacrylamide gel with the extracts.



b. Applying the cotton wicks to the gel on the electrophoresis apparatus. Note that each is fed from a different reservoir.

FIG. 5.1

leaf extract, containing bromophenol blue marker dye (FIG. 5.1, a), and the gel placed horizontally on to a water cooled glass plate in the 'Multiphore' electrophoresis tank. Cotton wicks were then attached along the top and bottom ends of the gel to allow contact with the electrode buffer (FIG. 5.1, b). With the anti-condensation lid in place, a potential difference of 260 V was applied across the gel (i.e. between the two buffer compartments) for a set time depending upon the isoenzyme under investigation. The bromophenol blue marker migrates in advance of the larger protein molecules.

The gel was then removed from the 'Multiphor' tank, placed in an incubation box with an enzyme-specific stain and incubated at 37°C until banding patterns could be seen (usually 20-45 mins). The gel was photographed on a light-table and drawings were also made of the, sometimes very faint, bands. Slight modifications to the compositions of the gel, tank and stain buffers had to be made for different enzymes (to produce optimal conditions for each enzyme) and therefore only one enzyme per gel and separation was stained for. The enzymes investigated were:

1. Succinate dehydrogenase = SDH
2. Isocitrate dehydrogenase = IDH
3. Glutamate-oxoalacetate transaminase = GOT
4. Malate dehydrogenase = MDH
5. Esterase = EST
6. Leucine aminopeptidase = LAP
7. Alkaline phosphatase = APP
8. Glucose-6-phosphate dehydrogenase = G6PD

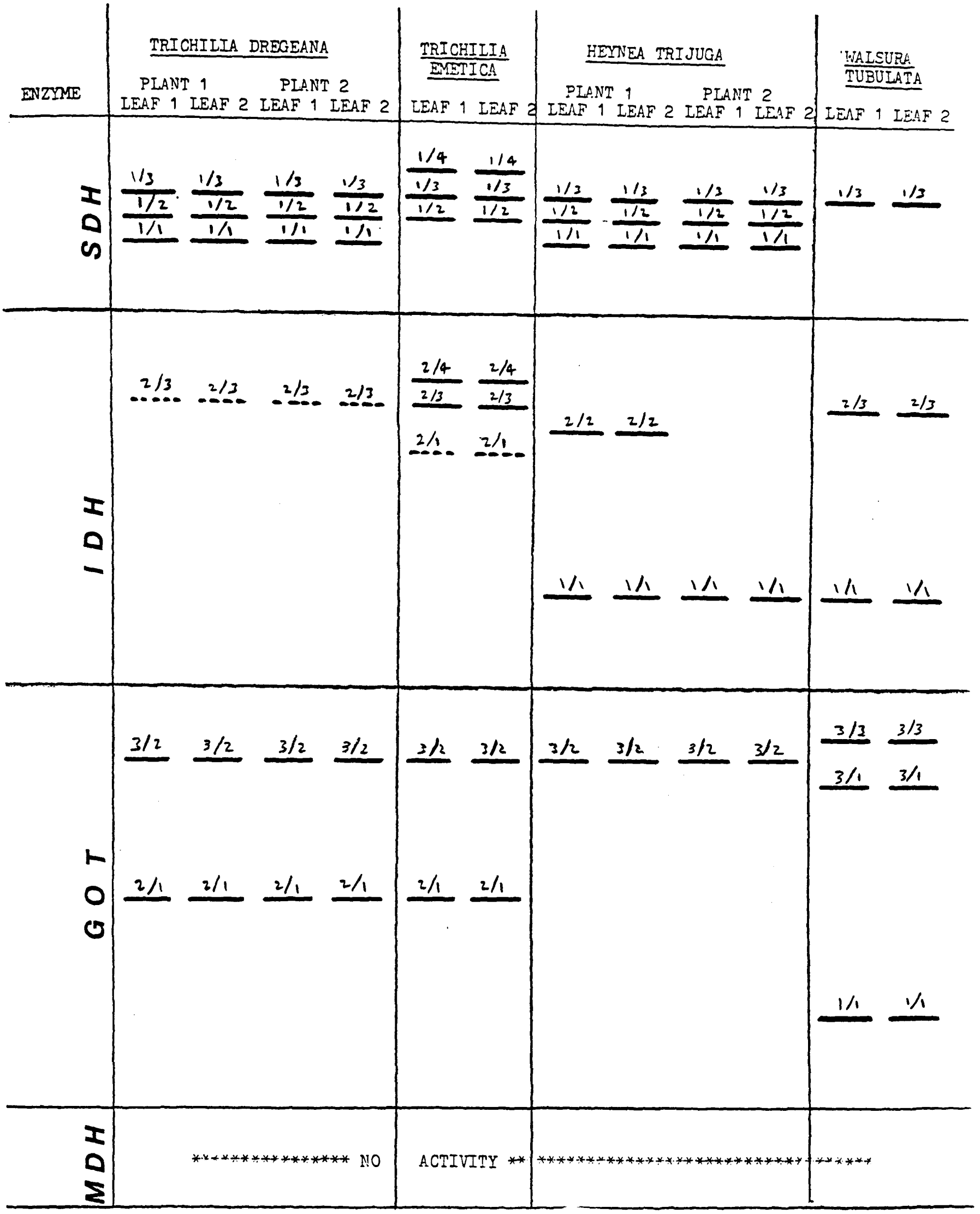


FIG. 5.2 Diagrams of banding patterns after electrophoresis and enzyme-specific staining of extracts from four species. Short horizontal lines indicate bands and a broken line indicates a weak band. Number coding is: X/Y, where X=locus number & Y=allele number. Diagrams are not to scale: see text.

↓ = direction of enzyme travel from reservoirs.

FIG. contd....

ENZYME	TRICHILIA DREGEANA				TRICHILIA EMETICA		HEYNEA TRIJUGA				WALSURA TUBULATA	
	PLANT 1		PLANT 2				PLANT 1		PLANT 2			
	LEAF 1	LEAF 2	LEAF 1	LEAF 2	LEAF 1	LEAF 2	LEAF 1	LEAF 2	LEAF 1	LEAF 2	LEAF 1	LEAF 2
EST							2/1	2/1	2/1	2/1	2/1	2/1
							1/1	1/1	1/1	1/1		
LAP	2/1	2/1	2/1	2/1	2/1	2/1						
	1/2	1/2	1/2	1/2	1/2	1/2	1/1	1/1	1/1	1/1	1/2	1/2
G6PD					2/2	2/2					2/2	2/2
					2/1	2/1	2/1	2/1	2/1	2/1		
	1/3	1/3	1/3	1/3	1/3	1/3						
							1/2	1/2	1/2	1/2	1/2	1/2
							1/1	1/1	1/1	1/1		
6 PGD					6/1	6/1						
	5/1	5/1	5/1	5/1			5/1	5/1	5/1	5/1	5/1	5/1
					4/1	4/1						4/1
	3/1	3/1	3/1	3/1			3/1	3/1	3/1	3/1	3/1	3/1
					2/1	2/1					2/1	2/1
							1/1	1/1	1/1	1/1	1/1	1/1

FIG. 5.2 continued.

FIG. contd.....

ENZYME	TRICHILIA DREGEANA PLANT 1 LEAF 1	TRICHILIA DREGEANA PLANT 1 LEAF 2	TRICHILIA DREGEANA PLANT 2 LEAF 1	TRICHILIA DREGEANA PLANT 2 LEAF 2	TRICHILIA EMETICA LEAF 1	TRICHILIA EMETICA LEAF 2	HEYNEA TRIJUGA PLANT 1 LEAF 1	HEYNEA TRIJUGA PLANT 1 LEAF 2	HEYNEA TRIJUGA PLANT 2 LEAF 1	HEYNEA TRIJUGA PLANT 2 LEAF 2	WALSURA TUBULATA LEAF 1	WALSURA TUBULATA LEAF 2
PER	2/1 1/2	2/1 1/2	2/1 1/2	2/1 1/2	2/1 1/2	2/1 1/2	2/1 1/2 1/1	2/1 1/2 1/1	2/1 1/2 1/1	2/1 1/2 1/1	2/3 2/2 1/2	2/3 2/2 1/2
ACP	3/3 1/1	3/3 1/1	3/3 1/1	3/3 1/1	3/4 3/3 3/1 1/1	3/4 3/3 3/1 1/1	3/4 3/3 3/2 1/1	3/4 3/3 3/2 1/1	3/4 3/3 3/2 1/1	3/4 3/3 3/2 1/1	3/4 3/3 3/2 2/2 2/1	3/4 3/3 3/2 2/2 2/1
AAP	********** NO				ACTIVITY		********** VERY HIGH CONCENTRATIONS IN HEYNEA & WALSUR.					

FIG. 5.2 continued to end.

9. 6-Phosphogluconate dehydrogenase = 6PGD

10. Peroxidase = PER

11. Acid phosphatase = ACP

Distances travelled by bands from the origins were measured for accuracy of comparison. Had time allowed, replicates of each gel would have been run and stained also.

RESULTS

The diagrams of the banding patterns (see Appendix 3) show the relative positions of the bands as seen in the gels, with the actual distances from the reservoir for each band. Having established (by careful study of the gels, photographs and drawings) that certain bands fall into groups or zones (and that they probably, therefore, indicate alleles of the same loci), FIG. 5.2 was drawn. This pictorially represents these groupings and emphasises the similarities and differences between the banding patterns in different species. FIG. 5.2 also has a numbering system for ease of comparison within each gel, but the spacing between the bands and between the groups of bands is constant and bears no relation to the distances given in App.3. Bands are numbered here in the conventional way (Brewer, 1970) with the fastest (i.e. farthest from the origin) band as '1', the second fastest as '2' and so on.

If unique combinations of (allele) characters are considered then by comparing the genera (Trichilia =T; Heynea =H; Walsura =W), the data can be simplified thus:

ENZYME	PRINCIPAL AFFINITY	GENUS SHOWING MOST AFFINITY WITH HEYNEA
SDH	H-T	T
IDH	W-H; W-T	W
GOT	H-T	T
EST	W-H	W
LAP	W-T	-
G6PD	H-T; W-T; W-H	-
6PGD	W-H	W
PER	H-T	T
ACP	H-T; W-H-T; W-H	-

DISCUSSION

Heynea, then, seems to exhibit practically equal affinity with both Trichilia and Walsura. This is perhaps over-simplified however, since there are other factors to consider.

For SDH, Heynea is clearly linked to Trichilia (by 1/2) and also to T.dregeana specifically (by 1/1) but not especially to Walsura. However,

for IDH the opposite situation exists with Heynea linked to Walsura (by 1/1) and not at all to Trichilia, but with Walsura linked to Trichilia (by 2/3). GOT shows clear Heynea-Trichilia affinity with Walsura very clearly distinct. It should be pointed out, however, that activity of this enzyme was very low and that perhaps not all bands were realised.

Esterase activity in these species seems pe culiar to Walsura and Heynea, with no trace of a band in either Trichilia species. This is the strongest difference between genera observed in the whole study. LAP illustrates another affinity between Walsura and Trichilia with Heynea being the exception, but the main affinity here is between species of Trichilia. G6PD seems to be of little use taxonomically with reticulation very much in evidence, thus emphasising the closeness of these genera.

For 6PGD, Walsura and Heynea share a unique combination of alleles (1/1, 3/1 & 5/1). At first sight, PER suggests greatest affinity of Heynea with Trichilia (in their sharing 2/1), but Walsura differs only in one allele (2/2). ACP again emphasises the reticulation but, on balance (considering 3/2), the greater affinity is between Walsura and Heynea. It should also be noted that levels of activity of this enzyme appeared high in Walsura and Heynea. In the light of all these additional considerations therefore, the balance of Heynea affinities now shifts slightly more towards Walsura.

There are some plant-plant differences in Heynea, which are a little worrying if this is an indication of the infra-specific variation generally in the Trichilieae. However, these differences are slight compared with the species-species and genus-genus differences. The data would be more

meaningful if more plants from more populations of more species had been considered, but this was not feasible because of the limited availability of fresh material.

CHAPTER 6

The Species of *Walsura* Roxb. and *Pseudoclausena* T.Clark *genus novum* (Meliaceae).

INTRODUCTION

Since the last monographic treatment (de Candolle, 1878) of the species included in this revision something in excess of 95% of specimens currently available for study have been collected and 72% (i.e. 28 out of 39) specific names have been published within *Walsura*. Of these new species, many were published with little attempt at comparison with previously described ones, hence synonyms abound. Of the fourteen species recognised here, three are newly described, and (for this revision) five have been studied in the field and flowering material of one (*W.dehiscens* T.Clark) was collected for the first time. In the light of infraspecific variation demonstrated by material collected since de Candolle's revision, five of his twelve species have been or need to be reduced, and his key to the species is found to be largely based on inaccurately described characters (which in some cases could have been avoided by close examination of any specimen of the species concerned). All of this, together with the removal here of several species to a new closely related genus, necessitates a new monographic treatment, so that material may be correctly identified and the affinities and relationships of the species be understood more clearly.

Where the term 'W.chrysogyne et al.' is used below it refers collectively to the species W.chrysogyne, W.brachybotrys, W.celebica, W.glabra, W.borneensis, W.hosei, W.palawanensis and W.velutina. The term Walsura sensu stricto refers collectively to all other Walsura species.

TAXONOMIC HISTORY

William Roxburgh described the genus Walsura in Flora Indica (1832) having invalidly published the name in his Hortus Bengalensis (1814). In 1832, he included only two species (W.piscidia Roxb. and W.robusta Roxb.). The genus therefore appeared just too late for incorporation in Adrien de Jussieu's revision of the family and its species then known, published in toto in 1832. Jussieu did however publish (1830) a new species of Heynea (H.trifoliolata) and it was not until 1940 that its synonymy with W.piscidia was pointed out (by Harms). W.robusta was removed from the genus by Roemer (1846) to a new genus Surwala, but was reinstated in Walsura by Hiern (1875) where it has remained.

W.pinnata was described by Hasskarl from Java in 1855 and W.gardneri by Thwaites from Sri Lanka in 1858. Clausena chrysogyne, described by Miquel in the Rutaceae in 1861, was transferred to Walsura by Bakhuizen f. (1968) as the correct name for the wide-ranging and highly variable species W.multijuga King (1895). W.trichostemon was also described by Miquel (1868) and Kurz (1875) reduced Wallich's unpublished W.villosa into it, though de Candolle (1878) chose to keep these two species separate.

Then followed two important regional floristic accounts. Hiern in J.D.Hooker's Flora of British India (1875) keyed out and described eight species of Walsura (including W.tubulata from Sikkim as new) and Kurz in his Forest Flora of British Burma (1877) did the same for seven species, but also illegitimately reduced Heynea Roxb. ex Sims (one species) to the genus. Walsura W.oxycarpa Kurz, from the Andamans, was also first described in 1875. 1878 saw the publication of Casimir de Candolle's epic species revision of the Meliaceae in which he described and attempted to key out twelve species of Walsura, including one new species (W.thwaitesii). Harms (1896 & 1940) gave descriptions of the genus but little or no information on individual species, and in the earlier work followed Kurz (1877) in including Heynea (at section status) but reinstated it as a distinct genus in 1940.

Since 1895, several species names have been published (see synonymies below), particularly based on material from Borneo, south eastern Indo-China and the Philippines. Only three are maintained in this revision, namely W.bonii Pellegrin (1910) and W.poilanei Pellegrin (1944) both from Vietnam and W.monophylla Elmer ex Merrill (1954, published invalidly by Elmer in 1937) from the Philippines.

Pennington (1965) gives the fullest description of the genus (but not species) to date and includes observations of wood structure and pollen morphology. Pennington and Styles (1975) in the most recent generic monograph of the family have a slightly abbreviated version of Pennington's earlier work for Walsura and also briefly discuss its relationship with other members of the tribe.

MORPHOLOGICAL NOTES

1. Habit

All species in wet evergreen forest are predominantly sub-canopy trees but in dry-zone evergreen forest in Sri Lanka, *W.trifoliolata* attains the same height as the other canopy trees (Holmes, 1956). *W.gardneri* of Sri Lanka is invariably a treelet to less than 3.5 m tall and its crown is more densely twiggy than any other species. All species, with the notable exception of *W.pachycaulon*, have slender twigs. Leaves can be all along the shoot (e.g. *W.robusta*) or clustered around the shoot apex (e.g. *W.pinnata* "villamilii").

2. Exudate

All species seem to lack exudate of any sort in slash bark and wood. Most of the species have glands on the undersurface of the leaf, however. These have been observed in *W.tubulata* (cultivated under glass at Oxford) to exude small quantities of sweet colourless liquid and the glands producing it are, therefore, probably extra floral nectaries. A colourless sweet sticky exudate has also been reported (Pennington 7815, Selangor) from the aril of *W.pinnata*.

3. Bark

Observations of bark morphology are sparse but seem to be of some taxonomic value. Most species have smoothish outer bark but that of W.trifoliolata is deeply fissured. Observations of some species are completely lacking.

4. Leaves

(i) Walsura sensu stricto

The leaf is unifoliolate (W.gardneri, W.monophylla and occasionally in W.pinnata "cochinchinensis") or imparipinnate with lateral leaflet pairs opposite (never subopposite). The primary rachis is slightly swollen at the point of insertion of the petiolules, as is the petiolule immediately below the base of the lamina, and the leaflet here can often be slightly geniculate. The unifoliolate species have a second petiolule swelling either just below or continuous with the swelling at the lamina base. The largest leaves are found in W.sarawakensis, at up to 80 cm long. W.trifoliolata and W.tubulata have one-jugate leaves and most species of Walsura are two-jugate. Three-jugate leaves occur in W.sarawakensis and in W.pinnata "villamilii" and the four- (and rarely five-) jugate state occurs in W.pachycaulon only. W.trifoliolata ssp. trifoliolata and W.tubulata grown from seed at the Oxford Botanic Garden both produced undivided leaves in the early stages and the latter was still producing a small proportion of such leaves when five years old (and flowering). Venation patterns do not seem to be of great use taxonomically. However, costae frequency is a good character with some species and W.pinnata "villamilii" is exceptional in having incomplete costae. These are 1/4-3/4 the length of normal costae

and taper distally, but for most of their length are the same width and prominence as complete costae.

(ii) W.chrysogyne et al.

This group exhibits a wide range of leaf division, from one- to seven-jugate, with two-, three- or four-jugate being the commonest states. The primary rachis and petiolule swellings typical of the other Walsura species are very slight or completely lacking in these species and, whilst most specimens have opposite leaflets, a small proportion have the slightly subopposite state. Venation patterns seem to provide no taxonomic characters.

For details of microscopical features of the leaf surface, see Chapter 2. Where, below, leaf epidermis is described as "glaucous in vivo", this implies that it is matt in sicco also. Species differ in the extent to which the abaxial surface is glaucous (i.e. papillae covered), from only in the islets between the smallest veins (giving the surface a white dotted appearance) in W.robusta and (to a lesser extent) in W.oxycarpa, to all areas except the midrib and costae, as in W.pachycaulon.

5. Inflorescence

In all species the inflorescence is a thyrse, which may be very short and dense as in W.brachybotrys (= W.chrysogyne) and W.dehiscens (as short as 0.8 cm) or long and open as in W.trichostemon and W.pachycaulon (up to 30 cm. in the latter). W. trifoliolata frequently has dense heads of florets at

the ends of the secondary rachides, a feature rare in other species. All species have a dense indumentum on the inflorescence, and in most this consists of minute simple trichomes only. In W.trichostemon the trichomes are so dense as to give the inflorescence a velutinous covering. Two-armed trichomes also occur (sparsely) in this species. In W.trifoliolata, W.gardneri and W.oxycarpa two-armed trichomes predominate on the peduncle and are replaced on all other parts by simple trichomes.

6. Flower

Most species seem to have hermaphrodite flowers only, but in W.trifoliolata, W.pinnata and W.chrysogyne et al. hermaphrodite or (on different trees) male only flowers occur. W.robusta seems to be dioecious but may also exhibit the hermaphrodite character.

Aestivation may vary considerably within a single specimen, from valvate to imbricate and, although much used in the past as a character in these species, is considered to be of little taxonomic value. W.robusta is the only species with discrete filaments only, all other species having an androecium which is tubular below with discrete filaments above. The proportion of the total androecium length (excluding anthers) which is a tube provides a useful taxonomic character. The form of the apex of the filament is in most species bifid to some degree, but in W.bonii is truncate.

All species of Walsura have a shallow cylindrical disk above the ovary around the style base, but apart from in W.robusta where it is pubescent, it is very constant and is of little taxonomic use. W.chrysogyne et al. lack a disk completely, however. All species have a dense covering of bristle-like trichomes on the ovary (being particularly dense in W.chrysogyne) but only in W.tubulata do they extend up the style. The stigma is normally capitate to conical, but in W.dehiscens a rather elaborate cone on top of a cap-like structure exists and in life the upper part is also covered by a layer of colourless gel-like substance, unknown elsewhere in the genus.

7. Pollen

See Chapter 3.

WOOD ANATOMY

The most detailed considerations of wood anatomy in these species are by Pennington (1965) and Datta & Samanta (1983), with a summary of Pennington's earlier work in Pennington & Styles (1975). The wood of W.robusta differs in some small features to that of W.trifoliolata and W.tubulata, and W.chrysogyne has a much larger vessel pore density (308/ sq.mm.) than these other three species (at 81-154/ sq.mm.). The paucity of data on individual species however severely limits the discussion of taxonomic worth of wood anatomical features.

Mehrotra (1989) has described (in English only) a new species of Walsura, W. deccanensis, on the basis of wood anatomical characters of fossil material*. He gives a detailed description of the wood structure of this fossil and compares it with wood samples of extant species of Walsura (W.robusta, W.piscidia = W.trifoliolata, W.villosa = W.trichostemon & W.glauca = W.pinnata), Heynea, Dysoxylum and Lansium.

FRUIT STRUCTURE AND SEED DISPERSAL

See Chapter 4.

GERMINATION

(After Pennington & Styles, 1975)

Cryptocotylar, cataphylls minute, followed by spirally arranged simple entire eophylls. See FIG. 3 for illustration of W.trifoliolata seedling.

* Mehrotra (1989) described fossil material from the ? early Tertiary deposits in Mandla district, India, presently c. 22° north of the equator, but in the early Tertiary almost equatorial. The single fossil 'holotype' specimen is deposited in the Birbal Sahni Institute of Palaeobotany, Lucknow Museum and is specimen number 35939.

CHROMOSOMES

W.trifoliolata is the only species to have been studied cytologically. Its chromosome count is n=14, 2n=28 (Ghosh, 1961; Khosla & Styles, 1975; Datta & Samanta, 1977).

CHEMOTAXONOMY

Chatterjee & Kundu (1968) describe a new pentacyclic alcohol, called Walsuranol, from W.tubulata, but they could not find limonoids in this species. Taylor (1984) however reports the occurrence of various limonoids in the other Indian species, W.trifoliolata. Purushothaman et al. (1985) and Umadevi et al. (1988) have also made chemical studies of W.trifoliolata. No other species seems to have been investigated from a chemotaxonomic viewpoint.

VARIATION WITHIN THE GENERA

Walsura was first divided into sections by Hiern (1875) when he reduced Roemer's (1846) genus Surwala to Walsura as the monospecific section containing W.robusta. All other species were accommodated in section Euwalsura. Harms (1896) maintained these two sections and added a third (un-named) which included W.trijuga (Roxb.) Kurz (= Heynea trijuga). In 1940, when Harms reinstated the genus Heynea, he included this species there setting up another, third, section within Walsura, called Neowalsura,

to accommodate W.glabra Merrill. However, this species is here (see below) moved to Pseudoclausena.

The section Euwalsura is here maintained, and its name amended slightly (to conform to the International Code) as section Walsura, and section Surwala is also maintained. A new section is described to accommodate W.dehiscens and is called Ruswala. Section Ruswala is characterised by the dehiscent fruit of its one species, and sect. Surwala by separate filaments and trichomes on the inner surface of the pericarp. The ordering of the sections posed some problems, particularly with respect to Ruswala. Fruit anatomical evidence (see Chapter 4) seems to suggest that sect. Surwala (i.e. W.robusta), may be nearer to Heynea than sect. Walsura is. Within sect. Walsura there is great diversity with, perhaps, those species centered on W.pinnata (see below) being the most different from W.robusta. The position of sect. Ruswala (W.dehiscens) depends largely on how the septicidal capsule character is treated. If it is regarded as a small evolutionary step from/to a loculicidal capsule (see FIG. 4.34) then it is best placed on the Heynea side of sect. Ruswala. If, however, it is considered quite different, and probably the product/origin of a completely different evolutionary line, then it should probably be placed further away, possibly beyond sect. Walsura. It is this second juxtapositioning which is accepted here. This decision is supported by W.dehiscens having a stigmatic form unlike that found in any other species of Walsura or Heynea. Its very short staminal tube (c. 1/5 of the total length of the androecium) is nearer than most species of the genus to the discrete filaments state of W.robusta but it could be pointed out that W.gardneri (in sect Walsura) can have a tube as short as 1/8 the total length of the androecium.

Accepting this order (i.e. sect. Surwala - sect. Walsura - sect. Ruswala), an evolutionary ordering can then be speculated. If Trichilia is seen as the core genus of the tribe with Heynea as a modified version of an African Trichilia species (see Chapter 4, "Discussion: taxonomy") then the evolutionary trend could be seen to be : Trichilia - Heynea - Walsura (sect. I, Surwala - sect. II, Walsura - sect. III, Ruswala) with the septicidally dehiscent species W.dehiscens being a relatively recent innovation derived from the normal berry bearing Walsura stock.

Section II, Walsura, accommodates the majority of the species and is here further divided informally into two species groups. Group 1 is defined by those species remaining when Group 2 is removed. Group 2 is centred on the highly variable and widely distributed species W.pinnata and is confined to the Malesian end of the distribution of the genus. Whilst the minor characters defining it are not sufficient to merit segregation as a separate section, it is considered useful to include the two groups in the current revision.

Group 2 is defined by the following characters, taken collectively: (i) petiole adaxially flattened to shallowly canaliculate along its whole length (i.e. to first node); (ii) leaf lamina abaxial surface glabrous or very sparsely pubescent; (iii) all leaf veins clearly prominent (in sicco) on abaxial surface; (iv) flower buds, just prior to opening, less than 4.6 mm long. W. walsura tubulata from Darjeeling is most similar to the Group 2 species (but differs in flower size and (see descriptions) in twig bark

lenticellation) and, perhaps, provides the link between the two groups and, possibly, between the Indian / Sri Lankan species and the Malesian species.

Walsura chrysogyne et al. are considered so different from all other species of Walsura (see morphological and anatomical notes above and the key and diagnosis below) that they are removed to a new genus, Pseudoclausena.

The taxonomic division of the genera in this revision is therefore as follows:

WALSURA Roxb.

Sect.I Surwala (M.Roemer) Hook.f.

1. W.robusta Roxb.

Sect.II Walsura GROUP 1:

2. W.trifoliolata (Adr.Juss.) Harms

   ssp. trifoliolata

   ssp. acuminata (Trimen) T.Clark comb.& stat.nov.

3. W.tubulata Hiern

4. W.trichostemon Miq.

5. W.gardneri Thw.

6. W.bonii Pellegrin

7. W.oxycarpa Kurz

8. W.poilanei Pellegrin

GROUP 2:

9. W.pinnata Hassk.

"pinnata"

"cochinchinensis"

"villamilii"

10. W.pachycaulon Mabb. ex T.Clark sp.nov.

11. W.sarawakensis T.Clark sp.nov.

12. W.monophylla Elmer ex Merrill

Sect.III Ruswala T.Clark, sect.nov.

13. W.dehiscens T.Clark, sp.nov.

+ two species (14 & 15) non satis cognitae.

PSEUDOCLAUSENA T.Clark, gen.nov.

16. P.chrysogyne (Miq.) T.Clark comb.nov.

forma chrysogyne

"chrysogyne"

"multijuga"

"brachybotrys"

forma velutina (Ridley) T.Clark comb.& stat.nov.

GEOGRAPHICAL DISTRIBUTION AND SPECIATION

The species of Walsura (excl. W.chrysogyne et al.) occur in India (west to the Western Ghats and north to Darjeeling), Sri Lanka, the Andaman Islands, Burma, Thailand, Indo-China, Yunnan, Hainan, the Malay Peninsula, Sumatra, Java, Borneo, the northern and western Philippines (Puzon to Palawan), Sulawesi, Halmahera and western New Guinea (Manokwari). W.chrysogyne et al. occur in peninsular Thailand, the Malay Peninsula, southern Sumatra, Borneo, the southern Philippines (Samar, Leyte, Mindanao and Palawan), Sulawesi, Halmahera, Seram and western New Guinea. Distribution maps for most individual species are given below.

W.pinnata, at the Indo-China - Malesian end of the range, is a complex species (sensu Pennington & Styles, 1981), which may correspond to an ochlospecies (White, 1962). Such a species is highly variable and occupies a wide geographic range but is not divisible into sub-species. One population may contain two or more distinct morphological entities which do not intergrade, but the intermediates may (now) occur in another population far removed geographically. Closely related to W.pinnata are at least three other species, all distributed within its range and each of very small range (viz. W.sarawakensis and W.pachycaulon in Borneo, and W.monophylla on Palawan). If W.chrysogyne et al. are treated as one species (see below) then this is also a complex species and is limited to the Malesian region (Whitmore, 1984; equivalent to the 'Malaysian region' of van Steenis,

1950), north to the isthmus of Kra and to Luzon in the Philippines and south east to New Guinea.

By contrast, those species in the India to continental-Malesia end of the range are predominantly monotypic, taxonomically isolated species (sensu Pennington & Styles, 1981), each of which is separable from all other species by several diagnostic characters and is not divisible into sub species, W.dehiscens being the only species from outside this range which falls within this category. alsura W. trifoliolata is the only species within this range which could be described as a polytypic species, i.e. which on the basis of morphological characters, supplemented by geographical or ecological evidence, can be subdivided into two or more sub species.

alsura
W.robusta seems to be of largely coastal occurrence whilst W.trichostemon, with a similar range, occurs much further inland as well. The velutinous indumentum of the latter may account for its tolerance of a more continental (i.e. seasonal) climate. The majority of specimens of the densely velutinous P.chrysogyne forma velutina are from localities above 300m altitude, possibly for similar reasons. alsura W.gardneri of Sri Lanka seems to be limited to hill country, although its shoots and leaves are glabrous, and the subspecies of W.trifoliolata generally occupy different climatic zones (see below), this being most pronounced in Sri Lanka. The distribution of W.monophylla in Palawan seems to be the only one which correlates with an edaphic factor, the trees being largely restricted to ultrabasic soils.

ECONOMIC BOTANY

Most of the widely occuring species seem to be used locally as a source of hard, durable timber* and W.robusta (in combinations with other timbers) has been used in paper manufacture (Hossain & Siddique, 1970). The specific epithet of W.piscidia Roxb. (= W.trifoliolata) reflects the widespread practice in India of using the bark in fishing. The bark is stripped off the tree, broken up and thrown into the water whence a toxin coming from it kills the fish (which float to the surface and can be collected) but does not render the fish flesh inedible (Roxburgh, 1832, p. 388). Most species of Walsura are known to have a succulent aril which is sweet and edible but no evidence of its use as a human foodstuff can be found.

Biomass production in dry evergreen forest (in Thailand) dominated by Hopea ferrea, Walsura trichostemon, Memecylon ovatum and Hydnocarpus ilicifolius has been studied by Sabhasri (1971).

*The properties of the timber of W.trifoliolata are listed in Nazma et al. (1981) pp.221-222.

SYSTEMATIC TREATMENT

Leaflet abaxial epidermis papillate, flower with well-defined disk; ovary 2-locular; fruit symmetrical; pericarp with sclerenchyma layer .....a. Walsura

Leaflet abaxial epidermis non-papillate; flower lacking disk; ovary 4-5-locular; fruit asymmetric; pericarp lacking sclerenchyma .....b. Pseudoclausena

a. WALSURA* Roxb. [Hort. Beng. 32 (1814) nom. nud.,] Fl. Ind. 2:386 (1832); C.DC. in DC., Monog. Phan. 1:633 (1878); Harms in Engl. & Prantl, Nat. Pflanzenfam. III,4:302 (1896) and in ed.2, 19b1:118 (1940); Penn. & Styles, Blumea 22:472 (1975). Type species: W.piscidia Roxb. = W.trifoliolata (Adr. Juss.) Harms, effectively selected by Roemer (1846).

[Monocyclis Wall. Report E.I.Co.Bot.Gard.: 26(1840) nom. nud. & ex Voigt, Hort. Suburb. Calc. 135 (1845), nom. nud.]

Surwala Roem., Synops. Hesp. Monogr. 1:108 (1846). Type species: S.robusta (Roxb.) Roem. = W.robusta Roxb.

Napeodendron Ridley, J.R.As.Soc.Straits Branch 82:179 (1920). Type species: N.altissimum Ridley = W.pinnata Hassk.

* From the Tamil name, "Walsura", for this species.

Trees, unbranched low down or (if tree less than 4 m tall) densely twiggy at breast height, sympodial, leptocaul to pachycaul, buttressed or not, indumentum of simple and/or 2-armed trichomes; leaves usually all along leafy twigs, unifoliolate or imparipinnate with opposite leaflets, 1-4-jugate, to 80 cm long; rachis swollen slightly at the node(s); petiolule usually swollen slightly immediately beneath base of lamina and sometimes slightly geniculate; lamina apex acuminate to obtuse to retuse and base symmetric or slightly asymmetric, abaxial surface glaucous (in vivo) and glabrous to velutinous and sometimes with small glandular-bodies (=black dots) on either side of and within 2 mm of the midrib; inflorescences axillary (cauliflory unknown), 0.8-30.0 cm long, each a thyrse with a very dense to open paniculate head, indumentum of simple and/or 2-armed trichomes; flower hermaphrodite or unisexual, just prior to opening +/- cylindrical and up to 6 mm long, at maximum opening up to 9 mm diam., short pedicel widening almost imperceptibly into calyx; calyx much shorter than the petals, shallowly- to deeply-5-lobed, each lobe triangular with entire margins and acute apex; petals 5, free, valvate to imbricate, oblong to narrow-elliptic, apex acute to obtuse and sometimes hooded after opening; androecium of 10 discrete filaments each narrowly triangular or a tube surmounted by 10 ligulate to narrowly triangular filaments, each filament with a truncate or short-bifid apex; anthers 10, deltoid, very short-beaked or not at all; disk annular, glabrous or pubescent; ovary very densely hairy with short erect trichomes or glabrous, 2-locular, each

locule with 2 collateral ovules; style cylindrical to inversely conical; stigma capitate to short-cylindrical, may have two short lobes at apex; fruit a 1-2 (-4 ?)-seeded berry or 1-2-seeded weakly dehiscent capsule, pericarp leathery with thin layer of sclerenchyma on inside, thin septum separating locules; seed +/- ellipsoidal, lacking endosperm, surrounded by transparent sweet fleshy aril.

16 species (including 2 non satis cognitae) in the Indo-Malesian region.

Type species, effectively selected by Roemer (1846) = W. piscidia Roxb. = W.trifoliolata (Adr. Juss.) Harms

ARTIFICIAL KEY TO WALSURA SPECIES

(N.B. W.yunnanensis excluded)

1a. Leaf undivided.....2

b. Leaf divided.....4

2a. Peduncle of inflorescence with 2-armed trichomes;
androecium tubular for less than 1/6 of length
(Sri Lanka) ..... 5. W.gardneri

Peduncle of inflorescence with simple trichomes
only; androecium tubular for greater than 1/3 of length 3

3a. Androecium tubular for 1/3-1/2 of its length;
berry 8-11 mm diam. when mature (Philippines).....12. W.monophylla

b. Androecium tubular for 1/2-2/3 of its length;

berry 12-24(-28) mm diam. when mature..... 9. W.pinnata ("cochinchinensis")

4a. Leaf 1-jugate.....5

b. Leaf 2 or more-jugate.....8

5a. Leaflets slightly asymmetric; filament apex truncate (Vietnam) .....6. W.bonii

b. Leaflets symmetric; filament apex shortly bifid 6

6a. Flower just prior to opening 5-6 mm long (Assam) .....3. W.tubulata

b. Flower just prior to opening 2-4 mm long 7

7a. Leafy twigs puberulous (India & Sri Lanka) .....2. W.trifoliolata

b. Leafy twigs glabrous .....9. W.pinnata

8a. Leaves 2-jugate.....9

a. Leaves 3-5-jugate.....15

9a. Leaflet abaxial surface white-dotted (matt/glaucous in islets); androecium of discrete filaments.....2. W.robusta

b. Leaflet abaxial surface not white-dotted (matt/glaucous uniformly); androecium tubular for part of its length.....10

10a. Leaflet abaxial surface velutinous (Vietnam).....8. W.poilanei

b. Leaflet abaxial surface glabrous to sub-densely pubescent.....11

11a. Fruit 4-winged to rhomboidal (in transverse section) and weakly dehiscent (Borneo).....13. W.dehiscens

b. Fruit terete and indehiscent.....12

12a. Fruit slightly beaked.....13

b. Fruit not beaked.....14

13a. Inflorescence velutinous; berries minutely tomentose (Burma, N.Thailand & Cambodia) .....4. W.trichostemon

b. Inflorescence glabrous or puberulous; berries glabrous or puberulous (Andamans) .....7. W.oxycarpa

14a. Petiole glabrous or extremely sparsely pubescent with prostrate simple trichomes; all veins prominent on abaxial surface of leaflet (in sicco) ..... 9. W.pinnata

b. Petiole densely puberulous with prostrate simple and 2-armed trichomes; only midrib and costae prominent on adaxial surface of leaflet (in sicco) (Borneo) .....15. W.species A.

15a. Leafy twigs 8-15 mm diam.; leaves 4(-5)-jugate (Borneo).....10. W.pachycaulon

b. Leafy twigs 2.5-8.0 mm diam.; leaves 3-jugate.....16

16a. Leaves 2(-3)-jugate; leaflet apex acute or acuminate for < 1.5 cm .....9. W.pinnata

b. Leaves 3-jugate only; leaflet apex acuminate for (2-)2.5-2 cm (Sarawak) .....11. W.sarawakensis

SECTION I: Surwala (Roem.) Hook.f.

Walsura sect. Surwala (Roem.) Hook.f. in Benth. & Hook.f., Genera Plantarum 1:336 (1862).

Surwala Roem., Syn. Hesperides 1:108 (1846). Type species: Walsura robusta Roxb.

1. WALSURA ROBUSTA Roxb. FIGS. 6.1 & 6.2

Walsura robusta Roxb. [Hort.Beng. 32 (1814), nom.nud.], Fl.Ind. 2:386 (1832); Wight & Arn., Prod.Fl.Pen.Ind.Or. 1:120 (1834) excl. specim.; Roem., Hesperides 1:108 (1846) excl. specim.; Miq., Ann.Mus.Bot.Lugd. Bat. 4:60 (1869); Hiern in Hook.f., Fl.Br.Ind. 1:565 (1875); Kurz, J.As.Soc.Beng. 44:148 (1875) and Prelim.Rep.Veg.Pegu App.B:37 (1875); Kurz, For.Fl.Br.Burma 1:223 (1877); C.DC. in DC., Monog.Phan. 1:638 (1878); King, J.As.Soc.Bengal 64:85 (1895); Harms in Engl. & Prantl, Nat.Pflanzenfam. III:4:302 (1896) and in ed.2, 19b1:119 (1940); Prain, Bengal Pl. 1:317 (1903) and ed.2, 1:221 (1963); Brandis, Ind.Trees 137 (1906); Lecomte, Fl.Gén.Indo-Chine 785 (1911); Lace, List Trees etc.Burma: 26 (1912); Schmidt, Fl.Koh Chang 405 (1916); Craib, Fl.Siam.Enum. 262 (1926); Kanjilal et al., Fl.Assam 1:241 (1937); Vidal, Nom.Vernac.Pl.Use.Laos 607 (1959); Nir, Burmese Fl.Pl. 1:173 (1963); Chun et al., Fl.Hainanica 3:71 (1974); Suvatti, Fl.Thai. 2:727 (1978); Balakrishman, Fl.Jowai 1:122 (1981); Deb, Fl.Tripura State 1:453 (1981); Haridasan & Rao, For.Fl.Meghalaya 1:214 (1985); Chen Ximu et al., J.Bot.Res. 4:177 (1986). TYPE: Roxburgh s.n., India, Silhet. (BM! lecto./selected here; K! syn.)

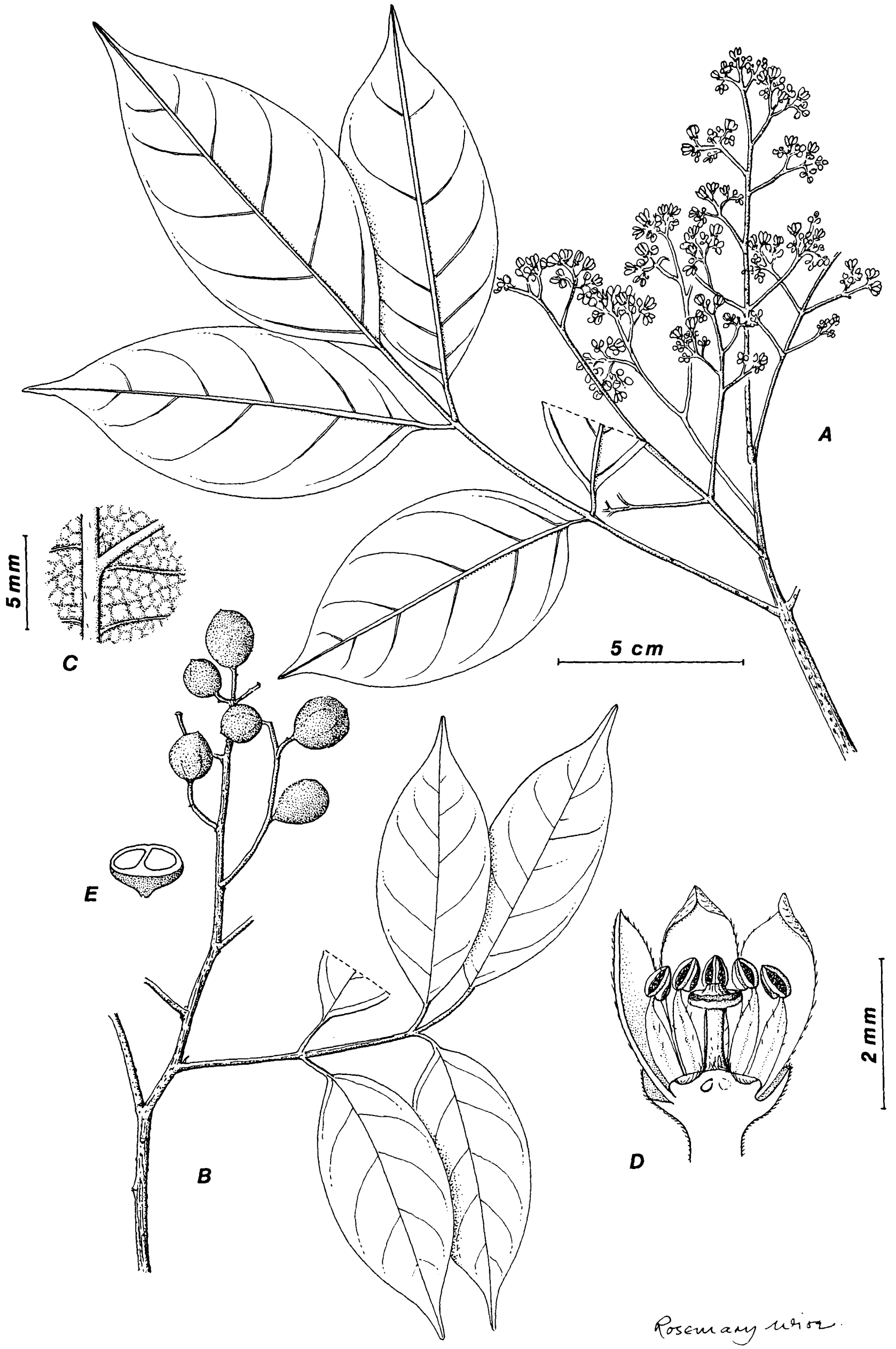


FIG. 6.1 W. robusta Roxb. A. habit; B. habit with infructescence; C. abaxial leaf surface detail (papillae islets); D. flower in L.S.; E. fruit in T.S. (A, C & D: Parkinson 283; B & E: Bunchuai 1822 = BKF s.n.)

[Monocyclis robusta Wall. ex Voigt, Hort.Suburb.Calcutt. 135 (1845), nom. Report E.I.Co.Bot.Gard.: 26(1840),
nud.]

Surwala robusta (Roxb.) Roem. Syn. Hesperides 1:108 (1846). Type: as for W.robusta.

[Scytalia glabra Buch. Ham. ex Wall., Cat. 8048E (1847), nom. nud.]

Scutinanthe boerlagii Hochr, Pl. Bog. 64 (1904); Lam, Bull.Jard.Bot. Btzg. III,12:422 (1932); c.f. Leenhouts, Fl.Mal. Ser.1, 5:249 (1956). TYPE: Hochreutiner 132, Indonesia, Java, Bogor Botanic Garden, Tree No. III T 27 (BO? holo?; L! iso.?; K! iso.?)

VERNACULAR NAMES: In Silhet: Upphing. Burmese: Gyopho or Gyobo. Thai: Maki ai, Lao.

Tree, to 25 (-31) m tall, d.b.h. to 1.5 m; outer bark grey-brown, inner bark pink-red; leafy twigs 2.0-3.5 mm thick, glabrous to puberulous with simple trichomes, bark dark-brown to black and very densely lenticellate; leaves 14-18 (-28) cm long, 2-jugate; petiole 2-4 (-6) cm long, 0.5-1.8 mm thick, semi-terete and flattened adaxially for entire length, glabrous to puberulous with simple trichomes, usually sparsely to densely lenticellate; petiolule +/- terete (to slightly flattened adaxially), (of distal pair leaflet:) 0.4-1.0 (-1.7) cm long & 0.5-1.0 mm thick; lamina (of distal pair leaflet:) 6.4-12.5 (-15.5) cm X 2.8-4.0 (-6.5) cm, (of terminal leaflet:)

6.5-10.5 (-16.5) cm X 2.9-4.0 (-7.0) cm, all leaflets (slightly obovate-) elliptic to ovate (basal leaflets usually slightly smaller and tending more to ovate), base acute to short-attenuate, apex acuminate, sub-coriaceous; adaxial surface with no veins prominent, abaxial surface with only midrib and costae prominent and glaucous (in vivo) only in islands between the smallest veins giving surface a whitish-dotted appearance, abaxial surface glabrous to extremely sparsely pubescent with simple trichomes (usually on the sides of the midrib); 5-7 (-8) (distal pair leaflet) and 6-8 (terminal leaflet) costae on either side of the midrib; glands present or absent and occasionally conspicuous.

Inflorescences clustered around shoot apex in the axils of caducous undeveloped leaves or below in the axils of caducous undeveloped or (far less commonly) fully expanded leaves, 5-10 (-18) cm long at anthesis, each an open thyrse, branched up to third order (excluding pedicels), first order branches up to (1.5-) 3.0-5.0 cm long, primary rachis glabrous to densely puberulous with simple trichomes and usually dark-brown to black and densely lenticellate; flowers unisexual (and hermaphrodite ?), scented, just prior to opening +/- cylindrical to inversely conical, 2.7-4.0 mm long X 2.1-3.0 mm diam., at maximum opening 2.5-4.3 mm diam. with no size differences between the sexes; calyx 0.9-1.3 mm long, lobes 0.7-0.9 mm long; petals 2.5-3.4 mm long X 0.9-1.0 mm wide, valvate (to slightly imbricate), apex acute with upper c.1/4 of petal incurved at c.90° prior to maximum opening, puberulous inside and out; androecium of discrete filaments, each filament triangular and 1.2-1.3 mm long X 0.6-0.7 mm wide at the base with acute apex, glabrous to sparsely puberulous inside and out; anthers 0.46-0.50 mm long with a blunt end and no beak, sessile on

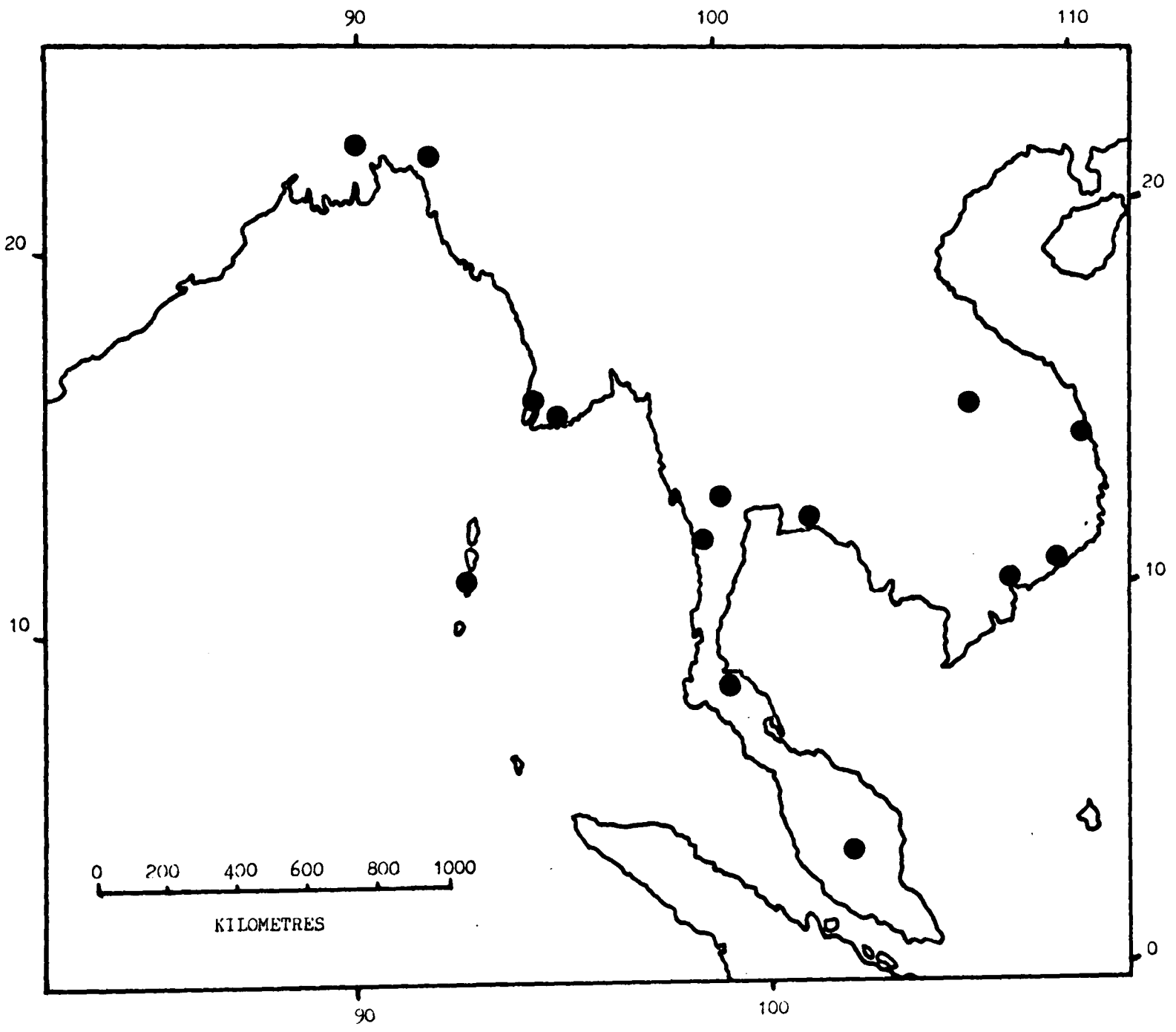


FIG. 6.2 Distribution of W. robusta Roxb.
N.E. India, Indo-China and Malay Peninsula.

filament apex, glabrous, the only difference between the sexes being that the female produces solely deformed (i.e. infertile) pollen; disk 0.2-0.4 mm high, minutely puberulous; style (in male flower:) 0.70-0.75 mm long X 0.27-0.33 mm diam., (in female flower:) 1.1-1.2 mm long X 0.4-0.7 mm diam., cylindrical to narrowly conical, glabrous except for ovary-type trichomes near the base; stigma capitate to short conical, 0.6-0.7 mm diam. at base X 0.2-0.5 mm high, with shallow depression at centre (in male) or slightly 2-lobed (in female), below (in male) or above (in female) the level of the anthers at anthesis; fruit a 1-2-seeded berry, globose, 1.1-1.9 cm diam., olive-green (in vivo) and brown (in sicco), puberulous, pericarp thin but coriaceous with very thin fibrous endocarp the inside of which (facing the seed) is densely pubescent with simple trichomes; seed +/- globose or (in 2 seeded fruit) hemi-globose and 0.7-1.3 cm long, completely to almost completely enveloped in an aril in vivo cream coloured and sweet to taste.

DISTRIBUTION: Bangladesh, Burma, Andamans, Thailand, Laos, Vietnam, Peninsular Malaysia.

NOTES: The only known collection of this species in Malaysia is (T.C.Whitmore) FRI 20163; Pahang, Taman Negara, Pahang Kuala (A!; FRI! incl. fruit in spirit; K!; SAR!). Seed harvested with this collection has given rise to a tree, c.9 m tall in 1987, at FRIM (Kepong) and FRI 27277 & T.Clark 89 are from this tree.

SPECIMENS STUDIED: Alfred 43/22(K); Amherst 1266(K), 8112(K); BKF 7545(L), 18203, 37444(L), 37511(L), 40246, 46507(K), 46868(L), 75654(L); Bunchuai 1555(K;L), 1822(K); Chatterjee s.n.(GH); T.Clark 89(FHO); Dickason

5503(GH), 7887(L); FRI 20163 (FRI;SAR), 27277(FRI); Gamble 7828(K), 7937(K); Geesink & Hiepko 7842(L); Griffith 335(L), 595(L), 1059(K), 1060(K), 1089(K), 1091(K); Harmand 713(K); Helfer 34(BM), 1059(K;L); Hochreutiner 132(K;L); Kerr 558(BM), 1288(BM), 1534(K), 5731(BM;K), 6007(BM;K), 6468(BM;K), 8520(BM;K), 8552(BM;K), 8594(BM;K), 8764(BM;K), 9866(BM;K), 10447(BM;K), 11648(K;L), 2606(BM), 12980(BM), 12983(K), 17055(BM;L), 17636(BM;K), 17890(BM;K), 20296(K;L); King s.n.(L); King's coll. 5(BM), 14(L), 89(K), 139(BM), s.n.(L); Koelz 27691(L); Kurz s.n.(L), s.n.(K); Lace 3015(K); Lakshnakara 561(BM;K;L); MADW 24507(K); Parker 2285; Parkinson 283(K), 14478(A); Parry 1161(K); Perry 11068(K); Phua 509; Pierre 1534(BM;L), 4244(K), 4255(BM;L), 4299(K); Pleyte s.n.; Poilane 1361(L), 3219(K;L), 3221(K), 9405(L), 19232(K;L); Put 558(K), 1288(BM;K;L); Siam 1891, 5744; Thorel 1227(BM); Vanpruk 116(K), 120(K), 509(K); Wall. Cat. 1266(BM;K-W), 8110(BM;K-W); Winit 22(K), 634(K), 1836(K), 1915(K).

SECTION II: Walsura

Walsura sect. Walsura, Hook.f. in Benth. & Hook.f. 1:336 (1862), 'sect. Euwalsura', emend; Hiern in Hook.f., Fl.Brit.Ind. 1:543 ('Euwalsura', 1875). Type species: W.trifoliolata (Adr. Juss.) Harms.

2. WALSURA TRIFOLIOLATA (Adr. Juss.) Harms FIGS. 6.3-6.5

Walsura trifoliolata (Adr.Juss.) Harms in Engl. & Prantl, Nat.Pflanzenfam. ed.2. 19b1:119 (1940), 'trifolia', emend.; Saldanha & Nicolson, Fl.Hassan Dist. 396 ('trifolia', 1976); Nair & Henry, Fl.Tamil Nadu 69 ('trifolia', 1982); Matthew & Britto, Fl.Tamilnadu Carnatic 3:I:242 ('trifoliata', 1983); Sharma et al., Fl.Karnatica (Anal.): 47 ('trifoliata', 1984).

Heynea trifoliolata Adr.Juss. in Mirb. & Cass. apud Guill. in Bull.Sci.Nat.Géol. 23:239# ['238'] (1830) and in Mém.Mus.Hist.Nat. Paris 19:235 ('trifoliata') & 274 ('Haenea trifolia') (1832)*;

*Although this paper (which is de Jussieu's monumental account of the family) is dated 1830, and was read at the Academy of Sciences on 25th January 1830, it was not published by November of that year when Guillemin (1830) gives a verbatim report of de Jussieu's classification and the diagnoses of his new genera and species. When de Jussieu's full account was published (1832 ?) this species is refered to by the specific epithets

Panigrahi & Mishra, Ind.J.For. 11:137 (1988) ('trifoliata').

TYPE: Sonnerat s.n., India (P! holo., FHO! photo).

[Trichilia trifoliolata Wall., List n. 8093. 1847, nom. nud.; Hiern in Hook.f., Fl.Brit.India 1:564 (1875) nom.in synon., non L. (1762) = T. trifolia L.]

[Trichilia coriacea Wall., List n. 1265. 1828, nom. nud.; Roem., Hesperides 1:115 (1846) nom. in synon.]

W.piscidia Roxb. [Hort.Beng. 32 (1814), nom.nud.], & Fl.Ind. 2:387 (1832); Wight & Walker-Arnott, Pro.Fl.Pen.Ind.Or. 1:120 (1834); Roem., Hesperides 108 (1846); Drury, Hndbk.Ind.Fl. 1:165 (1864); Miq., Ann.Mus.Bot.Lugd.Bat. 4:60 (1869); Hiern in Hook.f., Fl.Br.Ind. 1:564 (1875); C.DC. in DC., Monog.Phan. 1:634 (1878); Lisboa, Gaz.Bombay Pres. 25:44 (1886); Trimen, Fl.Ceylon 1:250 (1893); Nairne, Fl.Pl.W.Ind. 55 (1894); Talbot, Trees etc.Bomb.Pres. 41 (1894) and in ed.2, 78 (1902); Harms in Engl. & Prantl, Nat.Pflanzenfam. III:4:302 (1896) and in ed.2, 19b1:119 (1940); Dalgado, Fl. Goa 34 (1898); Cooke, Fl.Pres.Bomb. 1:213 (1903); Brandis, Ind.Trees 136 (1906); Talbot, For.Fl.Bomb.Pres.& Sind 1:241 (incl. plate) (1909); Haines, For.Fl.Chota Nagur 253 (1910); Rao, Fl.Pl.Travancore 75 (1914); Gamble, Man.Ind.Timb. 152 (1922); Haines, Bot.Bihar & Orissa 178

"trifoliata" and "trifolia" (one, perhaps, being a typographical error). In Guillemin's report, however, "trifoliolata" is used and this is accepted here as the first published name of this species.

(1925); Gamble, Fl.Pres.Madras 1:183 (1935); Worthington, Ceylon Trees 123 (1959); Penn. & Styles, Blumea 22:473 (1975). TYPE: Roxburgh s.n., India, 'Corrundel', (BM! lecto./ selected here, illus. Icon.Roxb. 3:t.17 (1969)).

W.piscidia var. typica Haines. Bot.Bihar & Orissa 2:178 (1921) nom. superfl. pro var. piscidia.

W.ternata Roxb. Fl.Ind. 2:388 (1832). TYPE: Roxburgh s.n., India, 'Corrundel', (BM! lecto./ selected here, illus. Icon.Roxb. 3:t.18 (1969)).

W.piscidia var. ternata (Roxb.) Haines, Bot.Bihar & Orissa 2:178 (1921).

H.trifoliolata var. ternata (Roxb.) Panigrahi & Mishra, Ind.J.For. 10(2):137 ('trifoliata'),(1988).

[Xylocarpus ? antila Buch.-Ham. in Wall., List n. 4893 (1831/32) nom. nud.; Wight & Walker-Arnott, Pro.Fl.Pen.Ind.Or. 1:20 (1834) nom. in synon.]

[W.antila Wight & Walker-Arnott ex Roem., Hesperides 108 (1846) nom. in synon.]

Illigera obtusa Meissn. in A.DC. Prod.Syst.Nat. 15:251 (1864); c.f. Kubitzki, Bot.Jarb. 89:180 (1969). TYPE: Wight 394 (G-DC holo. K! iso ; L! iso).



FIG. 6.3 W. trifoliolata (Adr. Juss.) Harms (i) ssp. trifoliolata A, seedling; B. habit; C. flower in L.S.; D. androecium exterior; E. infructescence; (ii) ssp. acuminata F. leaf. (A: Cult. Oxford = FHO s.n.; B, C, & D: Singhakumara 589; E: Singhakumara 304; F: Kostermans 25557).



FIG. 6.4 Walsura trifoliolata ssp. trifoliolata
Anthesing inflorescences on twig from tree at
Andiagala, Sri Lanka = B.M.P.Singhakumara 83.
(Photograph taken March, 1988 by B.M.P.Singhakumara).

VERNACULAR NAMES: Singhalese: Kiri-kon (also used of Aglaia roxburghiana Miq. = A.elaeagnoidea (A.Juss.) Benth.), Molpetta; Tamil: Chadavakku, Chokala.

Tree, to 12m tall, d.b.h. to 35cm, occasionally buttressed to 50cm; outer bark (smooth to) deeply fissured, light-grey-brown, brittle; inner bark orange-red, often showing through at fissures; leafy twigs 1.5-3.5 mm thick, sparsely to densely puberulous with simple and/or 2-armed trichomes, bark light to dark brown and usually lenticellate; leaves 9-18 cm long, 1-jugate; petiole 1.4-4.4 cm long, 0.75-1.0 mm thick, semi-terete and flattened adaxially near base but +/- terete for most of length, glabrous to puberulous with 2-armed trichomes; petiolule +/- terete, (of lateral leaflets:) 2-10 mm long, 0.5-1.0 mm thick; lamina (of lateral leaflets) 4.0-11.2 cm X 2.4-4.1 cm, (of terminal leaflet:) 5.0-12.8 cm X 2.5-4.5 cm, all leaflets slightly ovate to elliptic (to slightly obovate) with short attenuate base and retuse-obtuse to acuminate apex, sub-coriaceous, adaxial surface with no veins prominent (in vivo) or costae only slightly prominent (in sicco), abaxial surface glaucous (in vivo) except on most veins, with costae only slightly prominent (in vivo and in sicco) and sparsely pubescent with 2-armed trichomes; 7 (-8) (lateral leaflets) and 7-8 (-9) (terminal leaflet) costae on either side of midrib; glands sparse.

Inflorescences clustered around shoot apex in axils of caducous undeveloped leaves or solitary in axils of fully expanded leaves below, 2.8-10.5

(-14.0) cm long at anthesis, each a compact to open thyrse, branched up to third order (excluding pedicels) of which the first order branches can be up to 5 (-7) cm long , all parts puberulous with 2-armed trichomes predominating on the peduncle gradually replaced by simple trichomes on all other parts, peduncle occasionally lenticellate; flowers hermaphrodite or male only, just prior to opening +/- cylindrical and 2-3 mm long X 1.8-2.0 mm diam., at maximum opening 3.2-4.3 mm diam.; calyx 0.9-1.0 mm long, lobes c. 0.8 mm long; petals 2.6-3.3 mm long X 0.8-0.9 mm wide, +/- imbricate, apex acute to very slightly acuminate; androecium cylindrical to cask-shaped, 1.5-2.0 mm long X 1.9-2.3 mm diam., tubular for 1/4-1/2(-2/3) of length, filaments equi-long, the outside entirely glabrous or sparsely pubescent on filaments only (sometimes extending to below), the inside pubescent on the filaments and glabrous to very sparsely pubescent below, filament apex bifid with teeth c. 0.15 mm long; anthers 0.6-0.7 mm long, shortly-beaked, sparsely pubescent; disk 0.2-0.3 mm high; style 0.7-0.8 mm long, inversely conical, c. 0.2 mm diam. at base and c. 0.3 mm diam. at top, glabrous or very sparsely pubescent with erect trichomes; stigma +/- conical (to capitate) c.0.9 mm diam. at base X c.0.6 mm high, shortly two-lobed at the top; fruit a 1 (-2) seeded berry, globose to obovate to elliptic, 11-19 mm long X 8-18 mm diam., cream to light-brown (in vivo) and mid-brown (in sicco), surface smooth (in vivo) and minutely tomentose, pericarp thin but coriaceous with fibrous endocarp; seed +/- globose, 7-9 mm diam. (ssp. trifoliolata), enveloped in a succulent sweet colourless to white (in vivo) aril.

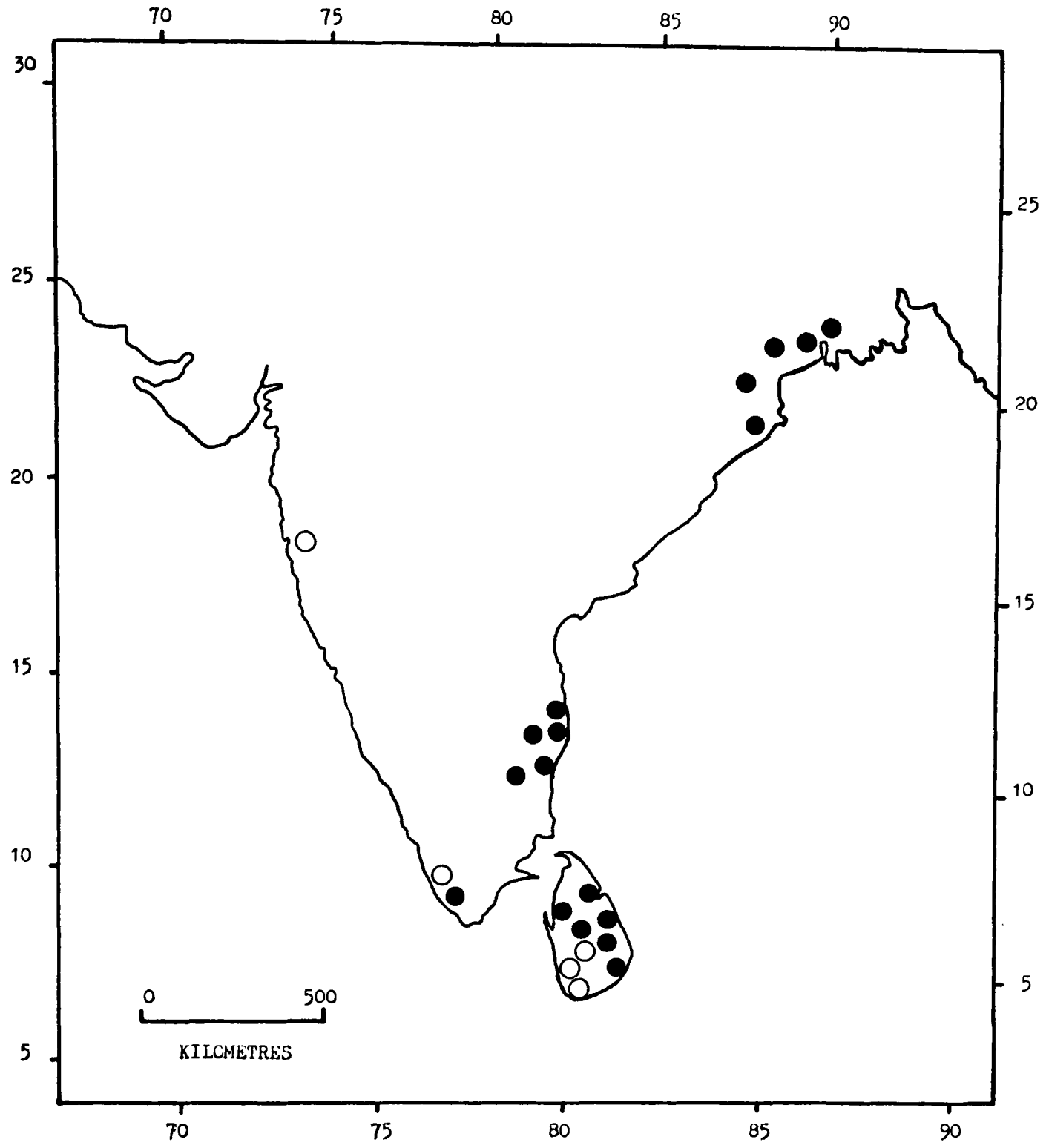


FIG. 6.5 Distribution of W. trifoliolata (Adr.Juss.)Harms India and Sri Lanka.
● : ssp. trifoliolata; ○ : ssp. acuminata

Two subspecies are recognised, separated on the basis of two good morphological characters and (especially in Sri Lanka) by geographic (and climatic) differences (see FIG. 5).

Leaflet apex retuse-obtuse to acute; mature fruit 11-14 mm long X 8-12 mm diam.; Sri Lanka (Intermediate- and Dry-zones) and southern & eastern India

..... (i) ssp. trifoliolata

Leaflet apex acuminate; mature fruit 14-19 mm long X 10-18 mm diam.; Sri Lanka (Wet-zone) and the S.W. coast of India

.....(ii) ssp. acuminata

(i) ssp. trifoliolata

(ii) ssp. acuminata (Trimen) T.Clark, comb. & stat. nov.

W.piscidia var. acuminata Trimen Fl.Ceylon 1:250 (1893). TYPE:

Thwaites C.P. 1162, Sri Lanka (PDA! holo.; B + iso.; BM! iso.)

W.thwaitesii C.DC. in DC, Monog.Phan. 1:635 (1878). TYPE: as above.

SPECIMENS STUDIED:

(i) ssp. trifoliolata

Alston 2227(K); Alzell s.n.(K); Beddome 298(K); Bernardi 14231(K); Bourne 822(K), 2281(K), 2282(K), s.n.(K); T.Clark 91(FHO); Comanor 850(K); Cooray

70031903R(K); Deschamps s.n.; Ellis 11791(K;L); Fosberg 50303(K); Gamble 1100(K), 14016(K), 18180(K); Haines 2350(K), 5533(K), 5534(K), 5535(K); Jayasuriya 1682(K), 1938(K), 2000(K); Kostermans 24314(K), 24814(K), 25161(K), 25258(K), 25291(K), 27398(K), 28140(K), 28603(K); Koyama 13322(K); Kuriakose s.n.; Meijer 200(K); Mooney 2120(K), 2215(K); Mueller-Dumbois 69030805(K), 69042609(K); Oxford B.G. s.n.(FHO); RHT 26244(A), 27043(K;L); Roxburgh s.n.(BM), s.n.(BM); Simpson 9223(FHO); Singhakumara 89(PDA), 304(PDA); Sonnerat s.n.(P); Thomson s.n.; Townsend 73/253(K); Wall. Cat. 1265(K-WALL), 1836(K-WALL), 8111(K-WALL); Walker s.n.(K); Wass 619(K); Wight 394(K), 415(K;L); Winit 8093(K); Wirawan et al. 941(K); Worthington 290(K), 533(K), 2656(K), 4751(A).

(ii) ssp. acuminata

Bourdillon 159(K), 395(K); Fernandes 1965; Kostermans 24197(K), 25557(L); Thwaites C.P. 1162(BM;K;PDA); Worthington 2616(K).

3. WALSURA TUBULATA Hiern

FIG. 6.6

Walsura tubulata Hiern in Hook.f., Fl.Br.India. 1:563 (1875); C.DC. in DC., Monog. Phan. 1:634 (1878); Harms in Engl. & Prantl, Nat. Pflanzenfam. III:4:302 (1896) and in ed.2, 19b1:119 (1940); Brandis, Indian Trees 137 (1906); Cowan & Cowan, Trees N. Bengal. 31 (1929); Kanjilal et al., Fl.Assam 1:II:240 (1937); Biswas, Pl.Darjeeling & Sikkim 1:229 (1966); Grierson & Long, Prov.Chklst.Trees & Shrubs



FIG. 6.6 W. tubulata Hiern A. habit; B. flower in L.S.; C. filament apices seen from the exterior; D. fruit. (A: Griffith 1058, lectotype; B & C: cult., Oxford = T. Clark 93; D: Univ. Michigan Plants of Assam 5567).

Bhutan & Sikkim 29 (1980). TYPE: Griffith 1058; Khasia Hills, Sikkim, India; (K! lecto./ selected here; GH! iso.).

Habit unrecorded: tree ?; leafy twigs 3-6 mm diam., glabrous to puberulous with light-brown very dense lenticellate bark; leaves 19-34 cm long, 1-jugate, brown or olive-green when dried; petiole 2.5-6.0 cm long, 1.5-2.0 mm thick, semiterete and flattened adaxially, glabrous; petiolule terete to semi-terete, (of lateral leaflets:) 0.6-1.8 cm long; lamina (of lateral leaflets:) 11.5-17.5 X 3.5-5.0 cm, (of terminal leaflets:) 9-19 X 3.5-7.0 cm, all leaflets elliptic to lanceolate and ovate to obovate, with short attenuate base and long acuminate apex, chartaceous, adaxial surface with costae very slightly prominent and all other veins faint or indistinct (in vivo and in sicco), abaxial surface (other than midrib and costae) glaucous (in vivo) and glabrous with midrib and costae very sparsely pubescent (with simple trichomes) and all veins prominent (in sicco); 7-10 (lateral leaflet) and 9-11 (terminal leaflet) costae on either side of midrib; glands sparse.

Inflorescences clustered around shoot apex in axils of caducous undeveloped and/or fully expanded leaves, and in groups of 1-4 in axils of fully expanded leaves below, 5-18 cm long at anthesis, paniculate, branched up to second order (excluding pedicels) of which the first order branches can be up to 6.5 cm long, all parts densely puberulous; flowers hermaphrodite, just prior to opening +/- cylindrical and 5-6 mm long X 3-5 mm diam., at maximum opening 5-9 mm diam.; calyx 1.75-2.0 mm long, lobes 1.1-1.5mm long; petals 4.5-5.8 mm long X 1.8-2.7 mm wide, valvate to imbricate, apex acute to obtuse and sometimes slightly recurved; androecium cylindrical to

cask-shaped* to flask-shaped, 3-4 mm long X 2.2-2.6 mm diam., tubular for c.2/3 of length, filaments equi-long, the outside glabrous or sparsely pubescent just below the filaments, the inside pubescent on and just below the filaments, filament apex bifid with teeth 0.2-0.3 mm long; anthers almost sessile, 0.6-0.8 mm long, shortly beaked, glabrous or sparsely pubescent; disk 0.2-0.3 mm high; ovary with very dense covering of short erect trichomes, c. 2/3 below the level of the disk base; style 0.8-1.0 mm long, terete and c. 0.4 mm diam. or conical and c.0.5 mm diam. at base and c. 0.8 mm diam. at top, sparsely pubescent with erect trichomes; stigma c. 1 mm diam. X c. 0.5 mm high, capitate with depression at centre, just below level of anthers at anthesis; fruit a 1 (2) seeded berry, globose to slightly obovate, 16-24 mm long X 14-18 mm diam., reddish-brown (in vivo) and mid-brown (in sicco), surface cerebriform and minutely velutinous, pericarp thin but coriaceous with very thin fibrous endocarp; seed globose to ellipsoidal and 12-13 mm long or (in 2-seeded fruit:) plano-ellipsoidal and 14-17 mm long, incompletely to completely enveloped in a thin aril.

DISTRIBUTION: Darjeeling.

SPECIMENS STUDIED: Biswas 2070(A;NY); Griffith 1058(K); Hort.Bog. VIII-B-92(BO); Wall.Cat. 843(K-WALL); Kurz s.n.(K).

4. WALSURA TRICHOSTEMON Miq. FIGS. 6.7 & 6.8

Walsura trichostemon Miq., Ann.Mus.Bot.Lugd.Bat. 4:60 (1868); Kurz,

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* "cask-shaped" is, throughout this chapter, taken to mean a symmetrical shape with convex sides and a circular cross-section widest at the equator:



J.As.Soc.Bengal, 39:72 (1870); Hiern in Hook.f., Fl.Br.Ind. 1:563 (1875) in nota; Kurz, J.As.Soc.Bengal 44:148 (1875); C.DC. in DC., Monog.Phan. 1:637 (1878); Harms in Engl. & Prantl, Nat.Pflanzenfam. III 4:302 (1896) and in ed.2, 19b1:119 (1940); Lecomte, Fl.Gén.Indo-Chine 790 (1911); Suvatti, Fl.Thai. 2:728 (1978). TYPE: Teijsmann 5968, Thailand: (? U, holo.; L! iso.)

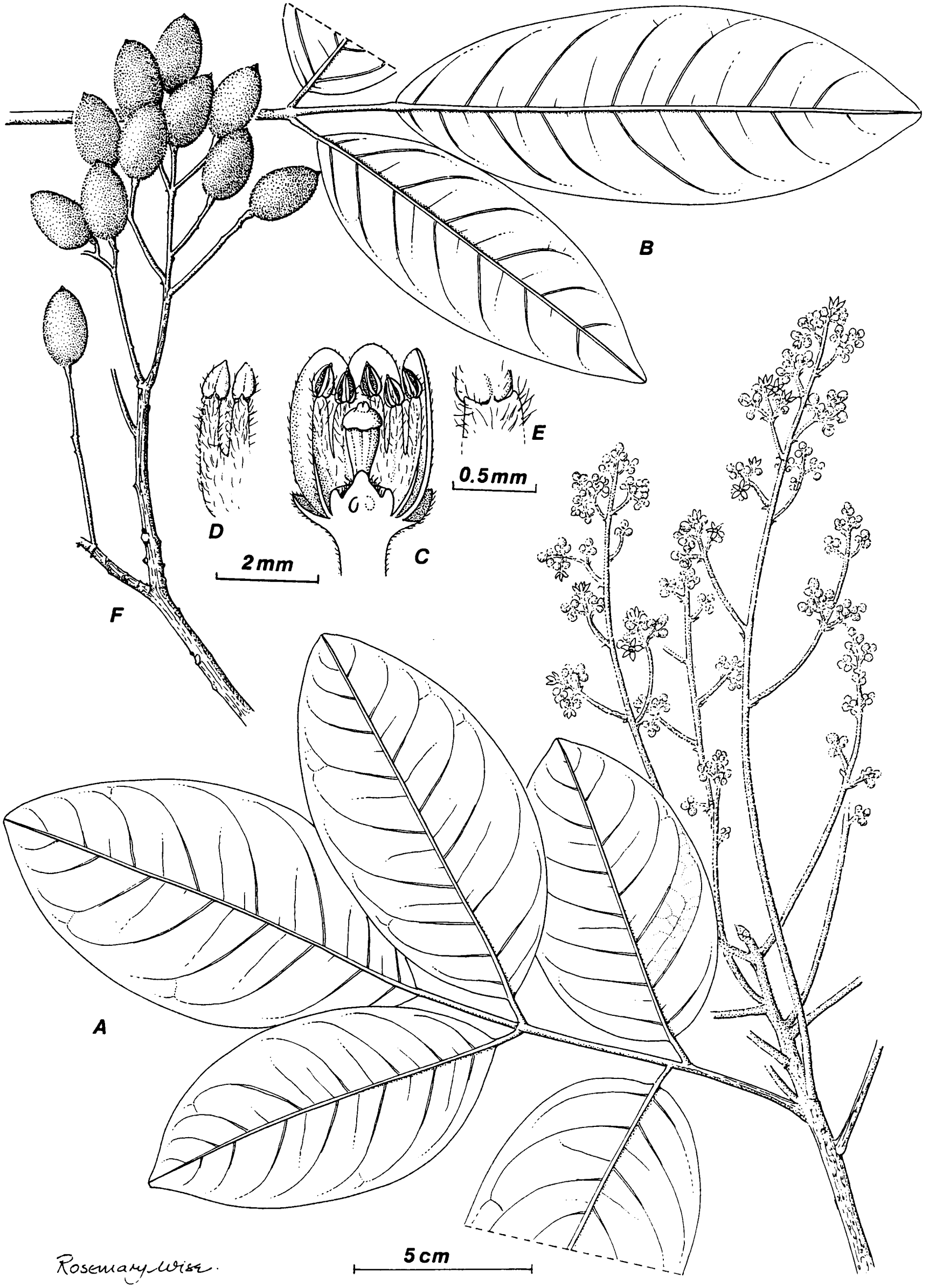
[Trichilia? villosa Wall., List n.1264 (1828), nom.nud.; Wight & Arn., Prod.Fl.Pen.Ind.Or. 1:120 (1834), nom.in synon.]

Walsura villosa [Wall. ex Voigt, Hort.Sub.Calc. 135 (1845); Roem., Hesperides 108 (1846); Mason, Flora Burmanica 568 (1851); Wight & Arn. ex Kurz, J.As.Soc.Bengal 39:72 (1870), nom. nud.;] Hiern in Hook.f., Fl.Br.Ind. 1:564 (1875); Kurz, Prelim.Rep.Veg.Pegu App.B:37 (1875) & For.Fl.Br.Burma 1:223 (1877); C.DC. in DC., Monog.Phan. 1:636 (1878); Harms in Engl. & Prantl, Nat.Pflanzenfam. III 4:302 (1896) and in ed.2, 19b1:119 (1940); Brandis, Ind.Trees 136 (1906); Lecomte, Fl.Gén.Indo-Chine 788 (1911); Lace, Lst.Trees Burma 27 (1912); Nath, Bot.Surv.Sth.Shan States 105 (1960); Suvatti, Fl.Thai. 2:728 (1978). nom. superfl. pro. W.trichostemon*

Walsura villosa var.cambodiana Pierre, Fl.For.Coch. 21-25:354 (1897). TYPE: Pierre 517, Cambodia (L! iso-syn.; P, syn.) & Pierre 4256, Cambodia (L! iso-syn.; P, syn.)

Vernacular names: Burmese: Gyobo (as for W.robusta)

* Therefore, same type.



IG. 6.7 W. trichostemon Miq. A. habit; B. leaf (part); C. flower in L.S.; D. ndroecium exterior; E. filament apices seen from exterior; F. infructescence. A, B, C & D: Dickason 7046; F: Kerr 1841).

Tree to 20 (-24) m tall; bark not known; leafy twigs 3.5-5.0 mm diam., (sparsely to) densely puberulous with simple trichomes, bark light to mid brown and lenticellate; leaves 11-24 cm long, 2-jugate; petiole 3.5-6.0 cm long, 1-2 mm thick, +/- terete or semi-terete and flattened adaxially, sparsely to densely lenticellate and glabrous to densely puberulous with simple prostrate to semi-erect trichomes; petiolule +/- terete, (of lateral pair leaflet:) 0.2-10.0 cm long, 0.8-1.3 mm thick, glabrous to sub-densely puberulous; lamina of distal pair leaflet 6-10 (-14) cm X (2.2-) 3.0-6.9 cm, the terminal leaflet slightly larger and the basal ones slightly smaller, oblong to elliptic to ovate (terminal leaflet tending more towards ovate than others) with very short attenuate base and retuse-obtuse to acute apex, sub-coriaceous, adaxial surface with all veins slightly prominent (in sicco), abaxial surface glaucous (in vivo) except on midrib and costae with costae prominent and all other veins slightly prominent (in sicco) and sparsely to densely pubescent on veins and sparsely pubescent on the inter-veinous lamina, trichomes simple prostrate and 2-armed, 7-8 (-10) (lateral leaflets) and (7-) 9-10 (terminal leaflets) costae on either side of midrib; glands absent or sparse.

Inflorescences densely clustered around shoot apex in axils of caducous, undeveloped leaves or occasionally in axils of fully expanded leaves near the shoot apex or below, 5.5-17.0 (-27.0) cm long at anthesis, each a compact to open thyrse, branched up to second (-third) order of which the first order branches can be up to 6.5 cm long, all parts velvety with simple (and few 2-armed) trichomes, peduncle and primary axis often

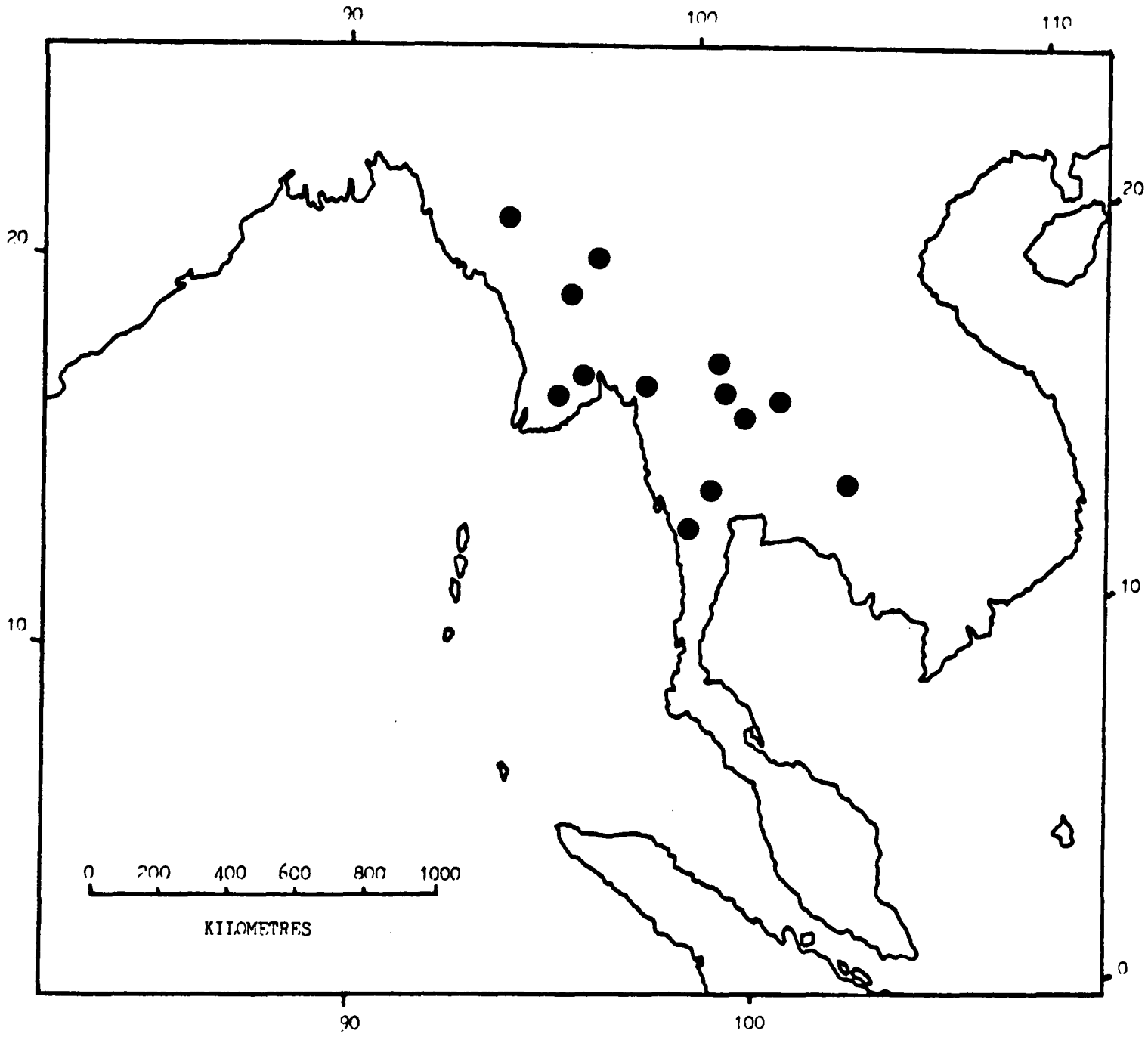


FIG. 6.8 Distribution of W. trichostemon Miq. Burma, Thailand & Indo-China.

lenticellate; flowers hermaphrodite, just prior to opening +/- cylindrical and 3.5-5.0 mm long X 2.5-3.5 mm diam., at maximum opening 0.4-0.6 mm diam.; calyx 1.7-1.9 mm long, lobes c. 1 mm long; petals 3.4-4.0 mm long X c. 1 mm wide, +/- imbricate, apex may be shortly acuminate, inside of petal may be sparsely puberulous; androecium cylindrical to slightly cask-shaped 2.3-3.1 mm diam., tubular for 1/3-1/2 of length with alternate filaments slightly shorter, densely pubescent on filaments and glabrous to sparsely pubescent below with long straggly trichomes, all parts sometimes with white flecks (like tiny lenticels), lobe apex very shortly bifid (to almost truncate) with teeth up to 0.13 mm long; anthers 0.65-0.78 mm long with short downward-curving beak, sparsely hairy with long straggly trichomes; disk 0.3-0.4 mm high; style cylindrical or cylindrical widening in the upper 1/3-2/3, 0.7-1.4 mm long, c. 0.2 mm diam. at base, c. 0.6 mm diam at top, glabrous or sparsely pubescent with erect trichomes in lower 1/3; stigma +/- capitate with two short lobes at the top, 0.5-0.8 mm diam. near base X 0.3-0.4 mm high; fruit a 1-seeded berry, ellipsoidal to slightly ovoidal with mammiform to very shortly acuminate apex, 2.2-2.5 cm long X 1.3-1.8 cm diam., light brown (in vivo and in sicco), minutely tomentose, pericarp thin but coriaceous with very thin fibrous endocarp; seed +/- ellipsoidal, enveloped in a thin aril.

DISTRIBUTION: Burma, Thailand and Cambodia.

SPECIMENS STUDIED: Beusekom & Santisuk 2842(L); BKF 2812, 11069(FHO), 38134(K;L), 40600(L); Brandis 718(K); Burma F.S.H. s.n. X40(FHO;L); Dickason 5524, 6880(L), 6952(L), 6989(L), 7046(L); Falconer 643(K;L); Fl.Burma 12321(L), 12341(L); Fl.Thailand 5372(L); 5741(L), 5830(L); Garrett

16; Geesink et al. 5611(L); Griffith 155(K); Harmand 335(K); Helfer 89(L), 1056(K;L); Kerr 1023(L), 1841(K), 2478(K), 5112(K), 5250(K), 5669(K), 19897(L); Khant 71; King,R.M. 5455(L), 5505(L); Kurz 1368(L); 2052(K); Lace 2757(K), 2802(K), 4567(K), 4695(K), 5211(K); Lakshnakara 997(K;L), 1312(K), 1313(K); Marcan 635(K); Maung Ba Pe 13022(K); Nai Noe 255(L); Pierre 517(L), 4256(L); Poilane 15258(A;K); Put 652(L), 2812(L), 3506(BM); Teysman s.n.(L); Vanpruk 121(K), 429(K); Wall. Cat. 1264(K-WALL); Winit 92(K), 128(K); Zimmerman 120(L).

5. WALSURA GARDNERI Thw. FIGS. 6.9 & 6.10

Walsura gardneri Thw., Enum.Ceylon Pl. 61 (1858); Hiern in Hook.f., Fl.Br.India. 1:563 (1875); C.DC. in DC., Monog.Phan. 1:633-634 (1878); Trimen, Fl.Ceylon 1:250 (1893); Harms in Engl. & Prantl, Nat.Pflanzenfam. III:4:302 (1896) and in ed.2, 19b1:119 (1940); Imp.For.Inst.Oxf., Descr.Chklst.Ceylon 4:46 (1939). TYPE: Gardner s.n. in Thwaites C.P. 1163. Sri Lanka, Kandy District, Hantane, Oct. 1845. (PDA! holo.; BM! ?iso.; K! ?iso.).

Small tree to 4 m tall; outer bark smooth, dark brown, flaking; inner bark red-brown; leafy twigs 2-3 mm thick, glabrous, bark mid to dark brown and lenticellate, leaves all along twig; leaves 10-14 (-18) cm long, unifoliolate; petiole plus petiolule 0.8-2.0 (-2.5) cm long X 0.5-1.0 mm thick, semi-terete and flattened adaxially, glabrous; lamina 8.5-14.0 cm

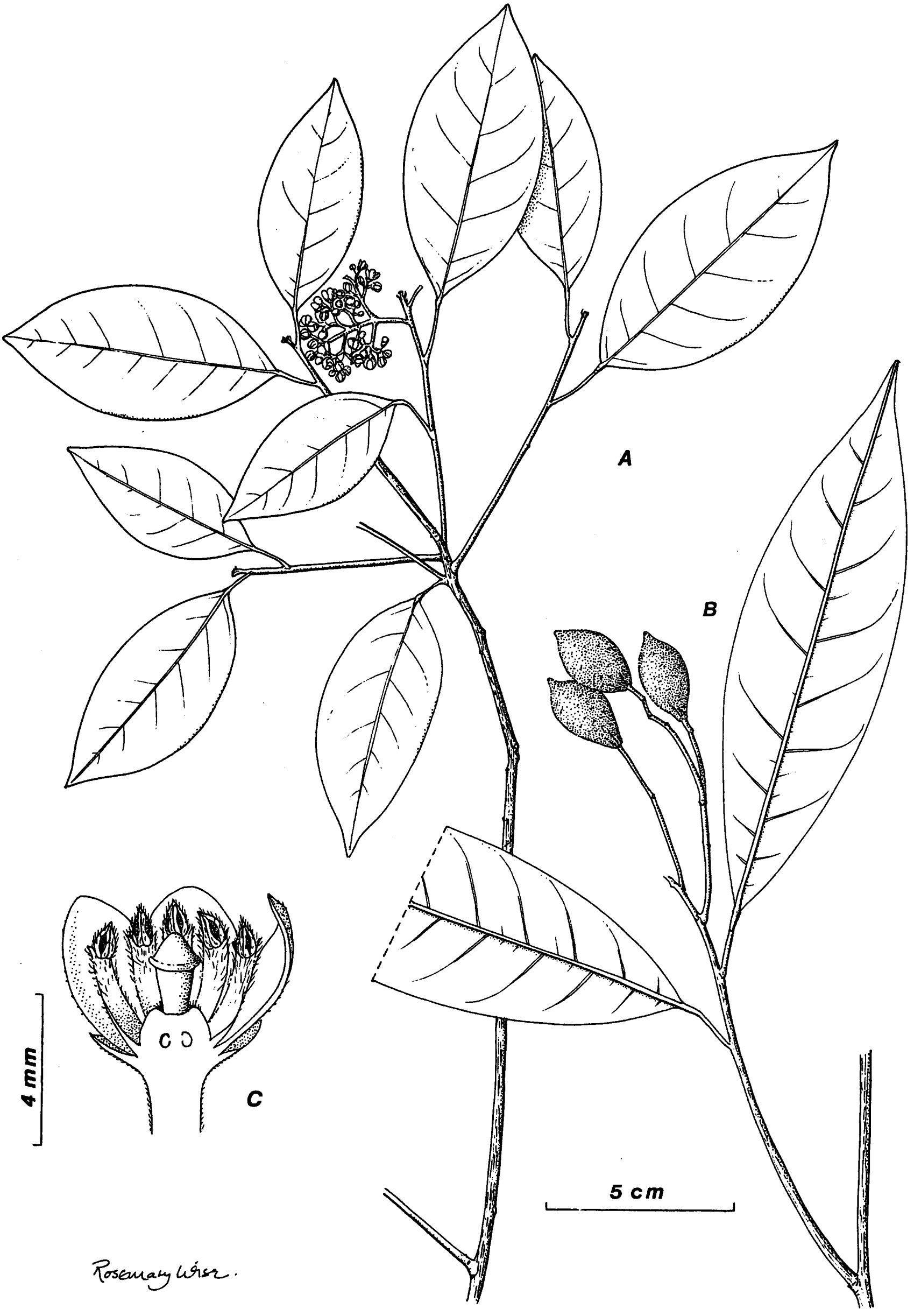


FIG. 6.9 W. gardneri Thw. A. habit; B. leafy twig with two infructescences; C. flower in L.S. (A: C.P. 1163; B & C: T. Clark 90).

long X 3.8-6.4 cm wide, elliptic (to slightly ovate), base acute to very short attenuate and usually slightly asymmetric, apex (acute to) very short acuminate, sub-coriaceous, adaxial surface with no veins prominent (in vivo) or most veins slightly prominent (in sicco), abaxial surface with most of venation prominent (in vivo and in sicco) and glaucous (in vivo) except on midrib and costae and glabrous or extremely sparsely pubescent (on the midrib) with prostrate simple trichomes; 6-7 (-8) costae on either side of the midrib; glands very small and sparse.

Inflorescences clustered around shoot apex in axils of caducous undeveloped leaves and never (?) below, 2.5-6.0 cm long at anthesis, each a compact thyrse branched up to second (to third) order (excluding pedicels), first order branches up to 2cm long, all parts sparsely to densely pubescent with 2-armed trichomes predominating on the peduncle gradually replaced by simple trichomes on all other parts, peduncle sometimes sparsely lenticellate; flower hermaphrodite, not scented ?, just prior to opening +/- cylindrical and 2.4-2.7 mm long X 2.3-2.5 mm diam., at maximum opening 2.5-3.8 mm diam.; calyx 1.0-1.1 mm long, lobes 0.3-0.6 mm long; petals 2.8-2.9 mm long X 0.9-1.2 mm wide, imbricate, apex acute; androecium cylindrical to cask-shaped, 1.0-1.8 mm long X 1.5-2.3 mm diam., tubular for 1/8-1/6 of length, alternate filaments slightly shorter, filaments pubescent with long trichomes inside and out and glabrous to sparsely pubescent below, filament apex bifid with erect teeth 0.1-0.2 mm long; anthers 0.5-0.7 mm long, shortly beaked, long hairy; disk 0.4-0.5 mm high, glabrous; style 0.3 (immature ? at anthesis) to 0.6 mm long, cylindrical to narrowly obconical, 0.2-0.3 mm diam. at base and 0.3-0.4 mm diam. at top, glabrous; stigma capitate to broadly conical, 0.6-0.7 mm diam. at base X

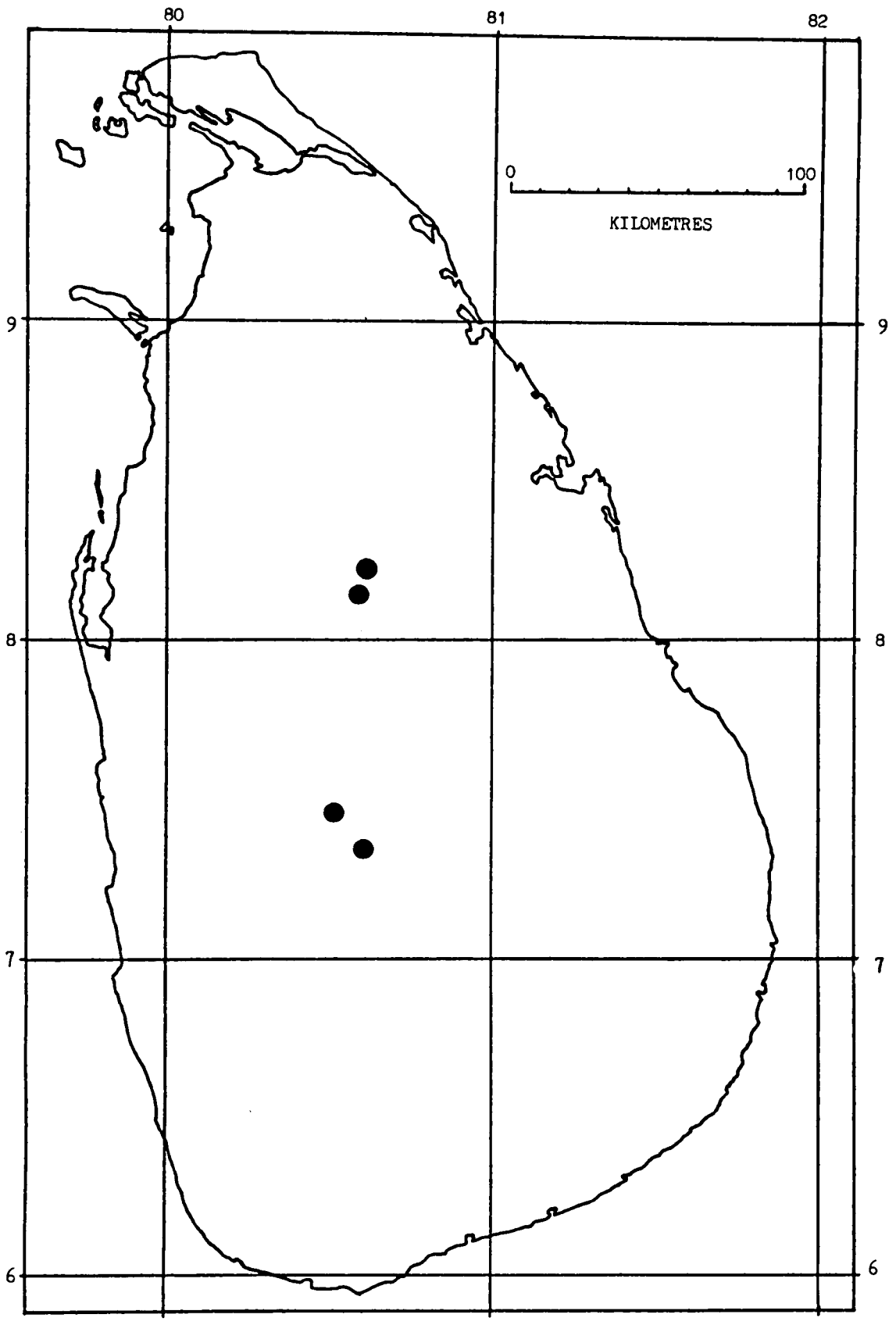


FIG. 6.10 Distribution of W. gardneri Thw.
Sri Lanka.

0.4-0.5 mm high, very shortly 2-lobed at top; fruit a 1-seeded berry, ovoid to ellipsoidal to slightly obovoid, 2.2-2.5 cm long X 1.2-1.5 cm diam., shortly beaked at apex for 1.5-2.5 mm, pale-green (in vivo) or brown (in sicco), surface rugose and densely but minutely puberulous with stiff simple trichomes, pericarp thick (1.0-1.5 mm) and coriaceous with thin fibrous endocarp; seed +/- ellipsoidal, 1.8-2.1 cm long X 1.1-1.8 cm diam., completely or almost completely enveloped in colourless sweet aril.

DISTRIBUTION: Sri Lanka

SPECIMENS STUDIED: Alston 2227(K); T.Clark 90(FHO); Gardner 136(K); Garston 2227(PDA); Jayasuriya 2208(PDA); Kostermans 24586(K;PDA), 27795(A;PDA;SAR), 27956(K;PDA), 28066(K); Thwaites C.P. 1163(BM;K;PDA); Waas 1640(PDA); Worthington 289(K).

6. WALSURA BONII Pellegrin

FIG. 6.11

Walsura bonii Pellegrin in Lecomte, Not.Syst. 277 (1910). Type: Bon 5217; Vietnam, Tonkin, Phu-dien; (P! holo.; FHO! photo.).

Habit unrecorded: tree ?; leafy twigs 1.7-3.0 mm diam., glabrous with dark-brown, lenticellate bark; leaves 11.5-19.5 cm long, 1-jugate, brown when dried; petiole c.1 mm diam., semiterete and flattened adaxially, glabrous; rachis 0.5-0.8 mm diam., terete to semi-terete, glabrous;



FIG. 6.11 W. bonii Pellegrin A. habit; B. flower in L.S.; filament apices seen from exterior (Bon 5217).

petiolule +/- terete, (of lateral leaflets:) 0.4-0.9 cm long, slightly swollen at point immediately below base of lamina; lamina of lateral leaflets 5.5-7.6 X 2.4-3.9 cm, lamina of terminal leaflet 9.5-12.8 X 4.6-5.6 cm, all leaflets elliptic and slightly asymmetric with short-attenuate base and long-acuminate apex, chartaceous, adaxial surface with costae prominent and all other veins slightly prominent (in sicco), abaxial surface (other than mid rib and veins) matt (in sicco) and glabrous, midrib very sparsely pubescent with prostrate trichomes and all veins prominent (in sicco), all leaflets with 8-10 costae on either side of the midrib; glands c. 0.18 mm diam., sparse, on the abaxial surface of the leaflet, seen as black dots within 1 mm of the mid-rib.

Inflorescences clustered around shoot apex in axils of undeveloped (not caducous) leaves and/or in groups of 1-4 arising from axils of expanded leaves near the shoot apex, 7.5-12.0 cm long at anthesis, a thyrse, branched up to second order (excluding pedicels) of which the first order branches can be up to 3.8cm, all parts densely puberulous; flowers hermaphrodite, just prior to opening +/- cylindrical and 2.3-3.5 mm long X 1.5-2.0 mm diam., at maximum opening 4- 6 mm diam.; calyx 0.8-1.0 mm long, pubescent on outside only; petals 4.0-4.3 mm long X 1.2-1.5 mm wide, valvate or very slightly imbricate, apex shortly acuminate and (when mature) recurved; androecium cylindrical, 2.1-2.5 mm long X 1.4-1.8 mm diam., tubular for 1/2(-3/4) of length with alternate filaments slightly shorter, pubescent on outside along whole length and inside on lobes only, lobe apex truncate with stalk to anther c. 0.07 mm long; anthers 0.6-0.8 mm long, shortly beaked, glabrous; disk annular, 0.2-0.3 mm high, wall +/- terete and c. 0.16 mm diam. in T.S., glabrous and smooth; ovary with dense

covering of short erect trichomes, c. 3/4 of ovary below the level of the disk; style 0.7-0.8 mm long, c. 0.2 mm diam. at base, c. 0.3 mm diam. just below stigma, terete, striate; stigma c. 0.5 mm diam. X c. 0.2 mm high, capitate with shallow depression at centre; fruit unknown.

DISTRIBUTION: Vietnam (only known from the type-collection).

SPECIMEN STUDIED: Bon 5217(P).

7. WALSURA OXYCARPA Kurz

Walsura oxycarpa Kurz in J.As.Soc.Bengal 44:200 (1875) & For.Fl.Br.Burma 1:224 (1877); C.DC. in DC., Monog.Phan. 1:637 (1878). TYPE: Kurz s.n., South Andaman. (CAL? holo?; K! iso.)

Walsura candollei King, J.As.Soc.Bengal 64:84 (1895); Parkinson, F.Fl.Andaman Is. 122 (1923). TYPE: Kurz s.n., Andaman Islands. (CAL? holo?; G! iso.). Syn. nov.

Small tree; leafy twigs 3-6 mm thick, dark-brown, lenticellate, glabrous to pubescent with prostrate trichomes; leaves 18-29 cm long, 2-jugate, brown when dried; petiole 3.5-7.0 cm long, 1.0-1.5 mm thick, semi-terete and slightly flattened adaxially, glabrous to sparsely pubescent with short simple and 2-armed trichomes, usually lenticellate; petiolule +/- terete, (of lateral leaflets:) (0.4-) 0.8-1.0 cm long and 0.5-1.0 mm thick,

glabrous to very sparsely-pubescent; lamina (of distal lateral:) 10-14 cm X 3.2-4.4 cm, (of terminal:) 10-16.5 cm X 3.1-5.5 cm, (basal:) 8-13 cm X 3.4-4.7 cm, all leaflets narrowly ovate (to narrowly elliptic) with short attenuate (and occasionally slightly asymmetric) base and short acuminate apex, sub coriaceous, adaxial surface with no veins prominent (in sicco), abaxial surface with most of venation prominent (in sicco) and matt (in sicco) usually only in islets between smallest veins and extremely sparsely puberulous with minute prostrate simple trichomes; glands present but very small.

Inflorescences clustered around shoot apex in axils of caducous undeveloped or fully expanded leaves, 4.5-16.0 cm long at anthesis, each an open thyrse branched up to third order (excluding pedicels), first order branches up to 3 cm long, primary rachis minutely pubescent with 2-armed trichomes for most of length replaced by simple trichomes distally, branches and all other parts densely puberulous with simple trichomes; flowers hermaphrodite, just prior to opening +/- cylindrical and 2.9-3.3 mm long X 2.4-2.6 mm diam., at maximum opening 3.0-4.5 mm diam., calyx 0.9-1.3 mm long, lobes 0.7-0.9 mm long; petals 3.1-3.2 mm long X 1.2-1.6 mm wide, imbricate, outside densely pubescent and inside sparsely to sub-densely pubescent, apex acute to short-acuminate; androecium +/- cylindrical, 1.8-1.9 mm long X 1.7-1.9 mm diam., tubular for 1/4-1/3 of length with alternate filaments usually slightly shorter, filaments densely hairy inside and out with long straggly trichomes but tubular part glabrous, filament apex very shortly bifid; anthers 0.7-0.9 mm long , shortly beaked, sparsely to sub-densely hairy with long straggly trichomes; disk c. 0.2 mm high; style obconical, 0.3-0.8 mm long X 0.2-0.3 mm diam. at the base and

0.2-0.7 mm diam. just below the stigma, glabrous; stigma capitate to broadly conical with two lobes on top, 0.2-0.3 mm long (excl. lobes) X 0.6-1.0 mm diam., lobes up to 0.18 (-0.20) mm long; fruit a one-seeded berry, ovoid and beaked, 1.8-2.3 cm long (excl. beak) X 1.2-1.7 cm diam., beak 2-3 mm long, minutely puberulous, pericarp coriaceous with a fibrous endocarp; seed ovoid, 1.3-1.6 cm long.

DISTRIBUTION: Andaman Islands.

SPECIMENS STUDIED: King s.n.(11-7-1891)(E); King's coll. 214(G), s.n.(24-6-1893)(K); Kurz s.n.(G), s.n.(K), s.n.(K); Parkinson 56(K).

NOTES: Kurz described his species from fruiting material, not having seen the flowers. It seems that C. de Candolle also saw fragmentary material of this species, sent to him by Kurz. de Candolle (in ignorance of Kurz's publication ?) seems to have decided that this material represented a new species and allowed King to describe it (as W.candollei) when King had obtained flowering material through Calcutta Botanic Gardens. Upon investigation of isotype specimens, however, W.candollei is undoubtedly the same species as W.oxycarpa.

8. WALSURA POILANEI Pellegrin FIG. 6.12

Walsura poilanei Pellegrin, Bull.Soc.Bot.France 91:177 (1944). TYPE: Poilane 1186; Vietnam, Quang-Tri prov., Mai-lanh. 23-iii-1920. (P!



FIG. 6.12 W. poilanei Pellegrin
The holotype. (Poilane 1186).

holo; FHO! photo.)

Tree 18 m tall, bole 15 m, girth 0.8 m; outer bark grey-brown; inner bark pink; leafy twigs 4-7 mm diam., glabrous or puberulous with simple trichomes, bark mid-brown and lenticellate; leaves 21-34 cm long, 2-jugate; petiole 4-7 cm long X 2.0-3.5 mm thick, semi-terete and flattened adaxially, sparsely pubescent; petiolule (of distal pair leaflet:) 0.7-1.1 cm long X 1.0-1.5 mm thick, sparsely puberulous with simple trichomes; lamina (of distal pair leaflet:) 12.0-17.5 cm X 6.5-8.4 cm and elliptic, (terminal:) 12-18 cm X 4.5-7.5 cm and (ovate to) broadly elliptic (to obovate), (basal:) 9.5-12.0 cm X 4.5-5.8 cm and ovate to broadly elliptic, all leaflets with a truncate (to short-acute) and usually slightly asymmetric base and very short-acuminate apex, sub-coriaceous, adaxial surface with all veins very slightly prominent (in sicco), abaxial surface with all veins prominent (in sicco) and matt and velutinous with simple erect trichomes; 12-13 (distal pair and terminal leaflets) or 10-11 (basals) costae on either side of the midrib; glands present but very small.

Inflorescences clustered around shoot apex in axils of caducous undeveloped leaves or fully expanded leaves in groups of 1-3, 10-23 cm long at anthesis, each an open thyrse, branched up to third order (excluding pedicels), first order branches up to 7 cm long, all parts tomentose with prostrate to semi-erect simple trichomes; flowers hermaphrodite, just prior to opening cylindrical and 2.5-3.0 mm long X 2.2-2.5 mm diam., at maximum opening 2.8-3.3 mm diam.; calyx 1.2-1.7 mm long, lobes 0.8-1.2 mm long; petals 2.9-3.1 mm long X 1.3-1.5 mm wide, imbricate, apex acute, inside

glabrous; androecium +/- cylindrical, 1.5-1.8 mm long X 1.5-2.1 mm diam., tubular for 1/3-1/2 of length, filaments sub-densely pubescent with straggly hairs inside and out, tubular part glabrous or sparsely and straggly pubescent inside and out, filaments all the same length, filament apex very shortly bifid with teeth c. 0.5 mm long; anthers 0.6-0.7 mm long, apex very shortly acuminate, glabrous except for a tuft of minute simple trichomes at the apex; disk c. 0.2 mm high; style obconical, 0.5-0.6 mm long X 0.2-0.4 mm diam. at the base and 0.3-0.4 mm diam. at the top, glabrous to sub-densely pubescent in the lower 1/4 with ovary-type trichomes; stigma capitate and slightly lobed on top, 0.4-0.5 mm high (excl. lobes) X 0.5-1.0 mm diam. at base; fruits unknown.

DISTRIBUTION: Vietnam (known only from the type-collection).

SPECIMEN STUDIED: Poilane 1186(P).

9. WALSURA PINNATA Hassk. FIGS. 6.13 & 6.14

Walsura pinnata Hassk., Retzia 1:147 (1855); Miq., Fl.Ned.Ind. 542 (1859); Miq., Ann.Mus.Bot.Lugd.Bat. 4:60 (1868); C.DC. in DC., Monog.Phan. 1:639 (1878); Koord. & Valeton, Bij.Boom.Java, 3:186 (1896); Koord., Exk.Fl.Java, 2:447 (1912); Backer & Bakh.f., Fl.Java, 2:129 (1965); Mabberley, Tree Flora Malaya 4:254 (1989). TYPE: Koorders 971 b.; Indonesia, Java, Bogor Botanic Garden, Tree No. IIIb20; 26th June 1892, (BO! neo./designated here).

W.hypoleuca Kurz, J.As.Soc.Bengal 42:296 (1872); Hiern in Hook.f., Fl. Br.Ind. 1:564 (1875); Kurz, Veg.Pegu 37 (1875) and For. Fl. Brit. Burma 1:224 (1877); TYPE: Kurz s.n.; South Andaman, Port Mowat (K! lecto./selected here). Syn. nov.

W.neurodes Hiern in Hook.f., Fl.Br.India 1:564 (1875); C.DC. in DC., Monog.Phan. 1:636 (1878); King, J.As.Soc.Bengal. 64:84 (1895); Ridley, Fl.Mal.Pen. 1:412 (1922); Wyatt-Smith & Kochummen, Mal.For.Rec. 17 (1979). TYPE: Maingay 344; Malay Peninsula, Malacca (K! holo.; L!).

Heynea cochinchinensis Baillon, Adansonia 11:265 (1879). TYPE: Lefévre 106; Vietnam, Ho Chi Min City, Bien-hoa (P? holo.?; L! iso.). Syn. nov.

W.cochinchinensis (Baillon) Harms in Engl. & Prantl, Nat. Pflanzenfam. III 4:302 (1896) and in ed.2, 19b1:119 (1940); Pierre, Fl.For.Cochinchine, 21-25 & t. 354 (1897); Pellegrin in Lecomte, Not.Syst.:227 (1910); Pham-Hoang-Ho, Fl.S.Vietnam: 244 (1960). TYPE: as for H.cochinchinensis.

W.elata Pierre, Fl.For.Coch. 21 & plate 355 (1897). TYPE: Pierre 4219; Vietnam (P? holo.; K! iso.?; BM! iso.?). Syn. nov.

W.aherniana Perk., Frag.Fl.Philip. 34 (1904); Merrill, Enum.Philip.Fl.Pl. 379 (1923). TYPE: Ahern 264, Philippines, Luzon, Camarines (B, holo.+; K! iso.; NY! iso.). Syn. nov.

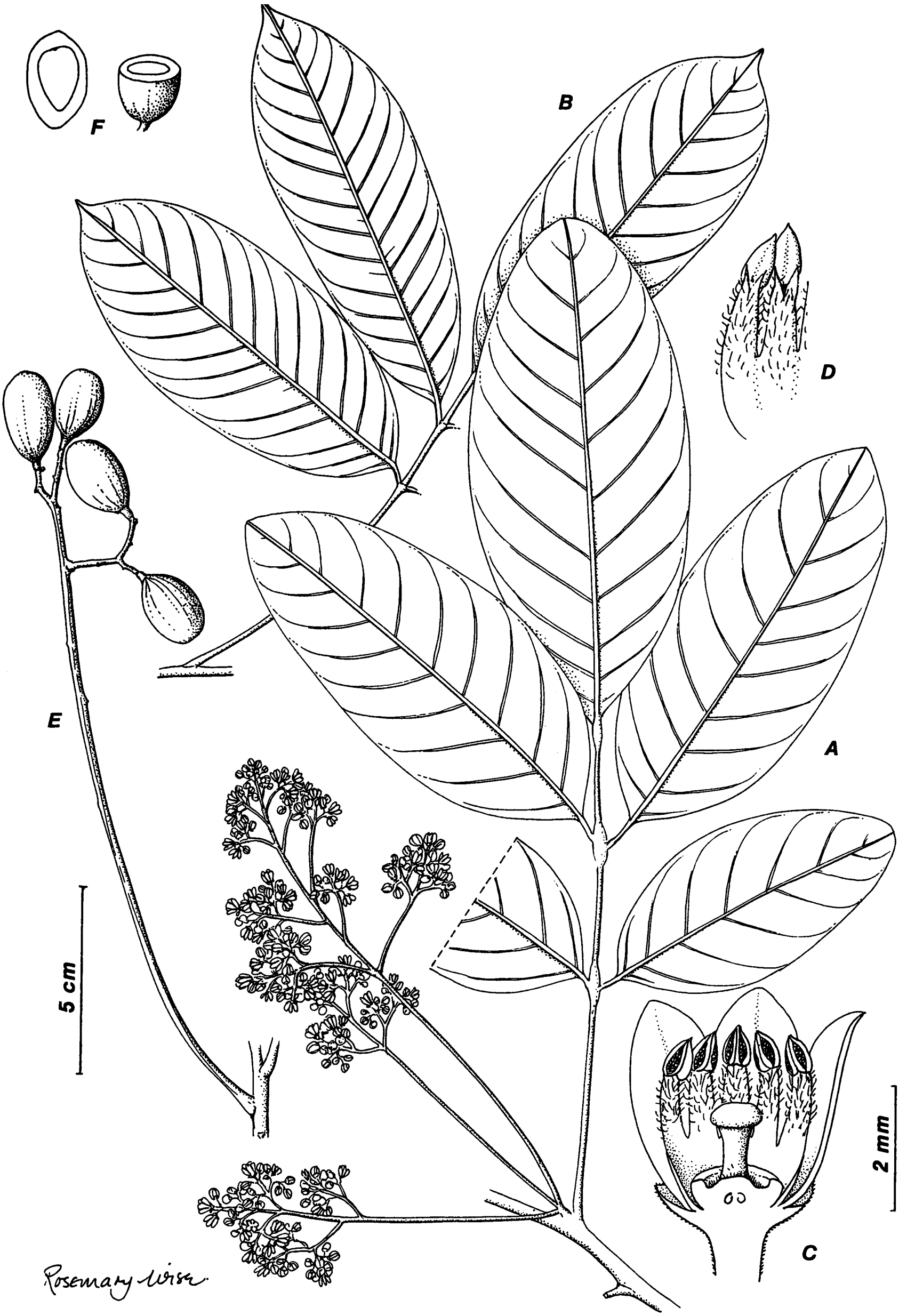


FIG. 6.13 W. pinnata Hassk. (i) "pinnata" A. habit; C. flower in L.S.; D. androecium (part) exterior; E. infructescence; F. berry in L.S. & T.S.; (ii) "villamilii" B. leaf (part). (A, C & D: Garrett 1237; E: K.L. 1640; F: Pennington 7815; B: SAN 61654).

W.villamilii Merrill, Philip.J.Sci. 9:308 (1914) and in Univ.Calif.Publ. Bot. 15:132 (1929). TYPE: FB 13764; Philippines, Mindanao, Zamboanga Dist., Margosatubig (PNH holo.?+; BM! iso.). Syn. nov.

Napeodendron altissimum Ridley, J.R.As.Soc. Straits Branch. 82:179 (1920); Symington, Bull.Misc.Info.Kew 1937:319 (1937). TYPE: Ridley s.n.; Malaysia, Selangor (K! holo.).

W.angulata Craib, Bull.Misc.Info.Kew 1926:344 (1926) & Fl.Siam.Enum. 1:261 (1926); Suvatti, Fl.Thai. 2:727 (1978); TYPE: Kerr 6793; Thailand, Srirachi, Nawng Kaw (K! holo.; BM! iso.). Syn. nov.

W.glauca C.Fischer, Bull.Misc.Info.Kew 1927:87 (1927). TYPE: Parkinson 1686; Burma, Sth. Tenasserim (K! holo.). Syn. nov.

W.grandifolia Ridley, Bull.Misc.Info.Kew 1930:370 (1930) TYPE: Haviland 1635; Borneo, nr. Kuching (K! holo.; SAR! iso.). Syn. nov.

Tree, height to 18 (-37) m, girth to 0.76 (-1.22) m, bole to 11 (-24) m; outer bark smooth and thin, light-grey-brown, often with lenticels, falling in parts to reveal pink-brown inner bark; sapwood very pink to pale-brown to pink-yellow, with slight aroma similar to that of the fruits; leafy twigs slender, 2.5-8.0 mm diam., glabrous with grey-brown usually lenticellate bark; leaves (9, if leaf undivided, to) 14-70 cm long,

undivided to 2 (to 3)-jugate; petiole 2.5-11.0 cm long, 1-4 mm thick, semiterete and flattened adaxially, glabrous or extremely sparsely pubescent, occasionally lenticellate near the base; petiolule semiterete and flattened adaxially, (of lateral leaflets) 0.4-1.4 cm long and 0.5-1.5 mm thick, geniculate just below base of lamina; lamina (of distal pair leaflet) 2.1-11.5 X 5.5-25.0 cm, the basal leaflets usually conspicuously smaller and the terminal a little larger, all narrowly oblanceolate, elliptic or oblong, with cuneate or cuneate-attenuate base and acute to short (<1.5cm) acuminate apex, sub-coriaceous, adaxial surface with most of veins slightly prominent (in sicco and in vivo), abaxial surface (other than midrib and costae) glaucous (in vivo) and glabrous or very sparsely pubescent on midrib and costae only with most (in sicco) or only to second order (in vivo) veins prominent, (of distal pair leaflet) 7-12 (-20) costae on either side of midrib or (in 'villamilii') with incomplete costae also (see above); glands usually present.

Inflorescences clustered around shoot apex in axils of caducous, undeveloped leaves and/or rarely solitary in axils of expanded leaves near the shoot apex, (4-) 8-35 cm long at anthesis, an open thyrse, branched up to 3rd order (excluding pedicels), 1st order branches up to 10 cm long, all parts densely puberulous, rachis occasionally lenticellate; pedicel 0.5-2.0 mm long; flowers hermaphrodite or male only, just prior to opening +/- cylindrical and 2-4 mm long X 2.0-2.8 mm diam., at maximum opening 3.5-5.0 mm diam; calyx 1.2-1.9 mm long, lobes 0.7-1.7 mm long, densely puberulous on outside only; petals 3.0-3.8 (-4.0) mm long X 1.5-1.8 (-1.9) mm wide, imbricate, apex sometimes slightly hooded when mature; androecium cylindrical or slightly ampuliform, (1.7-) 2.0-4.3 mm long X (1.5-) 2.0-2.5 mm diam., tubular for (1/4-) 1/2 (-2/3) of length with alternate filaments

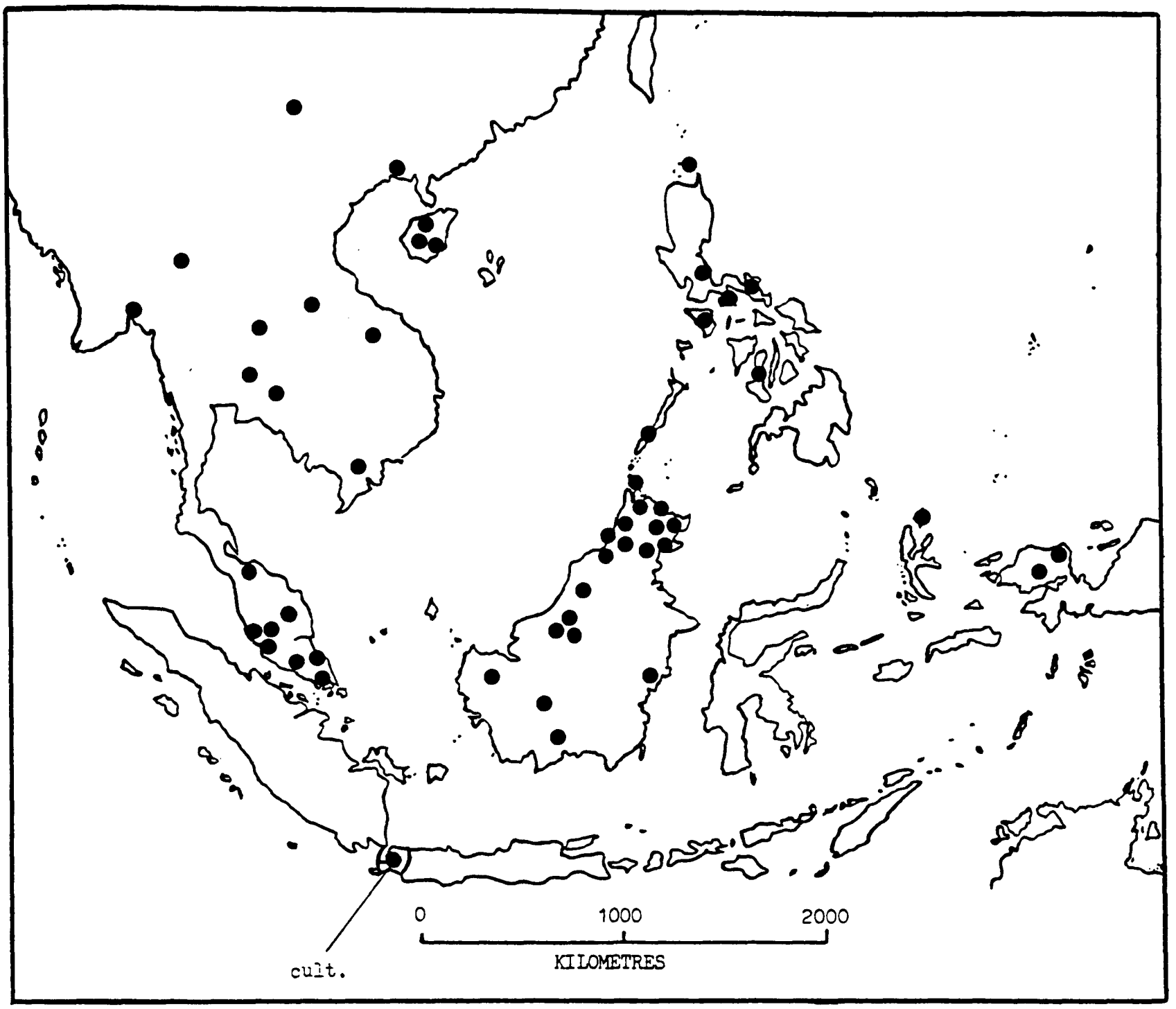


FIG. 6.14 Distribution of W. pinnata Hassk.
Burma, Thailand, Indo-China and the Malesian region.

slightly shorter or all to same length, outside glabrous or very sparsely pubescent on tubular part and sparsely to densely pubescent on filaments, inside glabrous on tubular part and densely pubescent on filaments, filament apex bifid with teeth c. 0.2 mm long, stalk to anther 0.2-0.3 mm long originating just below base of teeth; anther 0.6-0.8 mm long, occasionally shortly beaked, glabrous or (in 'villamilii') puberulous; disk 0.2-0.3 (-0.4) mm high; ovary densely hairy or very rarely glabrous (see below); style cylindrical to narrowly conical, 0.6-0.7 (-1.1) mm long and 0.3-0.4 mm diam. at base and 0.3-0.6 mm diam. at top, glabrous; stigma c. 0.4 mm long X 0.7-1.0 mm diam., capitate, just below the level of the anthers at anthesis; fruit a 1 (-2)-seeded berry, globose (to ovoid), 1.2-2.4 (rarely, 2.8) cm long X 1.2-2.4 cm diam., pale-green (or red: FUNG 20154) (in vivo) or brown (in sicco), sparsely and minutely puberulous, pericarp thin but coriaceous with very thin fibrous endocarp; seed +/- ellipsoidal and 1.3-2.3 mm long X 0.9-1.3 mm diam. or (in 2 seeded fruit:) hemi-ellipsoidal and up to 2.1 cm long, enveloped in a fleshy white or colourless sweet tasting aril which sometimes exudes a clear sticky liquid.

DISTRIBUTION: Burma, Thailand, Yunnan, Hainan, Cambodia, Vietnam, Malay Peninsula, Java (cult.: Bogor), Borneo, Philippines (Palawan to Luzon), Halmahera, extreme western Irian Jaya.

NOTES: W.pinnata has the largest range of all the species of Walsura or Pseudoclausena and is highly variable, mainly in leaf and leaflet size but also, to a lesser extent, in leaflet number. The type specimens of W.pinnata, W.neurodes and W.aherniana are clearly the same species

described from different geographical/political areas (viz. Indonesia, Malaysia and the Philippines respectively). Pierre (1897) seems to distinguish W.elata by its large (25-28 mm long X 20 mm diam.) berries and (26-31 cm long) leaves. Both of these characters can be accommodated within the morphological range of W.pinnata and even though the size of the fruit is at the upper end of the range for this complex, there are many intermediates. The angular (in transverse section) petiole with which Craib (1926) segregates W.angulata in fact occurs throughout this complex and particularly in specimens from Borneo, where much material of the complex has been collected since 1926. Leaf and leaflet size is of little use as a character in this complex, so W.grandifolia must also be reduced. Kurz's W.hypoleuca from Burma (at the north-western limit of the range of the complex) is defined by its very short staminal tube (as a proportion of the total length of the androecium) but Kurz specimens at Kew (including the lectotype, selected here) have androecia tubular for 1/4 or more of their length, which is fairly common within this complex. The only significant character which W.glauca, also from Burma, seems to possess is a glabrous ovary. This is unique within the genus but in all other features it seems to fit very well into the W.pinnata complex. Given the variation known to occur in floral pubescence throughout the genus, this single character is considered insufficient to support a distinct species. Ridley's monotypic genus Napeodendron seems to be distinctive only in that it has floral parts in 4s & 8s. Since the species was based on one specimen only, and since in all other respects it is typical of W.pinnata, Symington's reduction is maintained.

alsura
W. cochinchinensis and W.villamilii are defined by their degree of leaf division, being 1-3-foliolate and 7-foliolate respectively. In all other respects, W.cochinchinensis is identical with W.pinnata. Its range (N.E. Thailand to Vietnam) falls well within the range of 5-foliolate W.pinnata but 3-foliolate specimens do rarely occur elsewhere (in Luzon and Borneo). W.villamilii from Sabah and west Mindanao is additionally supported by a few minor characters, particularly the presence of incomplete costae (see above) and the degree to which the androecium is tubular (see below), but most of these characters, (including leaflet number) occur elsewhere within the range of W.pinnata. In view of this, although W.villamilii and W.cochinchinensis can be seen as largely distinct morphological entities within the species, the presence of many intermediates dictate their reduction. It may be useful however, with this proviso, to maintain an informal recognition of these entities, as Mabberley (1979) did within Chisocheton lasiocarpus (Miq.) Valeton, also in the Meliaceae.

KEY TO ENTITIES

1a. 9-foliolate & with incomplete costae & androecium tubular for 1/4-1/2; Borneo (Sabah) and west Mindanao. ...'villamilii'

b. 1-7-foliolate & without incomplete costae & androecium tubular for 1/2 (-2/3).....2

2a. 1-3-foliolate; N.Thailand to Vietnam and Hainan.....'cochinchinensis'

b. 5-7-foliolate.....'pinnata'

SPECIMENS STUDIED: Adduru 183; Ahern 264(K); bb 24108(L), 24848(L), 24891(L); Beccari 5/1888(K), 2665(K); Beusekom & Charoenpol 1900(L); BKF 12500(FHO), 13004(K), 34647(L), 35958(L), 37456(L) 46507(L), 47619(K;L), 52143(L), 54090(L); BNB A823(K), 10142(A); B.S. 257(K), 1257(GH;NY), 1613(GH), 3110, 13600, 21463(K), 26087, 29053, 49321(K), 79334(K;NY); BW 2588(L), 7051(L); Castro & Melegrito 1366(K); T.Clark 77(FHO), 80(FHO), 81(FHO), 82(FHO); Collins 386(K); Craib 17974(L); Ebalo 165; Elmer 2847(NY), 15628(K), 21487(FHO;K), 21574(FHO;K); FB 3110(NY), 3463, 13764(BM), 17933, FRI 6772(FRI), 11224(FRI), 14017(FRI;L), 14371(FRI), 16145(FRI), 17703(FRI), 19273(FRI), 19980(FRI), 20711(FRI), 27278(FRI), 29370(FRI),, 32646(FRI;L), 100120(FRI); Fung 20089(K), 20154(K); Garrett 1237(L); Geesink, Phanichapol & Santisuk 5611(L); Griffith 1057(NY); Groff 5676(K;NY); Hainan 20089(K), 20154(SING), 65053(K), 70644(L;SING), 70695(K); Haviland 1635(K:SAR); Henry 10849(NY), 12929(K); Hort.Bog. III-B-20(BO); How 70544(K), 70695(K); KEP 64310(FRI), 64423(FRI), 77866(FRI), 94022(FRI), 98187(FRI), 100120(FRI); Kerr 1923, 6793(BM;K), 17140(L), 17974(K), 20048(K), 20243(BM;K), 21208(BM;L); K.L. 1640(A); KLU 657(FRI), 888(FRI); Koorders 971b(BO), 974b(BO;K), 979b(BO;K); Kostermans 281(K), 470(L), 2885(L), 8106(K), 8206(K), 24022, 77866; Kurz s.n.(K); Lakshnakara 997(BM); Lau 291(NY), 3852(NY), 25975(NY); Le Févre 106(L), 551(L); Lei 253, 597(SING); Liang 65053(K), 65324(K); Loher 6819(K); Mabberley 1660(FHO;K;SAN), 1664(FHO;K;SAN); Maingay 344(K;L), 345(GH), 1638; Maxwell 75-176(L); Merrill 2534(K), 2847(K;P); Mogea 3711(L), 4163(K;L); Parkinson 1686(K), 5242(K); Pennington 7815(FHO;FRI), 8000(FHO); Pételot 1272(NY), 2007(NY), 4326(NY), 7857(NY); Pierre 1280(L;NY) 4219(BM;K); PNH 17046(K), 78185(K); Poilane 13229; Rastini 152(SING); Richards 2304; Ridley s.n.(K); SAN 823(K), 17583(K), 17678(SAN), 19616(K),

24558(SAN), 24979(K;SAN), 28613(SAN), 30551(K;L;SAN), 31339(K;SAN), 31560(L;SAN), 35161(K), 31564(SAN),35161(SAN), 35168(K;SAN), 35188(K;SAN), 36201(K;L;SAN), 38951(SAN), 39025(K), 39714(SAN), 39797(SAN), 43572(SAN), 44553(K;SAN), 52784(SAN), 52811(SAN), 57288(SAN), 58770(SAN), 61654(SAN), 63000(SAN), 70666(K;SAN), 72443(FHO;K;SAN), 72827(SAN), 73089(SAN), 73753(SAN), 76040(SAN), 76281(SAN), 76373(K;SAN), 76391(FHO;K;SAN), 76662(K;SAN), 77274(K;SAN), 77381(K;SAN), 77697(K;SAN), 82592(K;SAN), 83445(K;SAN), 83637(FHO;SAN), 83934(K;SAN), 84004(K;SAN), 86994(FHO;SAN), 87447(K;L;SAN), 90239(K;SAN), 93653(K;SAN), 93826(SAN), 95758(SAN), 96172(SAN); 96820(K;SAN), 97198(K;SAN), 100304(SAN), 108771(SAN), 110193(SAN), 114101(SAN); SAR 23939(K), 23959(K), 32633(K), 35017(L;SAR), 41069(SAR); Sinclair et al. 9334(K); Soepadmo 657(K), 884, 1200; Strugnell 12665(K;FRI); Thai F.D. 15461(K); Tsang 26690(K); Vidal s.n.; Wall. Cat. 1836(K-WALL); Wray 3798; Yunnan 31428(K).

10. WALSURA PACHYCAULON Mabb. ex T.Clark sp.nov. FIGS. 6.15-6.17

Arbor; rami frondosi pachycaules, (0.6-)0.8-1.5 cm in diametro; folia imparipinnata, 4 (5)-juga; petiolus ad insertiones petiolulorum tumidus, semiteres, parte adaxiali applanata vel leviter canaliculata; petiolulus leviter tumidus admodum infra basin laminae, plus minusve teres; foliolorum lamina anguste oblanceolata vel elliptico-oblonga cum apex brevis acuminatus, pagina abaxialis in vivo glauca, in sicco opaca, nervi laterales (primi ordinis) 9-13 (-19) in utroque latere; inflorescentiae circum apicem surculi in axillis foliorum immaturorum caducorum congestae,

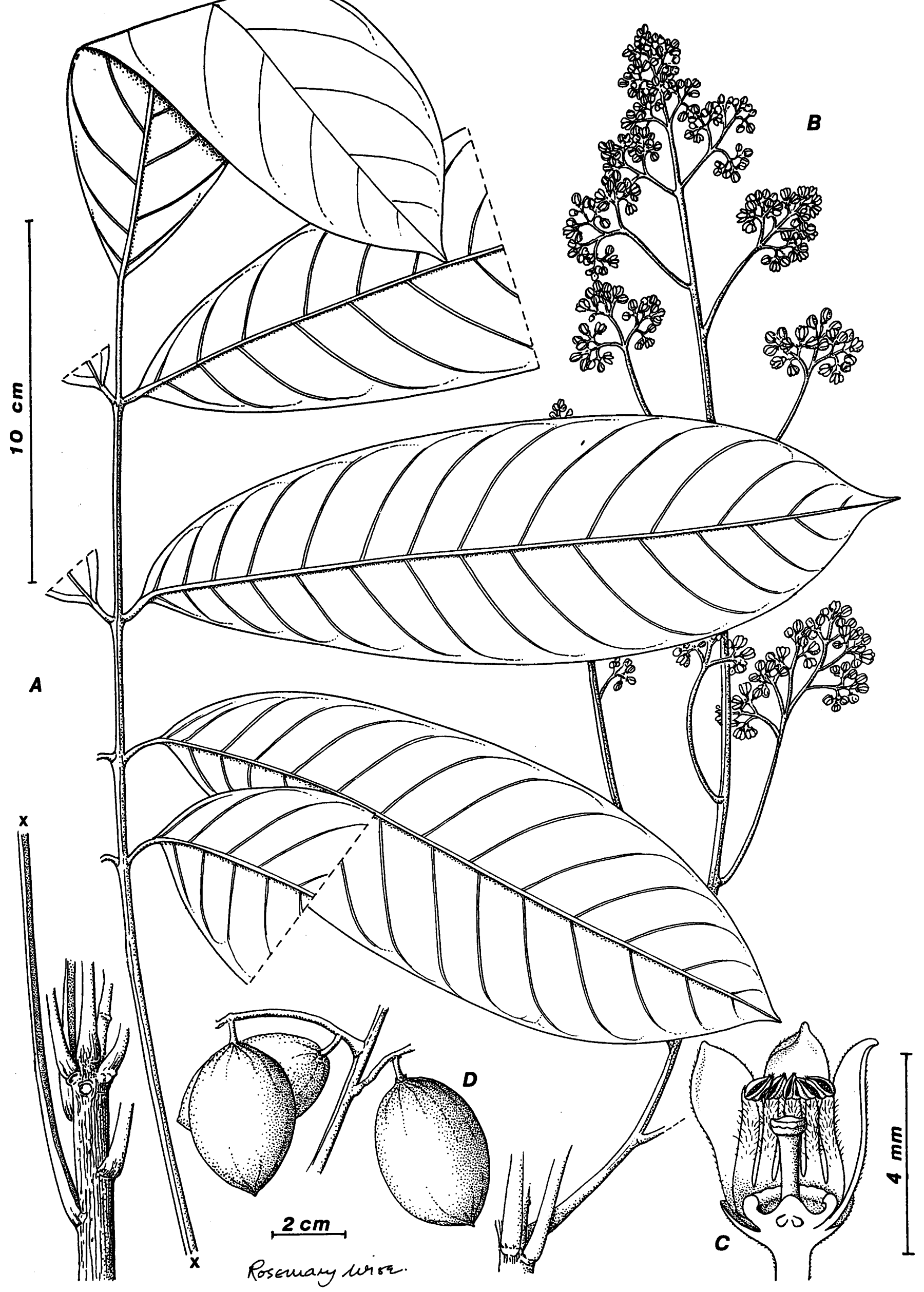


FIG. 6.15 W. pachycaulon Mabb. ex T. Clark A. leaf (part); B. inflorescence; C. flower in L.S.; D. fruits. (A: SAN 68486; B & C: SAN 53580, holotype; D: K4421).

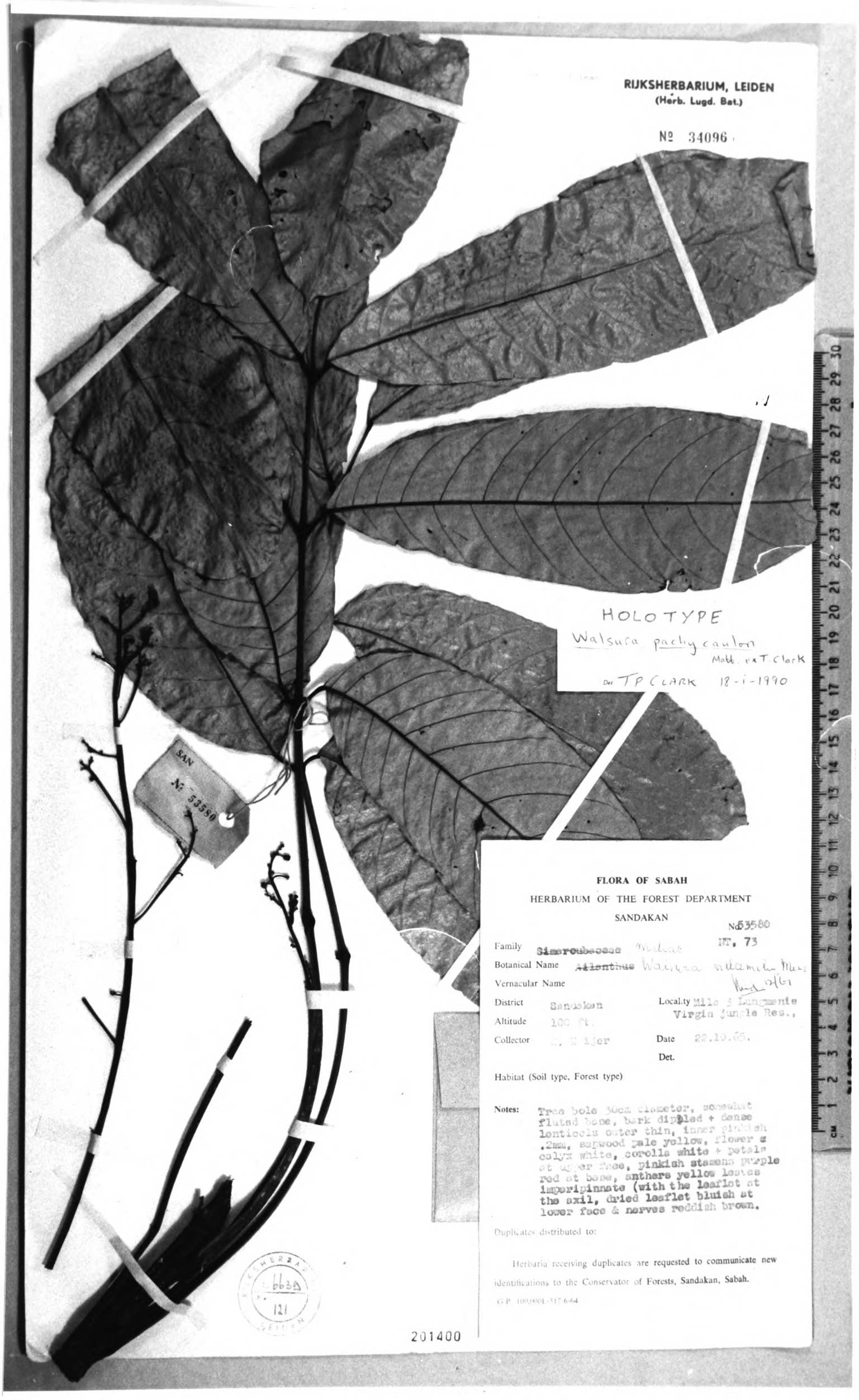


FIG. 6.16 W. pachycaulon Mabb. ex T. Clark
The holotype. (SAN 53580).

16-30 cm longae sub anthesi, unaquaeque thyrsus laxus; flores hermaphroditi; calyx parce 5-lobus; petala 5, libra, imbricata, oblonga, apice plus minusve acuta; androecium cylindrica vel leviter ampulliformis, c.1/4 eius longitudinis tubularis, filamenta 10, partim pubescens, apex filamenti bifidus, cum dentibus brevibus; stylus anguste et inverse conatus, glaber; stigma ad instar cylindri brevis cum apice leviter tholiformi; discus glaber; ovarium glabrum, biloculare, unusquisque loculus cum 2 ovulis collateralibus; fructus baccatus, monospermus, globosum vel ovoidus, pericarpium coriaceum, puberulus; semen anguste ellipsoideum, ab arillo gelineo circumcinatim ?. Typus: (W.Meijer) SAN 53580, Malaysia, Sabah, Sandakan Dist., Mile 3 Lungmanis Virgin Jungle Res., NT. 73., Oct. 1965 (L! holo.; SAN! iso., incl. flowers in spirit).

Tree to 29 m tall, girth to 90 cm; outer bark 0.6-3.8 cm thick and dark-grey-brown to blackish; inner bark pink; leafy twigs pachycaul, (0.6-)0.8-1.5 cm diam., sparsely to densely lenticellate, glabrous; leaves 38-60 cm long, 4 (5)-jugate; petiole 10-22 cm long and 3-7 mm thick, semiterete with flat to shallowly canaliculate adaxial surface, sparsely lenticellate and glabrous; petiolule 0.5-2.3 cm long and 0.8-2.0 mm thick, +/- terete; lamina (of distal pair leaflet:) 3.5-6.5 cm X 13.0-19.5 cm and basals slightly smaller and terminal slightly larger, all leaflets narrowly oblanceolate or elliptic or oblong, apex acuminate, base cuneate to cuneate-attenuate, sub-coriaceous, both surfaces with all veins slightly to conspicuously prominent (in sicco), abaxial surface glabrous to very sparsely pubescent with very short simple trichomes; 9-14 (distal pair

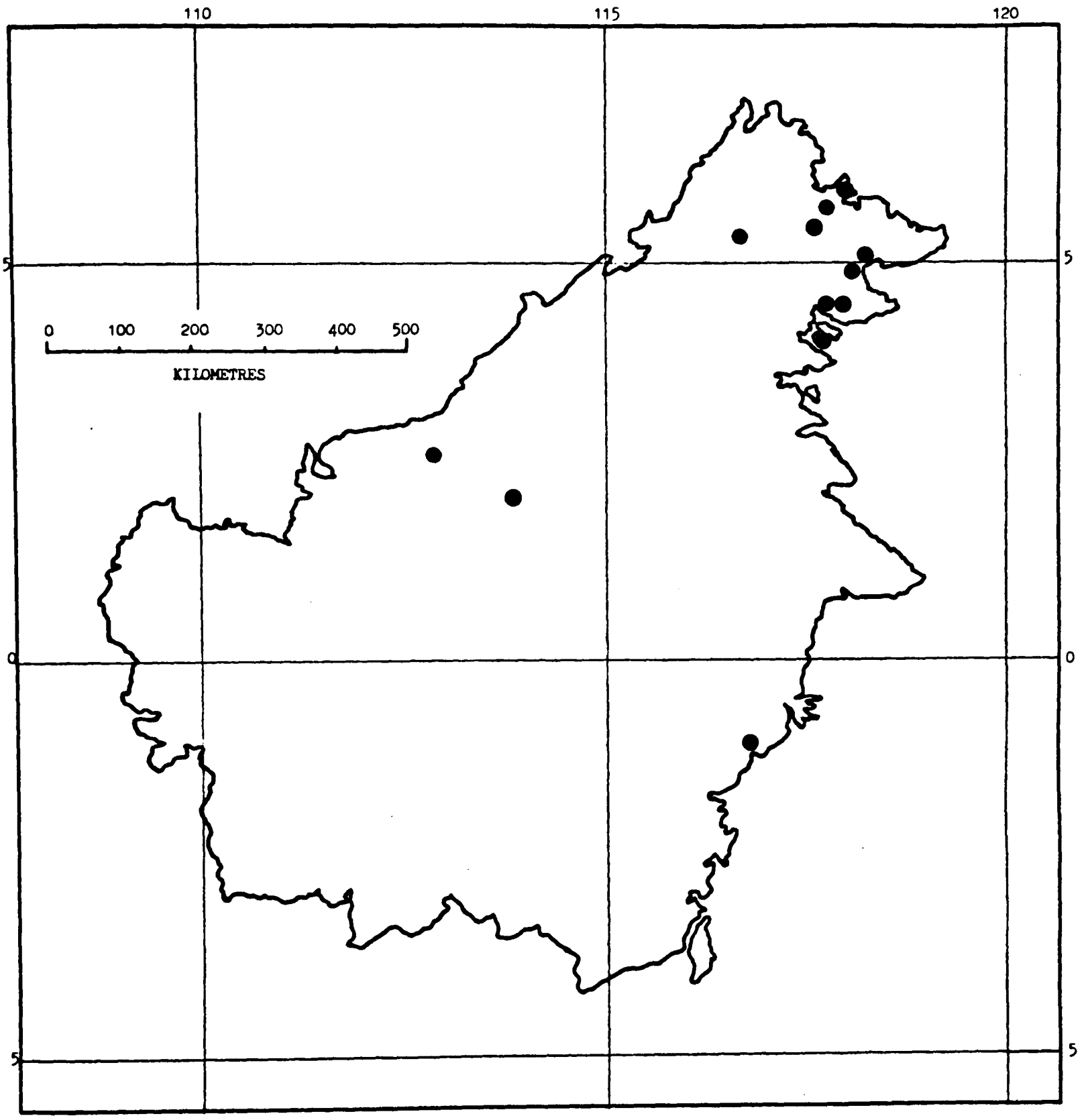


FIG. 6.17 Distribution of W. pachycaulon Mabb. ex T. Clark Borneo.

leaflets), 10-19 (terminals) and 9-13 (basals) costae on either side of the midrib; glands absent or very sparse and very small.

Inflorescences clustered around shoot apex in axils of caducous undeveloped leaves, 16-45 cm long at anthesis, each an open thyrse branched to third order (excl. pedicels) with first order branches up to 15 cm long, pedicels 1.0-2.5 mm long, all parts densely puberulous; flowers hermaphrodite, just prior to opening +/- cylindrical and 2.6-3.2 mm long X 2.5-3.0 mm diam., at max. opening c. 5.2 mm diam.; calyx c. 1.32 mm long, lobes c.0.5 mm long; petals c. 4.2 mm long X c. 2.2 mm wide, imbricate; androecium cylindrical to narrow-ampuliform, 2.1-2.4 mm long X 2.2-2.9 mm diam., tubular for c.1/4 of length, tubular part glabrous on both surfaces, filaments glabrous on outside and pubescent on inside, filament apex bifid with teeth c. 0.1 mm long; anthers c. 0.6 mm long and very short beaked, glabrous except for a short tuft of trichomes from the apex; disk c. 0.7 mm high, glabrous; style 1.0-1.5 mm long X 0.4-0.5 mm diam. (base) and 0.6-0.7 mm diam. (top), narrowly obconical, glabrous; stigma c. 0.4 mm high X c. 0.9 mm diam., cylindrical with low-domed top; fruit a 1-seeded globose (to ovoidal) berry, 1.8-4.2 cm diam., brown when mature (in vivo), sparsely puberulous, pericarp to 5 mm thick and coriaceous; seed narrowly ellipsoidal, to 2.8 cm long X 1.6 cm diam., incompletely (?) surrounded by sweet tasting jelly-like aril.

DISTRIBUTION: Borneo: Sabah & 4th Div. Sarawak.

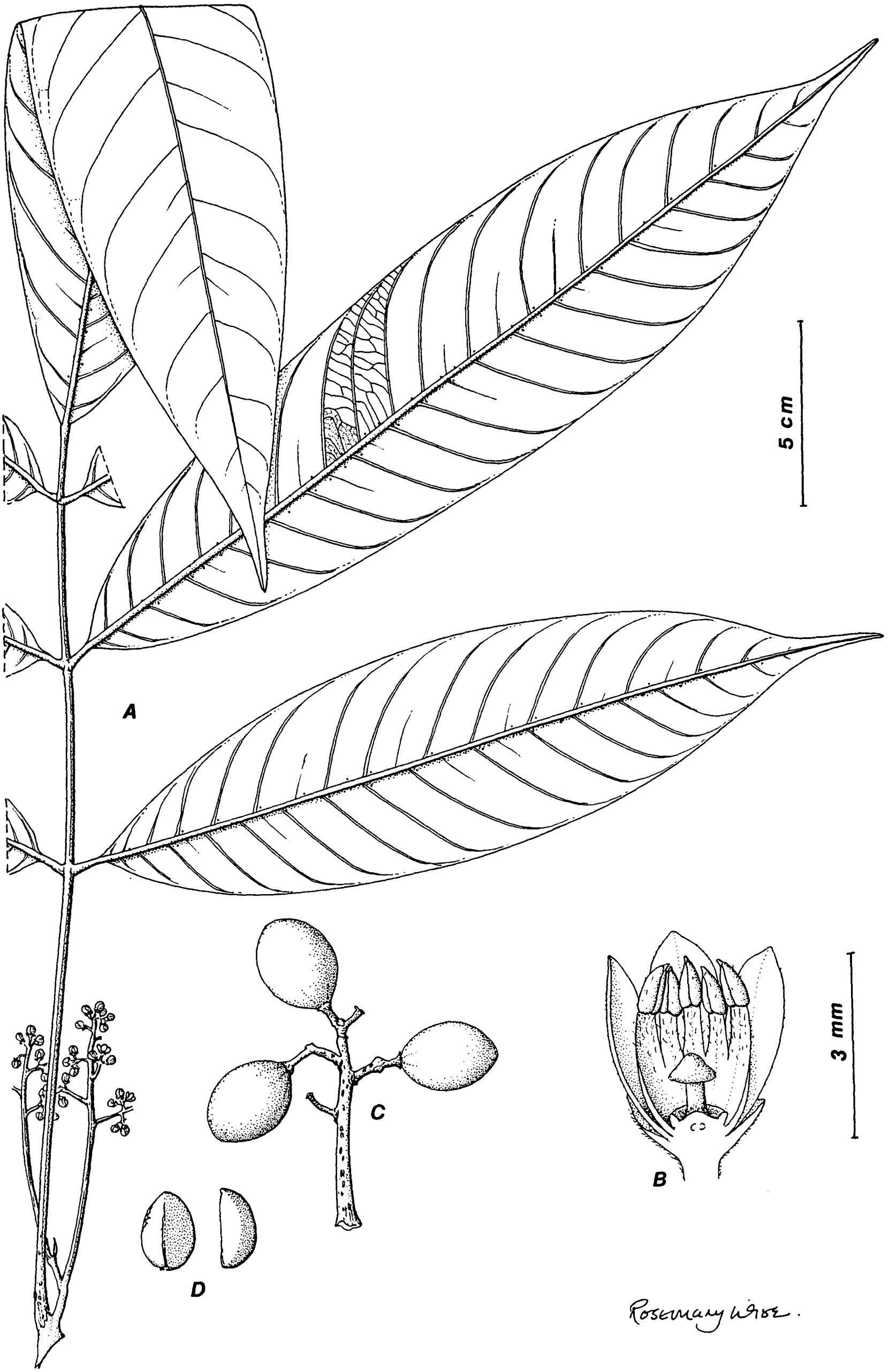
NOTES: This species is most closely related to W.pinnata and is a member of Group 2, see comments under "Variation within the genera" above. It is

distinguished from all other members of the genus by its pachycaul leafy shoots and large (i.e. 9 or 11) leaflet number. In addition to these characters, it differs from the other members of Group 2 in its very short staminal tube which is only c.1/4 of the total length of the andoecium.

SPECIMENS STUDIED: Kokawa & Hotta 2468(SAN); Kostermans 4421(K;L), 12630A(L); SAN 4050(K;L), 30573(K;L;SAN;SAR), 31564(L), 32921(K;L), 45151(K;L;SAN), 52784(K;L), 52811(K;L), 53580(K;L; SAN-incl. flowers in spirit), 65826(K;L;SAN;SAR), 67128(K;SAN), 68486(FHO;K;L;SAN;SAR;SING), 69355(K;SAN), 73181(K;SAN), 79176(K;SAN), 87447(K;SAN), 93826(K;SAN); SAR 21733(FHO;K;L;SAN;SAR), 21920(K;L;SAR), 28266(L;SAR), 29617(K;SAR).

11. WALSURA SARAWAKENSIS T.Clark sp.nov. FIGS. 6.18-6.19

Arbor; folia imparipinnata, 3-juga; petiolus ad insertiones petiolulorum tumidus, semiteres, parte adaxiali applanata; petiolulus leviter tumidus admodum infra basin laminae, plus minusve teres vel leviter applanatus in parte adaxiali, lamina elliptica vel late lanceolata, apex longe ((2-) 2.5-5 cm) acuminatus, pagina abaxialis in vivo glauca, in sicco opaca, nervi laterales (primi ordinis) 14-18 in utroque latere; inflorescentiae circum apicem surculi in axillis foliorum interdum caducorum immaturorum congestae; flores hermaphroditi; calyx non profunde lobatus; petala 5, libera, imbricata, oblonga vel elliptica, cum apice acuto; androecium cylindricum, 1/2-2/3 eius longitudinis tubularis, filamenta 10, partim sparse pubescens, apex lobi bifidus, cum dentibus brevibus; antherae



IG. 6.18 W. sarawakensis T. Clark A. habit; B. flower in L.S.; C. fruits; D. eeds. (A & B: Purseglove B5204; C & D: Purseglove B5143).

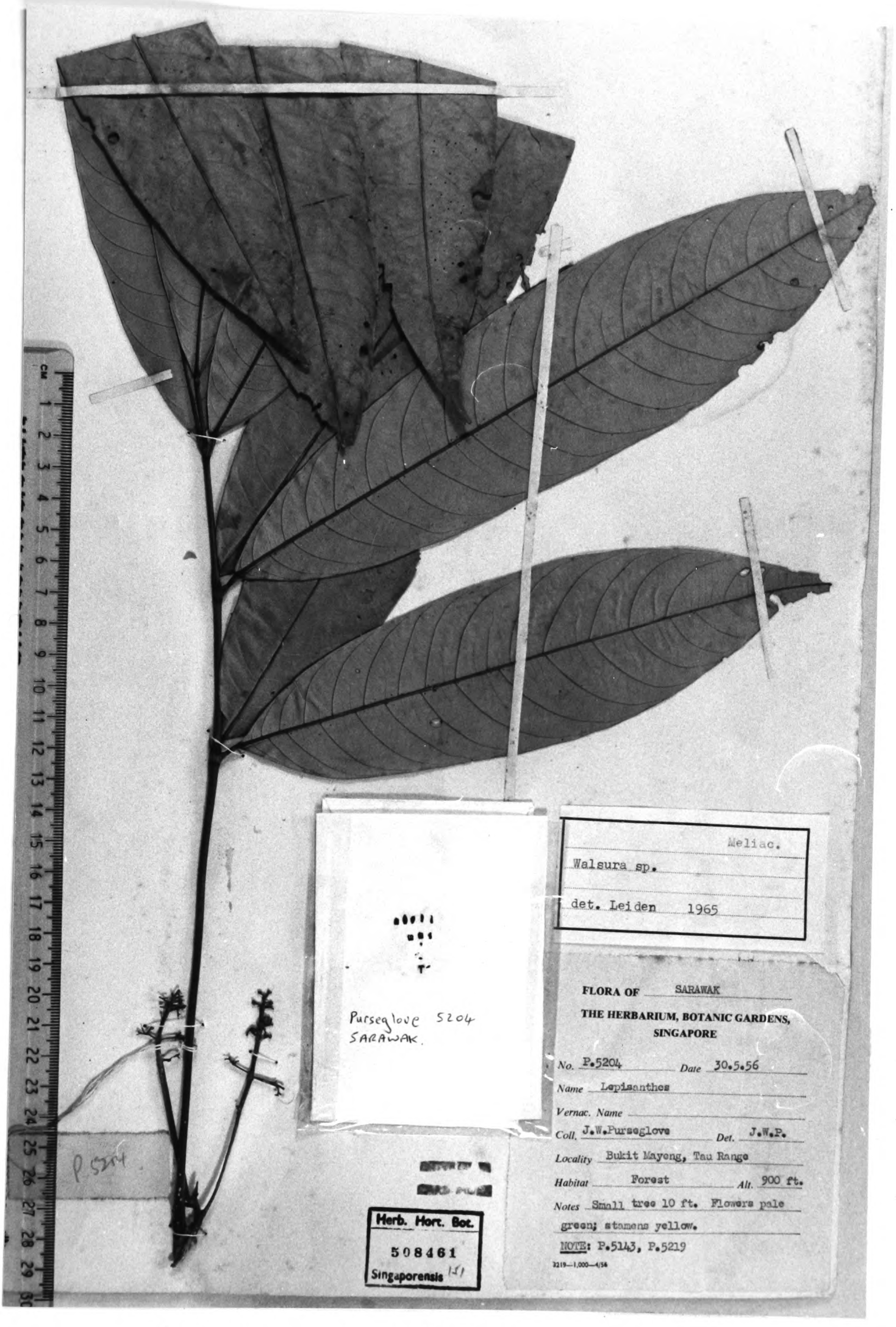


FIG. 6.19 W. sarawakensis T. Clark
The holotype. (Purseglove 5204).

puberulus; stylus cylindricus, glaber; stigma capitatum; discus glaber; ovarium trichomatibus brevibus erectis dense, 2-loculare, unusquisque loculus cum 2 ovulis collateralibus; fructus baccatus, cum 1-3 seminibus, ellipsoideus, pericarpium coriaceum, glabrum; semen ellipsoideum, ab arillo viscido albo circumcin$^{c}_{\wedge}$tum. Typus: Purseglove 5204; Malaysia, Sarawak, 4th Division, Bukit Mayeng (SING! holo.; L! iso.).

Tree to 6 m tall; leafy twigs 6-8 mm thick, glabrous with light brown sparsely lenticellate bark; leaves 52-80 cm long, 3-jugate; petiole 15-21 cm long, 0.2-0.4 cm thick, semi-terete and flattened adaxially, glabrous to very sparsely puberulous with very short erect trichomes, sparsely lenticellate; petiolule 5-18 mm long, 1.0-1.5 mm thick, +/- terete or slightly flattened adaxially; lamina (of distal pair leaflet:) 24-30 cm X 5-8 cm, (of terminal leaflet:) 28-41 cm X 5.8-10.0 cm, all leaflets lanceolate with short attenuate base and apex acuminate for (2-) 2.5-5 cm long, sub coriaceous, all veins prominent on both surfaces, abaxial surface matt on intervenous lamina and over most of smallest veins and very sparsely pubescent with simple trichomes; 14-17 (distal pair leaflet) and 17-18 (terminal leaflet) costae on either side of the midrib; glands conspicuous.

Inflorescences clustered around shoot apex in axils of (sometimes) caducous undeveloped leaves, 7.5-8.0 cm long at anthesis, a compact thyrse branched up to second order (excluding pedicels) of which the first order branches can be up to 1.3 cm long, all parts densely puberulous and primary rachis sparsely lenticellate; flowers hermaphrodite, just prior to opening

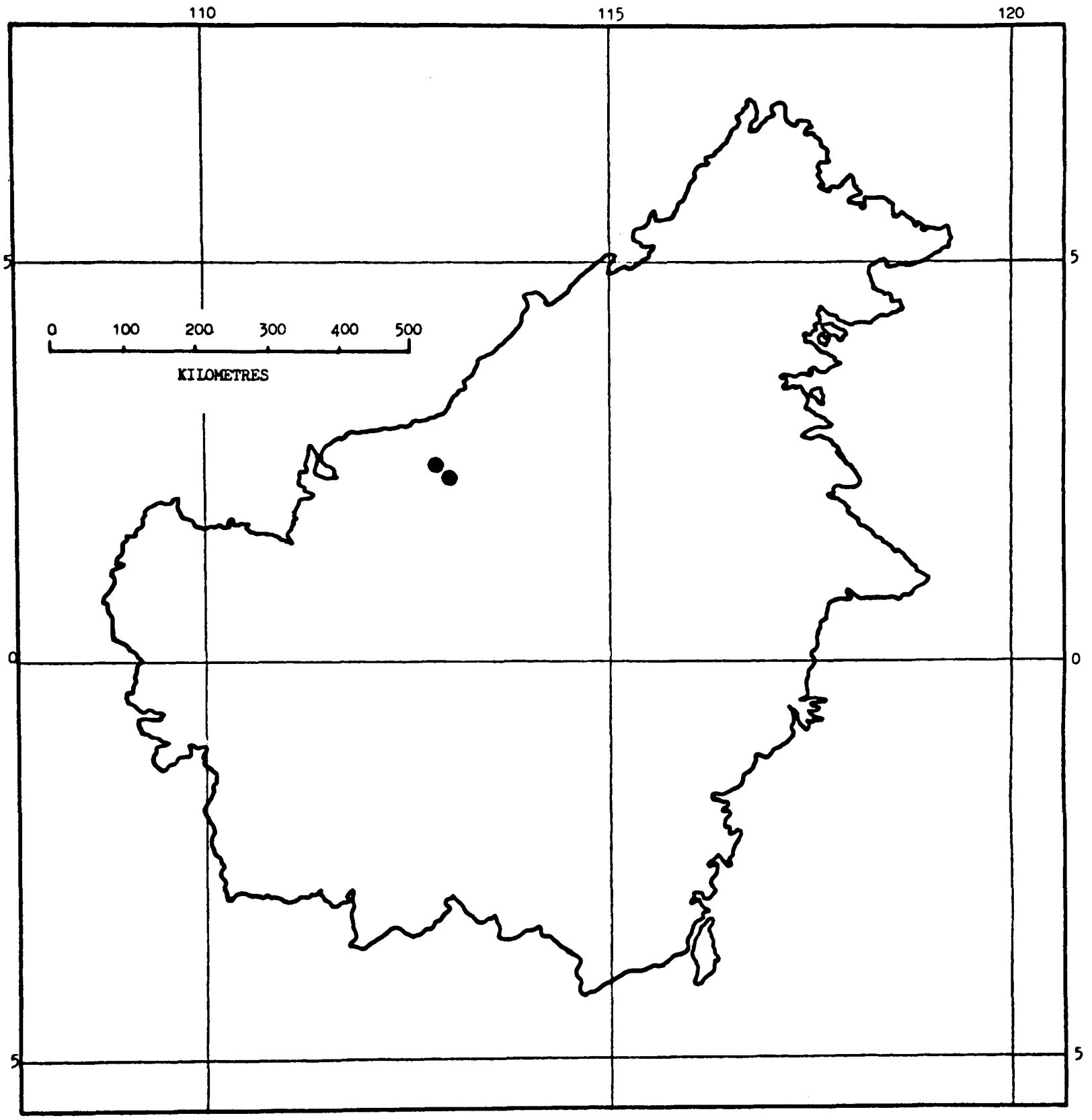


FIG. 6.20 Distribution of W. sarawakensis T. Clark Borneo.

cask-shaped and c. 2.6 mm long X c. 2.1 mm diam., at maximum opening c. 2.8 mm diam.; calyx c. 1.1 mm long, lobes c. 0.8 mm long; petals 3.2-3.5 mm long X 1.7-1.8 mm wide, imbricate; androecium cylindrical, c. 2.0 mm long X c. 1.6 mm diam., tubular for 1/2-3/4 of length, alternate filaments very slightly shorter, filaments (inside and out) sparsely pubescent and tubular part glabrous to very sparsely pubescent, filament apex bifid with erect teeth c. 0.3 mm long; anthers c. 0.8 mm long, apex acute to very shortly beaked, very sparsely and minutely puberulous; disk c. 0.3 mm high; style cylindrical, c. 0.5 mm long X c. 0.4 mm diam., glabrous; stigma capitate, c. 0.7 mm high X c. 1.1 mm diam. at base; fruit a 1-3 seeded berry, ellipsoidal, 2.0-3.0 cm X 1.7-2.5 cm, green to purplish-brown (in vivo) and brown (in sicco), glabrous, pericarp coriaceous; seed ellipsoidal, 1.8-2.3 cm X c. 1.4 cm, (in vivo) enveloped in a sticky white aril.

DISTRIBUTION: Known only from five collections from a small area north of Kapit (viz.: 1. P5143 from Sana on Sungai Tau; 2. P5204 from Bukit Mayeng in the Tau Range; 3. P5219 from Bukit Mersing in the Tau Range; SAR 5279 from "upper" Batang Rajang; Sarawak 'native collector'/ California Botanic Garden 5279 from "Upper Rajang.").

NOTES: This species is most closely related to W.pinnata and is a member of Group 2; see comments under "Variation within the genera" above. It differs from the members of the genus outside Group 2 in having a 7-foliolate leaf and from all members within Group 2 by its long acuminate leaflet apex. It is also the only species of the genus known to produce up to 3-seeded fruits.

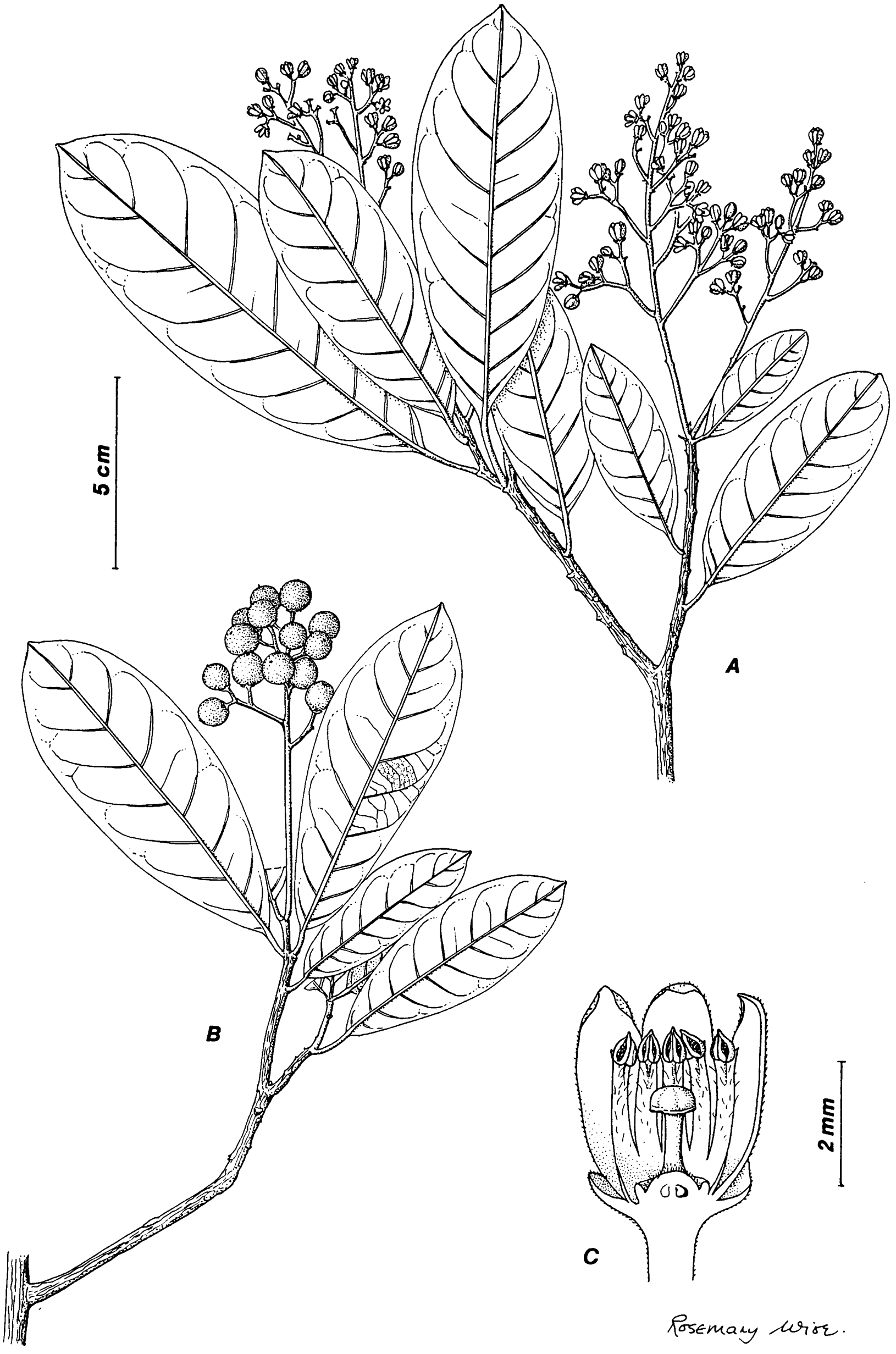


FIG. 6.21 W. monophylla Elmer ex Merrill A. habit; B. habit with infructescence; C. flower in L.S. (A & C: Edaño 252; B: SMHI 1607).

SPECIMENS STUDIED: Purseglove 5143(K;L), 5204(L;SING), 5219(L); Sarawak/California B.G. 5279(NY).

12. WALSURA MONOPHYLLA Elmer ex. Merr. FIG. 6.21

Walsura monophylla [Elmer, Lflts.Philip.Bot. 9:3391 (1937) descr.angl.,ex] Merr., J.Arn.Arb. 35:138 (1954) descr.lat. TYPE: Elmer 12903, Philippines, Palawan, Brook's Point (March, 1911): (PNH + holo.?; G! iso.; NY! iso.).

Tree, to 10m tall, d.b.h. 10cm when tree 3m tall; leafy twigs 2.0-4.5 mm thick, glabrous and frequently lenticellate, bark rough and dark brown; leaves 8-20 (-27) cm long, undivided; petiole plus petiolule 0.8-1.8 (-2.8) cm long, 0.8-1.8 mm thick, semi-terete and flattened adaxially, glabrous; lamina (8-) 12-17 (-25) cm long X (3.5-) 4.5-5.5 (-8.8) cm wide, lanceolate to elliptic to slightly obovate with very short attenuate base and acute to very short acuminate apex, sub-coriaceous to coriaceous, all veins prominent on both surfaces, abaxial surface glaucous (in vivo) on intervenous areas and over smallest veins and glabrous to very sparsely pubescent with short simple trichomes, (8-) 10-12 (-15) costae on either side of the midrib; glands conspicuous.

Inflorescences clustered around shoot apex in axils of caducous undeveloped leaves or solitary or in pairs in axils of fully expanded leaves below, 6-9

cm long at anthesis, each a +/- compact thyrse branched up to second order (excl. pedicels), first order branches up to 3cm long, all parts sparsely pubescent with short simple trichomes; flowers hermaphrodite, just prior to opening cylindrical to cask-shaped and 3.5-4.5 mm long X 2-3 mm diam., at maximum opening 4.0-7.5 mm diam.; calyx 1.5-1.7 mm long, lobes 0.8-1.2 mm long; petals 4.0-4.5 mm long X 1.8-2.0 mm wide, slightly imbricate to valvate, apex acute and often slightly hooded; androecium cylindrical to conical, 2.1-3.0 mm long X 2.1-2.3 mm diam. near base, tubular for 1/3-1/2 of length, alternate filaments slightly shorter, filaments (inside and out) pubescent and tubular part glabrous to very sparsely pubescent, edges of lobes often slightly recurved, lobe apex bifid with erect teeth 0.2-0.4 mm long; anthers 0.8-0.9 mm long, very shortly beaked, glabrous; disk c. 0.4 mm high; ovary very densely pubescent with short simple rigid trichomes; style 1.0-1.2 mm long, narrowly and obconical, c. 0.3 mm diam. at the base and c. 0.5 mm diam. at top, glabrous; stigma capitate with flattened or trapezoidal top, not lobed but with a shallow depression at the centre, c. 0.5 mm high X 0.9 mm diam. at base; fruit a 1-2 seeded berry, globose, 0.8-1.1 cm diam., pale-green to cream (in vivo) or olive-green to mid-brown (in sicco), sparsely puberulous, pericarp very thin and sub-coriaceous, surface rugose but almost smooth; seed +/- spherical or +/- hemi-spherical and c.8 mm long, enveloped in a thin aril ?

DISTRIBUTION: Palawan.

NOTES: This species seems most closely allied to W.pinnata but differs in its small, thin-walled fruits (showing greater affinity with W.trifoliolata) and short inflorescence. Also, whilst all specimens of

W.monophylla have unifoliolate leaves, in W.pinnata they occur only rarely (in some specimens of 'cochinchinensis'). It is an understory tree, often of stunted forest, and usually found on ultra-basic rocks. It is a hyperaccumulator of nickel and has a very specialised Ni detoxification system (Baker, pers.comm., 1989)

SPECIMENS STUDIED: Edaño 727(K); Elmer 12903(G;NY), 12907; PNH 252(L), 1137(L), 12162(L), 12399(A;L), 14103(A); SMHI 1588(A), 1593(A), 1598(L), 1607(A), 1721(A;FHO), 1755(A), 2157(A).

SECTION III: Ruswala T.Clark sect. nov.

Inflorescentiae brevissimae, 1.0-1.7 cm longae sub anthesi, densae; androecium tubulare, c. 4/5 eius longitudinis lobatum; fructus longitudinaliter quadrialatus (immaturus), rhomboidalis (in sectione transversali) ad subglobosus, septicidalis, leniter dehiscens in duabus valvis. Typus: Walsura dehiscens T.Clark sp. nov.

13. WALSURA DEHISCENS T.Clark sp. nov. FIGS. 6.22-6.25

Arbor, rami frondosi leptocaules, 1.5-3.5 mm diametro; folia imparipinnata, bijuga; rhachis leviter tumidus ad insertionem petiolulorum et admodum infra basin laminae, teres, excepta pars proprie basalis adaxialiter leviter applanata; petiolulus teres; lamina (foliolorum terminalium et lateralium) elliptica (ad obovata), (foliolorum basalium) ovato-elliptica;

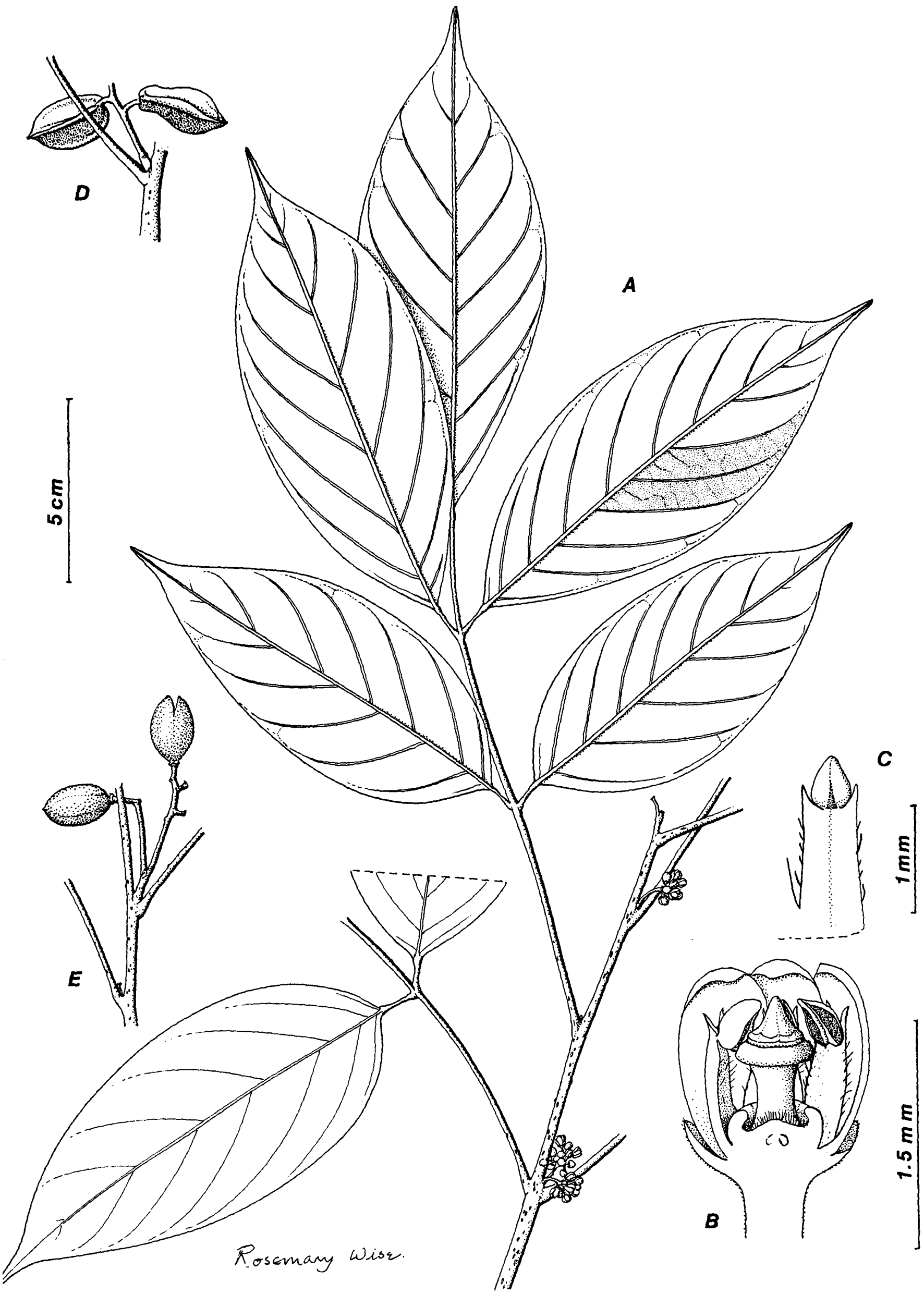


FIG. 6.22 W. dehiscens T. Clark A. habit; B. flower in L.S.; C. androecium (part) exterior; D. immature (winged) fruits; E. mature fruits, one just beginning to dehisce. (T. Clark 78).

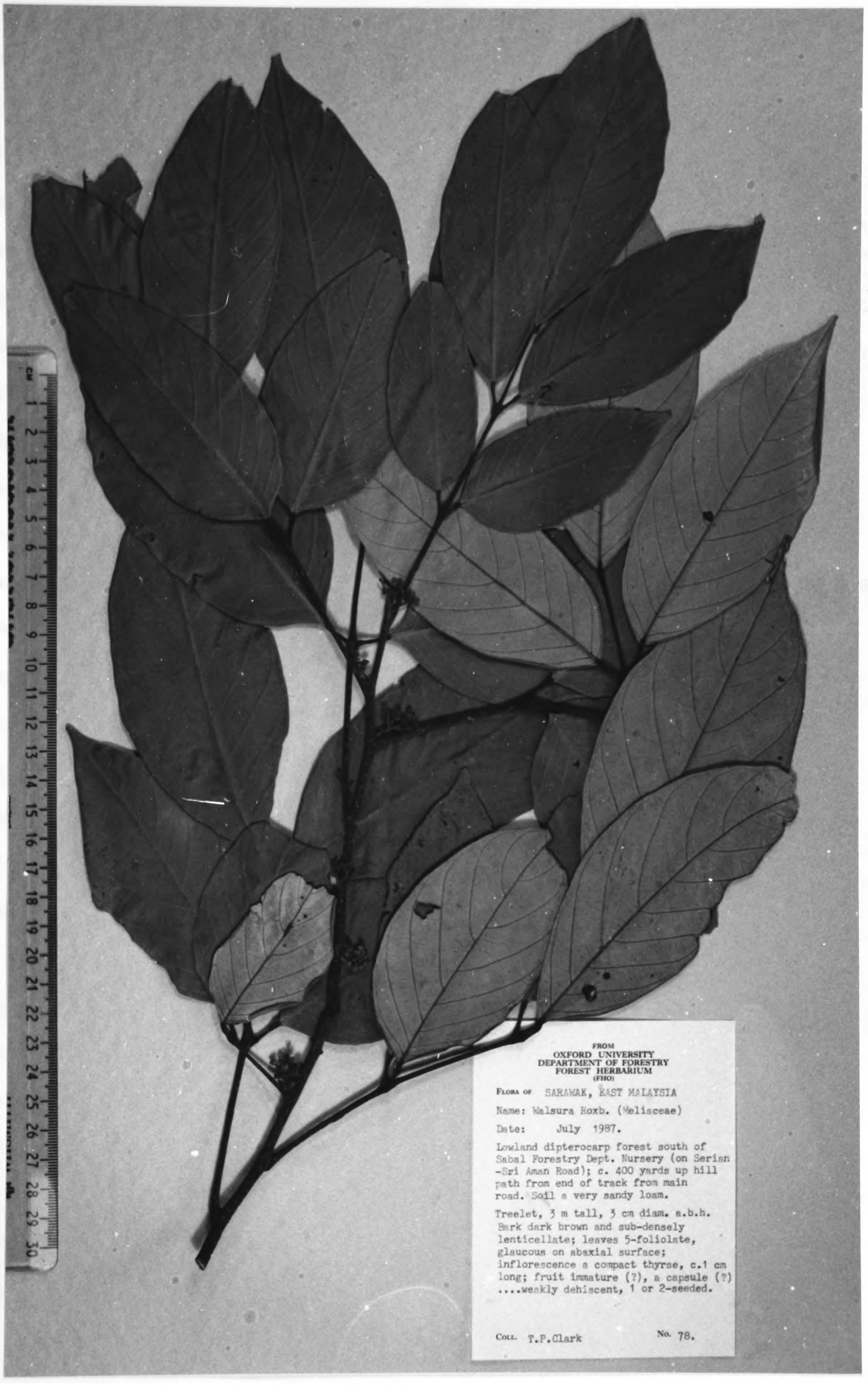


FIG. 6.23 W. dehiscens T. Clark
The holotype. (T. Clark 78).

pagina abaxalis cum nervatura leviter prominente (in vivo et in sicco), in vivo glauca, in sicco opaca (costa media et nervi laterales primi ordinis excepti); corpora parva glandulosa in utroque latere costae mediae et nervorum lateralium primae ordinis; inflorescentiae in axillis foliorum immaturorum vel plene expansorum prope apicem surculi vel infra orientes, sub anthesi 1.0 - 1.7 cm longae, omnes thyrsi arcte compacti; flores hermaphroditi; calyx 5-lobus; pet la 5, libera, imbricata, anguste elliptica vel oblonga, apice acuta; androecium cylindricus vel leviter cupiformis, c.1/5 eius longitudinis tubularis, filamenta 10, tantum margines filamenta pubescentes, apex filamenti bifidus cum dentibus brevibus; antherae 10, glabrae; stylus anguste et inverse conicus, stigma capitatum, apice cum 2 lobis brevibus; discus glaber; ovarium trichomatibus brevibus rigidis dense obtectum, biloculare, unusquisque loculus cum 2 ovulis collateralibus; fructus cum 1 (-2) semine (-ibus), longitudinaliter quadrialatus (immaturus), rhomboidalis (in sectione transversali), subglobulosus, septicidalis, leniter dehiscens in duabus valvis, pericarpium coriaceum; semen plus minusve ellipsoideum. TYPUS: T.Clark 78, Malaysia, Sarawak, 1st Div., Sabal; July 1987; (L! holo.; FHO! iso.; SAR! iso.)

Tree to 9 (-13) m tall, girth to 25 (-40) cm; outer bark smooth and grey; inner bark pale yellow; leafy twigs 1.5-3.5 mm thick, dark-brown to black-brown and densely lenticellate, glabrous to puberulous with occasional simple trichomes; leaves 25-30 (-35) cm long, 2-jugate; petiole 4.5-9.5 cm long, 1.5-2.0 (-2.5) mm thick, +/- terete and slightly flattened adaxially near the very base, sub-densely lenticellate, very sparsely puberulous; petiolule +/- terete, (of distal pair leaflet:) 0.7-1.4 (-2.4)



FIG. 6.24 Walsura dehiscens
Two inflorescences in a leaf axil. Fresh material from treelet at Sabal, Sarawak (= T. Clark 78). Photograph taken July, 1987.

cm long and 0.6-1.2 mm thick; lamina (of distal pair leaflet:) (9-) 11-16 (-19) cm X 4-6 (-8) cm, (terminal leaflet:) 11-15 (-19) cm X 5-8 cm, (basal leaflet:) 8-16 cm X 4-6 (-8) cm, lateral and terminal leaflets elliptic (to obovate), basal leaflets ovate to elliptic, chartaceous to sub-coriaceous, adaxial surface with all veins slightly or not at all prominent (in vivo & in sicco), abaxial surface with most veins slightly prominent (in vivo & in sicco) and surface glaucous (in vivo) except for midrib and costae and (usually) intercostae, abaxial surface very sparsely to densely pubescent (to sub-tomentose) with +/- erect simple trichomes; 7-9 (lateral and terminal leaflets) and 6-8 (basal leaflets) costae on either side of the midrib; glands conspicuous and dense and usually extending along either side of the costae also.

Inflorescences in axils of undeveloped or fully expanded leaves near the shoot apex or lower down, 1.0-1.7 cm long at anthesis each a tightly compact thyrse, branched to first (to second)-order, first-order branches up to 4 mm long, peduncle sparsely lenticellate, all parts densely puberulous with simple trichomes; flower hermaphrodite, not scented, just prior to opening cylindrical and 1.5-1.6 mm long X 1.2-1.3 mm diam.; calyx 1.0-1.4 mm long, lobes c. 0.6 mm long; petals 2.2-2.5 mm long X 1.0-1.8 mm wide, glabrous on inside; androecium cylindrical to slightly cask-shaped, c. 1.5 mm long, tubular for c. 1/5 of length, filament edges only pubescent, filament apex bifid with teeth c. 0.2 mm long; anthers 0.4-0.5 mm long and very short beaked; disk c. 0.4 mm high; style narrowly obconical, c. 0.5 mm long X c. 0.3 mm diam. at base & c. 0.5 mm diam. just below stigma; stigma capitate with two lobes on top, c. 0.4 mm diam. long (excl. lobes) X c. 0.9 mm diam. at base , lobes c. 0.2 mm high; fruit a 1(-2)-seeded septicidally

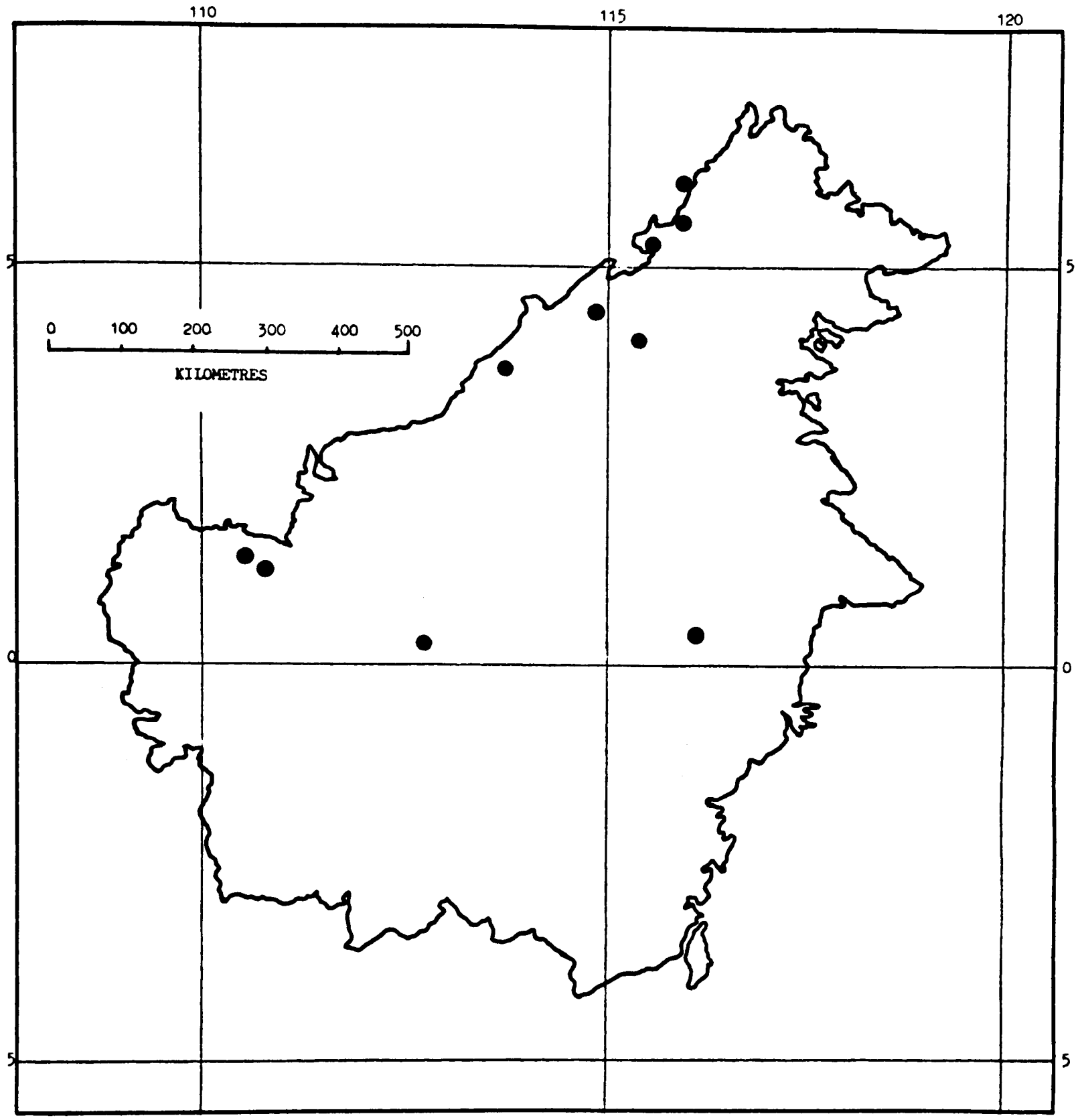


FIG. 6.25 Distribution of W. dehiscens T. Clark Borneo.

dehiscent capsule, longitudinally 4-winged (immature) to rhomboidal (in transverse section) to almost globose, 1.7-2.5 cm long X 0.6-0.9 cm diam., green or glaucous (in vivo) and brown (in sicco), puberulous with simple trichomes, pericarp 0.7-1.0 mm thick generally but up to 1.3 mm thick at the four edges, fibrous endocarp 0.13-0.18 mm thick, septum c.0.18 mm thick between the two locules connected to pericarp at two opposite suture lines, fruit weakly dehiscent into two (or 4 ?) valves commencing at the distal end, the septum spliting into two membranes (see Chapter 4, above) at dehiscence.

DISTRIBUTION: Borneo (1st & 4th Divs. Sarawak; Beaufort and Kota Kinabalu areas, Sabah; Longbleh area, East Kalimantan).

SPECIMENS STUDIED: T.Clark 78 (FHO;K:SAR), 79(FHO;K); Geh & Samsuri 1105(SAR); Hallier 312(L), 355(L); Kostermans 10324(L), 12553; SAN 28427(L;SAN), 28527(K), 33572(SAN), 47852(L;SAN;SAR), 78226(FHO;SAN); SAR 16648(A;K;L;SAR), 32293(L;SAR), 34325(SAR), 35597(L;SAR), 40128(K;SAR), 42881(K;L;SAR), 43064(L;SAR); Winkler 2414(L).

SPECIES NON SATIS COGNITAE

14. W. sp. A. FIG. 6.26

Tree to 35 m tall, d.b.h. to 0.75 m, buttressed to 1.2 m; bark smooth to flaky, reddish; leafy twigs 2.5-4.0 mm diam., glabrous, bark light-brown to

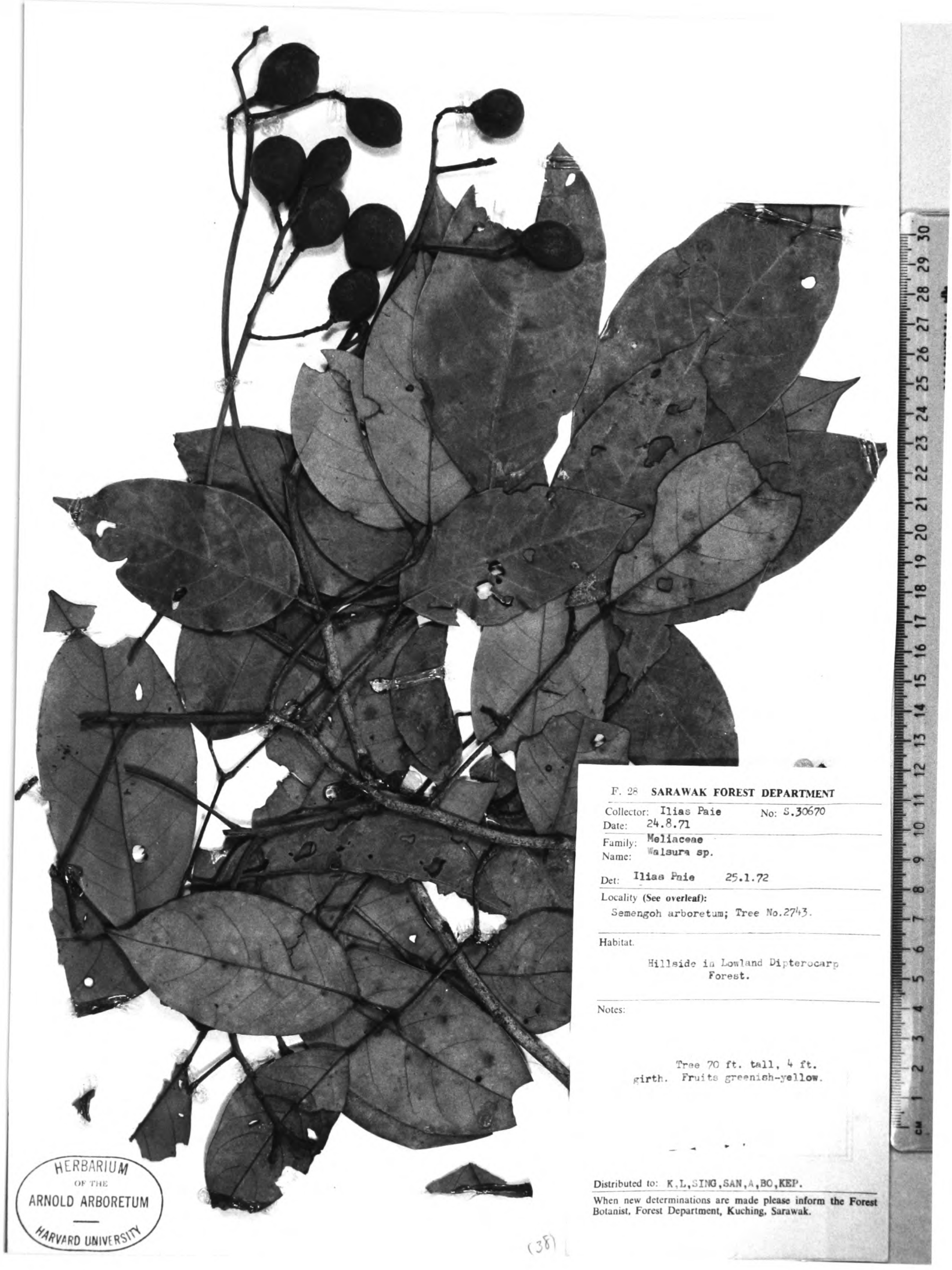


FIG. 6.26 W. sp. A (SAR 30670).

whitish, lenticellate; leaves 13-24 cm long, 2-jugate; petiole 2.5-5.0 m long, 1.5-2.0 mm thick, +/- terete and slightly flattened adaxially near the base, densely puberulous with prostrate simple and 2-armed trichomes; petiolule +/- terete, (of distal lateral:) 0.7-1.2 cm long, 0.7-1.0 mm thick; lamina (of distal lateral:) 8-12 cm X 3.5-5.0 cm, (of terminal leaflet:) 8-14 cm X 4.0-5.5 cm, (of basal leaflet:) 7.5-11.5 cm X 3.5-4.0 cm, all leaflets elliptic with acute base and very short acuminate apex, sub-coriaceous, adaxial surface with no veins prominent, abaxial surface with midrib and costae only prominent and very sparsely pubescent with prostrate simple and 2-armed trichomes; 7-9 (distal lateral), 9-10 (terminal) and 7-8 (basal) costae on either side of the midrib; glands present; flowers unknown; fruit a 1-2-seeded berry, (globose to) ellipsoid, 2.2-2.6 cm long X 1.5-1.8 cm diam., olive-green (in vivo) and brown (in sicco), puberulous with prostrate simple and 2-armed trichomes, pericarp coriaceous with a very thin fibrous endocarp; seed 1.0-1.5 cm long, completely enveloped in a fleshy sweet-tasting aril.

DISTRIBUTION: Sarawak (1st & 4th divisions).

NOTES: This species superficially resembles W.pinnata, and in fruit anatomy (except for the 2-armed trichomes) is very similar, but the degree of vein prominence on the undersurface of the leaflet (especially after drying) is very different.

SPECIMENS STUDIED: T.Clark 76 (FHO); SAR 27213 (K;L;SAR); 27982(K;SAR); 30670(L;SAR), 37776(K;SAR).

15. Walsura yunnanensis C.Y.Wu, Flora Yunnanaica 1:226 (& drawing) (1977). Type: Y.H.Li 2927; Yunnan (KUN ? holo.?). The author comments that this species is allied to W.tubulata but the description gives it a 5-foliolate leaf and its other features do not seem to be particularly compatible with this suggestion.

b. PSEUDOCLAUSENA T.Clark genus novum

[Melospermum Scortech. ex King, J.As.Soc.Beng. 64:83 (1895), nom. in synon.]

Walsura sect. Neowalsura Harms in Engl. & Prantl, Nat.Pflanzenfam. ed.2, 19b1:119 (1940). Type species: W.glabra Merrill = P.chrysogyne.

Arbores; folia imparipinnata, (1-) 2-4 (-7)-juga; lamina foliolorum integra, epidermide in pagina abaxiali tantum simplici, trichomata foliaria multicellularia, glandulae absentes; inflorescentia axillaris, thyrsus valde compactus vel plus minusve laxus, cum indumento trichomatum tantum simplicium; flos aut hermaphroditicus aut masculinus; calyx profunde 5-lobus, petala 5, libera, imbricata, anguste elliptica vel oblonga, apicae acuminata; androecium plus minusve cylindricus, ad 1/4-1/2 eius longitudinis tubularis, filamenta 10, unusquique filamenta linearis pro maiore parte eius longitudinus et cum apice breviter bifido; antherae 10, praeter apicem cum caespite brevi trichomatum glabrae; stylus glaber vel in parte inferiore sparse pubescens; stigma capitatum, apice cum 2 lobis brevibus; discus nullus; ovarium trichomatibus brevibus rigidus densissime obtectum, aspectu aureo, 4-5-loculare, loculis uniovulatis; fructus baccatus, cum 1-2 seminibus, plus minusve globosus, brevissime rostellatus, leviter asymmetricus, coriaceous sed sclerenchymate omnio destitut semen plus minusve ellipsoideum. Typus: Clausena chrysogyne Miq. = P.chrysogyne (Miq.) T.Clark.

Diagnosis: Foliolum epidermide in pagina abaxili tantum non papillatus; flos nullus discus; ovarium 4-5-loculare; fructus brevissime rostellatus, leviter asymmetricus, sclerenchymate omnio destitute.

Diagnosis: Leaf abaxial surface epidermis non papillate; flower lacking a disk; ovary 4 or 5 locular; fruit with short beak, slightly asymmetric and completely lacking sclerenchyma.

The generic name Pseudoclausena is given since the type species was originally placed in the genus Clausena Burm.f. (Rutaceae) by Miquel. Similarly, Pseudobersama mossambicensis (Sim)Verdcourt, also a mono typic genus of the Trichilieae, was originally placed in the genus Bersama (Melianthaceae).

PSEUDOCLAUSENA CHRYSOGYNE (Miq.) T.Clark comb.nov. FIGS. 6.27 & 6.28

Clausena chrysogyne* Miq., Fl.Ind.Bat.Suppl. 502 (1861). TYPE:

Teysmann HB 3805; Indonesia, Sumatra, Palembang (L! holo.; U! iso.).

Walsura chrysogyne (Miq.) Bakh.f., Blumea 16:359 (1968); Mabberley, Tree Flora Malaya 4:254 & tab. (1989). TYPE: as above.

*Gr., chryso = gold, gyne = woman, referring to the golden colour of the ovary, due to its covering of short, stiff, golden trichomes.

Cipadessa borneensis Miq. Ann.Mus.Bot.Lugd.Bat. 4:6 (1868); c.f. van Steenis & Bakh.f., Bot.Jb. 86:399 (1967). TYPE: Korthals 115; Borneo (Kalimantan?) (L! holo.).

W.multijuga King, J.As.Soc.Beng. 64:83 (1895); Ridley, Fl.Mal.Pen. 1:412 (1922). TYPE: King's Coll. 10622; Malaysia, Perak (CAL ? holo?; K!, L!).

[Melospermum rubro-stamineum Scortech. ex King, op.cit. (1895). nom. in syn.]

[W.quadriloculare Val., Ic.Bogor 2:156 (1906) nom. nud.; Dakkus, Bull. Jard.Bot. Btzg.Suppl. 295 (1930) & Ed.2 pg. 237 & Ed.3 pg. 244; Bakh.f., Blumea 16:359 ('W.quadrangularis', 1968). nom. in syn.]

W.brachybotrys Merr., Philip.Journ.Sci. 8:378 (1913). TYPE: Wenzel 295; Philippines, Leyte, Dagami. 3 July 1913. (PNH + holo.; E! iso.; GH! iso; NY! iso). Syn. nov.

W.celebica C.DC., Mededeelingen van's Rijks Herbarium Leiden 22:10 (1914). Type: Elbert 3188; Sulawesi, Penango, 24 Sept 1909. (L! holo.). Syn. nov.

W.glabra Merr., Philip . Journ. Sci. 13:76 (1918). TYPE: "Native collector", B.S. 2438; Malaysia, Sarawak, Feb.-June 1914. (PNH holo.?+, A! photo.). Syn. nov.

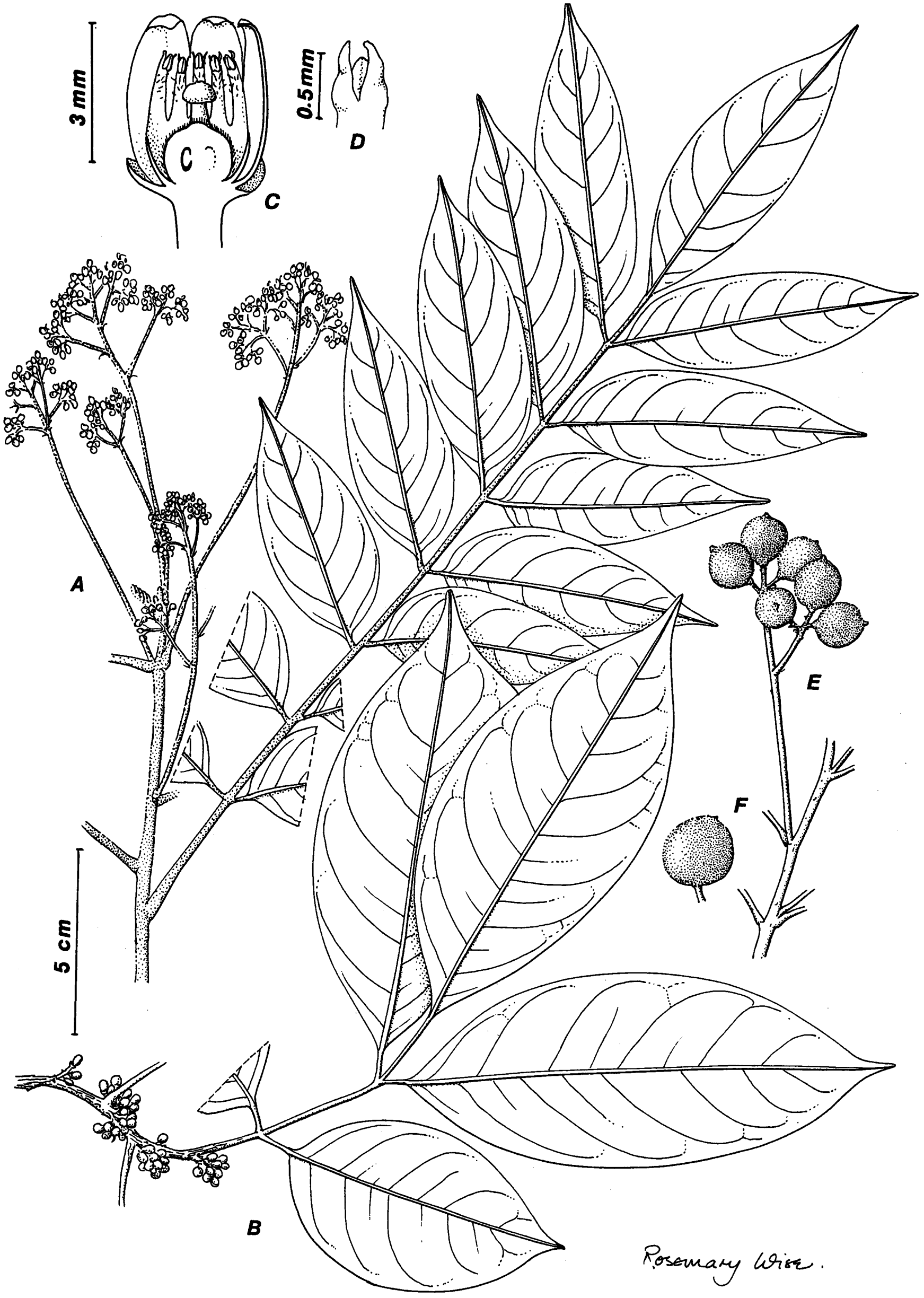


FIG. 6.27 P. chrysogyne (Miq.) T. Clark (i) "chrysogyne" A. habit; C. flower in L.S.; D. filament apex seen from exterior; E. infructescence; F. mature berry; (ii) "brachybotrys" B. habit. (A: Pennington 7983; C & D: SAN 81144; E & F: SMHI 20; B: Wenzel 295).

W.borneensis Merr., Un.Cal.Publ.Bot. 15:213 (1929); Bakh.f., Blumea 16:359 (1968). TYPE: Elmer 20167; Malaysia, Sabah, Sandakan. Oct-Dec 1921. (PNH holo?; A! iso.; K! iso.; NY! iso.; SING! iso.).

W.hosei Ridley. Bull.Misc.Info.Kew 1930:371 (1930). TYPE: Hose 394; Malaysia, Sarawak, Baram. Dec 1894. (K! holo.; L! iso.). Syn. nov.

[W.palawanensis Elmer Leaf. Philipp. Bot. 9:3393 (1937). nom. non rite publ. (descr. angl.)]

Tree to 25 m tall, bole to 15 m tall, d.b.h. to 60 cm; outer bark smooth and c. 2 mm thick, unfissured and pale-brown to greyish-brown; inner bark 3-4 mm thick and red-brown; sapwood whitish with red or pink tinge; leafy twigs 1.1-3.5 mm thick, glabrous or puberulous or velvety, trichomes simple, bark mid brown to very light brown or greyish and sometimes sparsely lenticellate; leaves 18-42 cm long, (3-) 5-9 (-15)-foliolate, brown (to olive green) when dried; petiole 2.5-8.5 cm long and 0.8-2.1 mm thick, terete or semi-terete slightly flattened adaxially, glabrous or puberulous or velvety, trichomes simple; petiolule +/- terete, (of distal lateral leaflet:) 1.5-10.0 mm long X 0.4-0.9 mm thick, glabrous or puberulous or velvety; lamina (of distal lateral leaflet:) (5.3-) 7.2-14.0 (-18.5) cm X 2.3-5.0 (-6.5) cm, (of terminal leaflet:) (6.4-) 7.2-16.5 (-19.5) cm X 2.4-5.0 (-6.8) cm, (of basal leaflet:) 4.0-12.5 cm X 1.9-5.5 cm, lateral leaflets on any one leaf of similar areas and basal leaflets usually 1/4-1/2 of this area, ovate to elliptic (to lanceolate) the basal

leaflets tending towards a smaller length:width ratio, base attenuate and slightly asymmetric, apex shortly acuminate, sub-coriaceous, adaxial surface with no veins or only midrib prominent (in sicco), abaxial surface with only midrib and costae prominent (in sicco) and not glaucous (i.e. epidermis is non-papillate) and glabrous to tomentose with simple decumbent to erect trichomes; 6-9 (-15) (distal pair leaflet) or 7-10 (-15) (terminal leaflet) or 6-9 (-14) (basal leaflet) costae on either side of the midrib; glands absent.

Inflorescences clustered around shoot apex or below in axils of fully expanded or expanding leaves, 1-6 (-10) cm long at anthesis, each a very compact to open thyrse, branched up to second (to third) order (excl. pedicels) of which the first order branches are up to (0.7-) 7.5 cm long, primary rachis and all branches lacking lenticels and glabrous to tomentose with simple trichomes; flowers hermaphrodite (with little pollen) or (on different plant) male only (with much pollen), just prior to opening cylindrical to cask-shaped and 3.0-3.6 mm long X 1.4-2.6 mm diam.,at maximum opening 2.9-6.0 mm diam.; calyx 1.5-1.8 mm long, deeply 5-lobed, each lobe 0.8-1.2 mm long with a blunt apex; petals 5, free and imbricate, 2.8-4.8 mm long X 1.5-1.8 mm wide, narrow-elliptic to oblong, apex acute; androecium +/- cylindrical, 1.5-3.3 mm long X 0.9-1.8 mm diam., tubular for 1/4-1/2 of length, each filament linear or slightly narrowed towards the apex, filament apex bifid with erect to spreading teeth 0.4-0.5 mm long; anthers 0.4-0.5 mm long, glabrous or with a short tuft of trichomes from the apex; disk absent; ovary very densely pubescent with short stiff trichomes, appearing golden or extremely rarely (see below) glabrous, 4-5 locular, each locule with one ovule; style +/- cylindrical, 0.4-0.6 mm long X

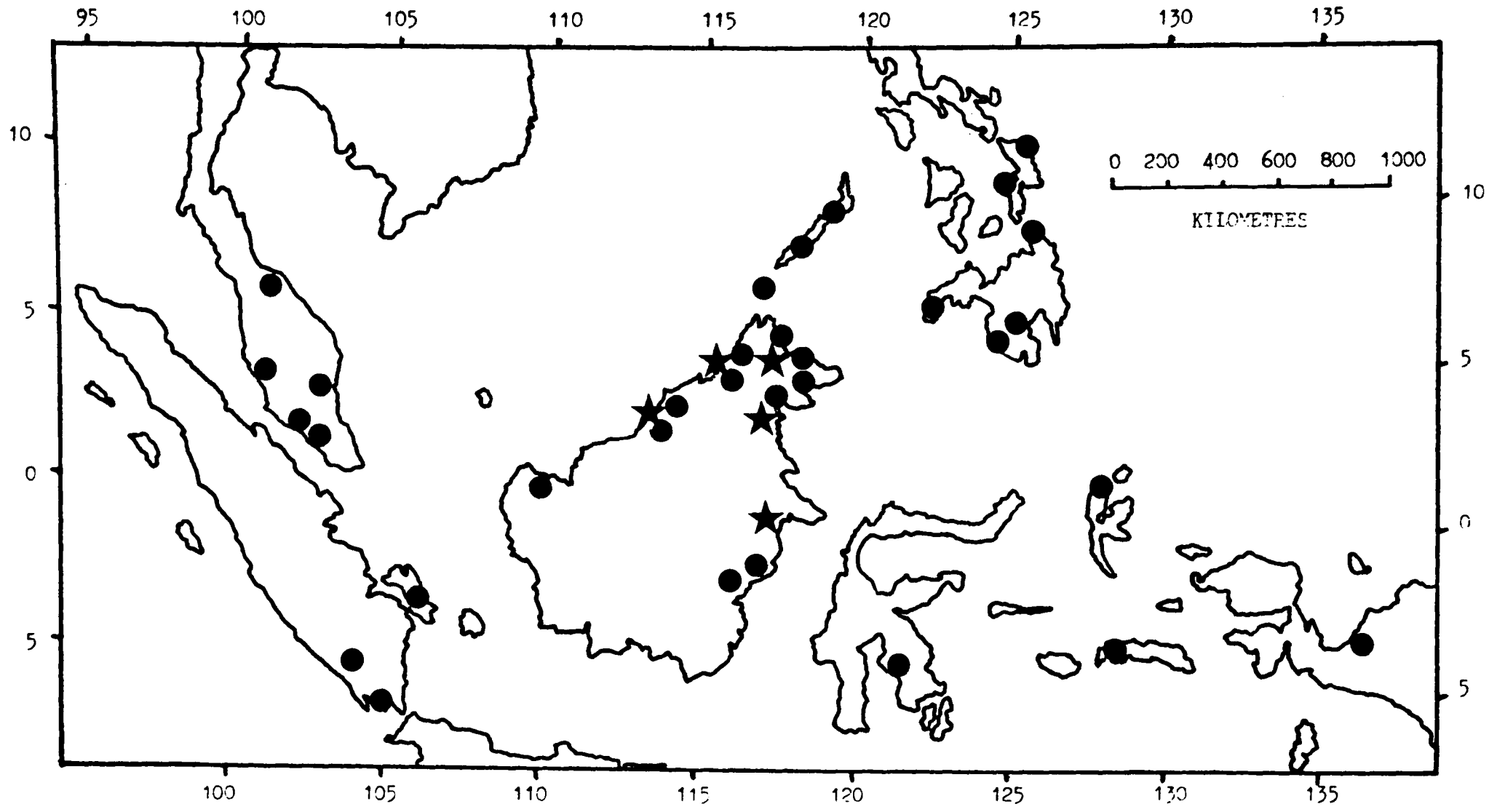


FIG. 6.28 Distribution of P. chrysogyne (Miq.) T. Clark Malesia.
● : forma chrysogyne; ★ : forma velutina

0.2-0.3 mm diam., glabrous to sparsely pubescent in the lower half; stigma +/- capitate and shortly two-lobed on top, (excl. lobes:) 0.5-0.6 mm diam at base X 0.3-0.5 mm high, below the level of the anthers at maturity; fruit a 1-2 seeded berry, +/- globose, 1.3-1.8 cm diam. with a short beak,3-5 mm long, positioned asymmetrically on the fruit, pericarp coriaceous but lacking sclerenchyma, parenchyma with high levels of tannins only; seed 0.8-1.3 cm long and +/- ellipsoidal, dark brown and shining but lacking an aril.

Two forms are recognised:

Young parts glabrous or puberulous on axes and
leaflet midrib and costae only.....a. forma chrysogyne
Young parts (incl. leaf lamina) velutinous.....b. forma velutina

forma velutina (Ridley) T.Clark comb. & stat. nov.

W.velutina Ridley, Bull.Misc.Info.Kew 1930:371 (1930). Type: Hose 643; Sarawak, Baram (K! holo.)

NOTES: Most of the variation within this species is accounted for by three characters: 1. degree of pubescence on the young aerial parts, 2. number of leaflets, 3. length of inflorescence.

W.velutina was distinguished by its dense (tomentose) covering of erect trichomes on all young parts, including the whole undersurface of the

leaflet, W.chrysogyne and the other species here reduced being glabrous or very sparsely pubescent or densely pubescent only on the midrib and costae of the leaflet undersurface. This is a good character but in the absence of any supporting character the species has had to be reduced to forma status. Its distribution is fairly small, occuring only in Borneo and Mindanao.

Leaflet number varies considerably and more so than in any species of Walsura, from 3 to 15 per leaf, with the range 5 - 9 predominating. At the Philippines end of the range (e.g. W.brachybotrys type-specimen) there is a tendency towards 3 - 5-foliolate specimens, but only one specimen (from Mindanao) has exclusively 3-foliolate leaves. Specimens with 9+ leaflets predominate at the Sumatra end of the range (e.g. W.chrysogyne type-specimen) but also occur in Borneo and Palawan (e.g. W.palawanensis 'type'-specimen). Inflorescence length also varies considerably in this complex. In the 100+ specimens examined, those at anthesis ranged along a continuum from 0.8 cm to 10 cm. The graph of inflorescence length against leaflet number was plotted and no group segregated out. The distribution was continuous with the mode at 7cm/7-9 leaflets. No combination of characters will maintain those species here reduced and the whole is held tightly together by several very good morphological and anatomical characters (see above).

It may be useful to distinguish informally between the three main morphological entities within forma chrysogyne however, even if they are all linked by intermediates (see also W.pinnata above).

1a. Inflorescence <2 cm long at anthesis (Philippines) ......'brachybotrys'

b. Inflorescence >4 cm long at anthesis.....2

2a. Leaf 5-9-foliolate .....'multijuga'

b. Leaf 11-15-foliolate (Sumatra) .....'chrysogyne'

In view of the variation demonstrated in this complex, the species W.celebica, W.glabra and W.hosei are here reduced since they have formerly been maintained by minor characters (of floral pubescence and/or leaf division), the intermediates of which are now known. W.hosei is perhaps the most unusual of the four with its glabrous ovary. Since the type-specimen is the only known example of this in the Pseudoclausena species, and considering the great variation shown in floral pubescence in the genus, this character is considered insufficient to maintain a distinct species (see also W.glauca = W.pinnata, above).

(i) forma chrysogyne

Agama 10222; Alston 17211(K); Amiruddin 24(L); Balgooy 4977(L); bb 24892; BKF 119(K), 45581(L); Bloembergen 4609(L); BNB 1952, 4817(L); B.S. 24140(K), 2438(A), 27052, 28223, 29126, 39167(L); CF 2265(K); Clemens 3397(U), 4449(U); Elbert 3188(L), 3225(L); Elmer 13138(L), 13158(L), 20167(A;K;L;NY;SING); FB 27052(K); Forbes 1154, 1216(GH); FRI 2986(FRI;L), 3497(FRI;L), 6713(FRI;L), 6788(FRI;L), 11145(FRI;L), 11250(FRI;L), 11684(FRI;K;L), 11873(L), 13007(FRI;K;L), 13198(FRI;L), 13206(FRI;L), 13224(FRI;L), 13770(FRI;L), 14269(L), 14371(FRI), 14413(FRI;L), 15756(FRI), 16649(FRI), 16658(FRI), 17320(FRI;L), 23380(FRI;L), 26068(FRI), 29155(FRI),

64747(FRI), 66524(FRI;K), 73759(FRI), 76521(FRI), 94087(L), 98187(FRI), 99474(FRI), 104269(FRI;L), 104977(FRI;L); Hallier 4715(L); Hort.Bog. 429(L), III-D-20(BO), III-F-23(BO); Hose 394(K;L); Kerr 7845(K), 12606(L); King's coll. 5473(L), 6915(K), 8400(L), 10622(K;L), 10798(K); Kokowa & Hotta 3069(SAN), 5948(L;SAN); Korthals 115(L); Kostermans S.133(L), 281(FHO;L) 4348(L), 4385(L), 7454(L), 7475(K), 7477(L), 10064(L), 12323(L); Kuswata & Soepadmo 12(A;K;L), 77(L), 109(L), 184; Lakshnakara 997(K); Maingay 2571(K); Maxwell 81-199(L); Merrill 715; Minjulu 79224; Musser 77(L); Nooteboom 1638(L); Pennington 7831(FRI;L), 7899(L), 7907(L;SAN), 7921(L;SAN), 7983(FHO;L); Peyte 233(L); PNH 4134(L), 4715, 38022(L), 38058(L), 41949(L); Prawiroatmodjo & Soewoko 1275(L), 1691(L), 1962(L); Ridley s.n.(K); SAN A1952(L), 10142(L), 10222(L), 16479(L), 30498(L;SAN), 32556(K;L;SAN;SAR;SING), 32586(L;SAN), 35619(L), 37688(L;SAN), 39135(L;SAN), 39726(L;SAN), 41085(SAN), 43057(SAN), 43756(K;L;SAN), 43760(L;SAN), 46098(L;SAN), 47886(SAN), 49165(L), 62513(K;L;SAN), 66696(SAN), 70646(FHO;K;L;SAN), 71276(L), 74599(L;SAN), 74887(K;L;SAN), 79219(SAN), 79224(SAN), 80970(FHO;FRI;K;L;SAN;SING), 81144(L;SAN), 81150(L;SAN), 81373(L;SAN), 81934(SAN), 82008(L;SAN), 87381(SAN), 87738(SAN), 89258(L;SAN), 89780(L;SAN), 91777(SAN), 94945(L;SAN), 107255(SAN), 109629(SAN); SAR 13377, 22156, 24268(FHO), 26985(FHO), 27267(FHO), 32163(L), 35236(FHO), 39029; Sargent s.n.; Scortechini s.n.(SING), 1562(K), 1569; SF 28969(A;BM;K;L); SMHI 20(FHO); Sosrodihardjo 28; Teysmann HB3805(L;U), s.n.(L); Univ.San Carlos 809(L); Vidal 2325(K); Vogel 3093(L), 3746(L), 3770(L), 3771(L); Wenzel 295(E;GH;NY), 1621(L), 2600(K;NY), 3260(GH;K;NY); Williams 2093(K).

(ii) forma velutina

BKF 51943(K;L), 52047(L); BNB 3995; Hose 629(K), 643(K); Kostermans 4844(L), 4890(L), 7156(L), 7275(L); Meijer 2099(L); PNH 13660(L); SAN 81180(L;SAN), 84007(SAN), 84153(FHO;K;L;SAN;SAR), 85708(SAN); SAR 24459(L;SAR); 41048(SAR).

FULL LIST OF SPECIMENS STUDIED

See Appendix 4.

SPECIES EXCLUDENDAE

Walsura intermedia Craib, Bull.Misc.Info.Kew 1926:345 (1926). TYPE: Kerr 4959; Thailand, Nan, Doi Pu Ka (K! holo.; BM! iso.) = Heynea trijuga Roxb. ex Sims.

[Walsura lanceolata Wall., List n.4886 (1828). nom.nud.] = Aglaia elaeagnoidea (Adr.Juss.) Benth. (det. C. Pannell).

W. pallida Craib, Bull.Misc.Info.Kew 1926:345 (1926). Type: Kerr 5813; Thailand, Dan Sai, Hui Nam Man (K! holo.) = Heynea trijuga Roxb. ex Sims.

Walsura perrottetii C.DC., An.Conserv. & Jard.Bot.Genève 10:152 (1907). TYPE: Perrottet s.n.; India, Nilgherries (G! holo.?). = Heynea trijuga Roxb. ex Sims.

Walsura pubescens Kurz, J.As.Soc.Bengal 41:297 (1872) & For. Fl. Brit.Burma 1:225 (1877), TYPE: Kurz s.n. (CAL ? holo?). =? Heynea trijuga Roxb. ex Sims. N.B. Kurz described this species, from Burma, as having a capsule which splits into two leathery valves containing a single seed enveloped in a white aril. This is almost certainly a Heynea species.

Walsura punctata Suesseng., Mitt.Bot.Staatss.Münch. 2:58 (1950). TYPE: Clemens 28201; Malaysia, Sabah, Mt.Kinabalu (M holo.?; K! iso?). = Heynea trijuga Roxb. ex Sims.

Walsura punctata Suesseng. var. papillosa Suesseng. & Heine, Mitt.Bot. Staatss. Münch. 2:58 (1950). TYPE: Clemens 28649 = 28668; Malaysia, Sabah, Mt. Kinabalu (M, holo.; K!). = Aphanamixis borneensis (Miq.) Merr.

Walsura quinquejuga Kurz, Prel.Rep.Veg.Pegu App.A:33, App.B:37 (1875) perhaps based on Heynea quinquejuga Roxb. (Hort. beng., 1814) nom. nud., (Fl. Indica 2:391, 1832) = H.trijuga teste Bentv. (Acta Bot. Neerlandica 11:11, 1962) non H.quinquejuga Roxb. ex Sprengel (Syst.Veg. 4:252, 1827) = Aglaia rufinervis (Bl.) Bentv.

'Walsura sumatrana' = Heynea sumatrana Miq. Ann.Mus.Bot.Lugd.Bat. 4:60 (1869), 'Walsura sumatrana', emend.; Lam, Bull.Jard.Bot.Btzg. III:12:422 (1932); c.f. Leenhouts, Fl.Mal. Ser.1, 5:249 (1956); c.f. Bentvelzen, Act.Bot.Neerl.

11:11 (1962). N.B. Lam seems be the first to use "Walsura sumatrana" when he refers to Merrill's reduction of Scutinanthe engleri Elm. to it (Enum.Philip.Pl. 2:380, 1923), when in fact Merrill, rightly, uses Heynea sumatrana Miq. = Heynea trijuga Roxb. ex Sims.

Walsura tenuifolia Ridley, J.Roy.As.Soc.Straits Branch 75:17 (1917). TYPE: Ridley 3022; Malaysia, Perak (K! holo.). = Heynea trijuga Roxb. ex Sims.

Walsura trijuga (Roxb.) Kurz, J.As.Soc.Beng. 44:148 (1875). TYPE: as for H.trijuga Roxb. ex Sims, incl. var. 'genuina' and var. pubescens (Kurz) Kurz TYPE: as for W.pubescens, above. Also, var. microcarpa (Pierre) H.H.Hu, J.Arn.Arb. 5:299 (1924), TYPE: Balansa 4040 (P). = Heynea trijuga Roxb. ex Sims.

Walsura xixangensis C.Y.Yu & H.Li Acta Phyt. Sinica 18:110 (1980). Type: Qinghai-Zizang (Tibet) Complex Exped. 74-4540; China, Xizang; (PE! holo.; FHO! photo.). = Glycosmis sp. (Rutaceae) (det. M.van Balgooy).

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CHAPTER 7

CLADISTICS

INTRODUCTION

Whilst revising the genus Walsura and considering these species in relation to those of Heynea and the rest of the tribe, ideas about apomorphy (advanced character states) and phylogeny naturally came to mind. Taxonomists seem to rely heavily on their intuition and a thorough knowledge of their group(s) to establish apomorphies, but outgroup comparison is not strange to them. A character state represented in an outgroup is considered likely to be primitive and that in the 'ingroup' newly derived and therefore advanced. Those who advocate the method of classification termed cladistics routinely use outgroup comparison in a formalised way to establish character polarity as a basis for phylogenetic reconstruction (Hennig, 1966; Mayr, 1974). Using this method in isolation however places much on the assumptions that advanced character states are uniquely derived and that resemblance is more likely to reflect homology than homoplasy or convergence. Multiple outgroups are sometimes used (Donoghue & Cantino, 1984) but if only one outgroup is taken then it is usually the sister-group, if indeed this can be determined.

Phylogenetic systematics (as laid down by Hennig, 1966) classify and rank organisms exclusively on the basis of recency of common descent, which is

evinced only by shared derived character states (synapomorphies). Shared primitive character states (symplesiomorphies) inherited from a more remote common ancestor are irrelevant or misleading in the search for phylogenetic relationship. Monophyletic groups are characterised by shared derived characters (evolutionary novelties). The relationships thus defined can be represented as branching tree diagrams (cladograms). For a given set of data, one or several trees may be constructed and the 'best' tree is determined usually by applying a parsimony criterion, to find the shortest possible tree(s). Characters may also be weighted, unlike characters in a phenetic analysis.

In the past ten years, cladistics has gained considerable impetus amongst botanical and (especially) zoological taxonomists but, like phenetic classification methods, has some major flaws (see below). Not so much to jump on the bandwagon (Cronquist, 1987) but rather to evaluate this method on a group of species which I know intimately, it was decided to subject them to a cladistic analysis. It is also important for those of us working on tropical tree groups to test cladistic methodology on our taxa since its main testing ground to date has been (after all manner of animal groups) predominantly herbaceous groups (e.g. Zandee & Geesink, 1987, on legumes; Knapp, 1990 on Solanum species).

Whilst there is no rule about the number and type of characters necessary for a cladistic analysis, it is a good policy to cover features from as many organs/ tissues of the plant as possible. This helps to avoid misleading results due to parallelism in one or two organs/ tissues. It is also wise to consider biochemical and cytological data, if available. In

the normal course of a taxonomic revision, microscopical (especially anatomical) features are rarely investigated in all species and so the characters available for an analysis at the end of the revision are somewhat limited. In the present study, a cladistic analysis was planned from the earliest stages.

In the course of the study, a wide range of data was collected for all species of Heynea, Walsura and Pseudoclausena (gen.nov., segregated from Walsura - see previous chapter) but, because of time constraints, for few species of Trichilia or of any of the other genera. The analysis was necessarily, therefore, restricted to Heynea, Walsura and Pseudoclausena and a sister group was sought. Since these three genera are clearly more closely related to each other and each to Trichilia than any one is to any other genus in the tribe (see Pennington and Styles, 1975, and Chapters 1 to 5, above), Trichilia was the clear choice of sister- /out-group.

CHARACTERS AND POLARITY

Selection of characters was not so much governed by subjective choice as by data available for the species concerned. Since the investigations of leaf surface and fruit anatomy had provided a number of taxonomically useful characters (see Chapters 2 & 4, above) these figure heavily alongside the more conventional (and, again, very useful) characters such as degree of leaf division.

FIG. 7.1 Summary of character states and their respective codes for cladistic analysis of Heynea, Walsura and Pseudoclausena.

1. Leaves: 7- or more-foliolate (1); 5-foliolate (2); 3-foliolate (3); unifoliolate (4).

2. Rachis: not swollen (1); rachis swollen (2).

3. Lamina abaxial epidermis: non-papillate (1); papillae islets (2); papillate (3).

4. Leaf trichomes: unicellular (1); multicellular (2).

5. Leaf trichomes: simple only (1); incl. 2-armed (2); incl. stellates (3).

6. Incomplete lateral veins: absent (1); present (2).

7. Inflorescence: >4 cm long (1); <2.5 cm long (2).

8. Inflorescence trichomes: simple only (1); incl. 2-armed (2).

9. Filaments: united for >1/4 (1); united for <1/4 (2); discrete (3).

10. Disk: present (1); absent (2).

11. Stigma: not lobed (1); lobed (2).

12. Ovary: 3-locular (1); 1-2-locular (2); 4-5-locular (3).

13. Endocarp sclerenchyma: thin (1); thick (2); absent (3).

14. Endocarp sclerenchyma: broken (1); complete (2); absent (3).

15. Sutures: incl. complex (1); simple only (2); absent (3).

16. Fruit: loculicidal capsule (1); septicidal capsule (2); berry (3).

17. Pericarp inner-surface: glabrous (1); pubescent (2).

18. Aril: coloured (1); colourless (2); absent (3).

Characters were allocated primitive (plesiomorphous) and advanced (apomorphous) states. Multi-state (e.g. 1 - 3) characters are allowed in most modern cladistics computer programs and in the one used here (see below) the computer then breaks them down into series of binary (i.e. 2-state) characters. The characters used here have two or three states. Unknown data can be allowed for in most cladistics programs. The only data missing in this analysis were of the fruits of W.bonii and W.poilanei and these data were entered as "-1" in the data matrix.

The character state represented in the outgroup is taken as most primitive. One of the difficulties with this is that, especially with a large outgroup, a state other than the most primitive may occur there. When this happens, possibly subjective decisions have to be made or a new outgroup found. Where this has occurred in Trichilia, the former option was taken. Should all of the states (i.e. the whole character) be absent from the outgroup (as was the case with fruit characters of Pseudoclausena chrysogyne) then it is considered particularly advanced since it is so different from anything else that it is almost certainly newly derived and is given the highest number in the character state transition sequence. This seems to be a reasonable extension of the polarisation by out-group comparison method, especially as there is no evidence of these highly advanced fruit characters in Trichilia, Heynea or Walsura.

The characters and their states are listed (FIG. 7.1) and briefly considered in turn here. (Data on the character states in Trichilia species are partly from this study and partly from De Wilde (1968) and Pennington & Styles (1981)).

The unifoliolate leaf is very rare in Trichilia species (e.g. T.pallida from C. & S. America), most species being imparipinnate and 3+ jugate. In dried material, the primary rachis is normally of fairly uniform thickness in all Trichilia species. Papillate epidermis is unknown in Trichilia, as are multicellular leaf trichomes, 2-armed or stellate leaf trichomes and incomplete lateral veins (see Chapter 6 for definition).

Very short inflorescences do occur in a few species of Trichilia (e.g. T.prieureana Adr.Juss. & T.trifolia L.) but, by far, the majority have an inflorescence longer than 4 cm at anthesis. Two-armed inflorescence trichomes are not known in the sister group and neither is a staminal tube lobed for greater than 3/4 (T.capitata from Africa coming closest).

Although a disk, or what Pennington and Styles (1981) refer to as a nectary, occurs in some form in only about 30% of Trichilia species (T.capitata Klotzsch, T.prieureana A.Juss. and T.rubescens Oliv. in Africa and e.g. T.glabra L., T.elegans A.Juss. and T.septentrionalis C.DC. in America) they do occur in a wide range of forms right up to the Walsura-type well defined annular form. Also, going beyond sister group comparison, disks occur (in some form) in all other genera of the tribe except Lepidotrichilia. Tentatively therefore, possession of a disk is considered plesiomorphous. Lobing of the stigma occurs in only a very small proportion of Trichilia species and so is considered advanced. A three-locular ovary is by far the the most typical state in Trichilia with two- and four-locular ovaries occurring very rarely in normally three-locular species. In Heynea and Walsura, a two-locular ovary is normal, with Pseudoclausena being four- or five-locular. Polarising this

	CHARACTERS																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. Heynea trijuga	1	1	3	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
2. Heynea velutina	1	1	3	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
3. Walsura dehiscens	2	2	3	1	1	1	2	1	2	1	1	2	1	1	2	2	1	2
4. Walsura robusta	2	2	2	1	1	1	1	1	3	1	2	2	2	2	3	3	2	2
5. Walsura trifoliolata	3	2	3	1	2	1	1	2	1	1	2	2	1	2	3	3	1	2
6. Walsura tubulata	3	2	3	1	1	1	1	1	1	1	1	2	1	2	3	3	1	2
7. Walsura trichostemon	2	2	3	1	1	1	1	2	1	1	2	2	1	2	3	3	1	2
8. Walsura gardneri	4	2	3	1	1	1	1	2	2	1	2	2	1	2	3	3	1	2
9. Walsura bonii	3	2	3	1	1	1	1	1	1	1	1	2	-1	-1	-1	-1	-1	-1
10. Walsura oxycarpa	2	2	2	1	2	1	1	2	1	1	1	2	1	2	3	3	1	2
11. Walsura poilanei	2	2	3	1	1	1	1	1	1	1	1	2	-1	-1	-1	-1	-1	-1
12. Walsura pinnata	2	2	3	1	1	2	1	1	1	1	1	2	2	2	3	3	1	2
13. Walsura pachycaulon	1	2	3	1	1	1	1	1	2	1	1	2	2	2	3	3	1	2
14. Walsura sarawakensis	1	2	3	1	1	1	1	1	1	1	1	2	2	2	3	3	1	2
15. Walsura monophylla	4	2	3	1	1	1	1	1	1	1	1	2	1	2	3	3	1	2
16. Pseudoclausena chrysogyne	1	1	1	2	3	1	1	1	1	2	2	3	3	2	3	3	1	3
OUTGROUP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

FIG. 7.2 Data-matrix for cladistic analysis of the species of Heynea, Walsura and Pseudoclausena using CAFCA program (Zandee, 1987).

character is therefore difficult, with perhaps both two-locular and four-five-locular being advanced. However, since the three-locular state occurs more often in Trichilia species, this is taken as primitive. This decision might be backed up by the fact that, in the fruit, species of Trichilia, Heynea and Walsura have well defined specialised septa separating the locules but in Pseudoclausena there is no septum but only undifferentiated parenchymatous tissue separating the seeds.

The fruit anatomy of ten species of Trichilia (including both Old and New World species) has been investigated (see Chapter 4). All species except P.chrysogyne have a sclerenchymatous endocarp and this is either thin relative to the whole thickness of the pericarp (i.e. <1/4), as in Trichilia species, or thick (i.e. >1/4). All Trichilia species have a loculicidally dehiscent capsule where the endocarp is broken at the sutures with a complex dehiscence apparatus (see Chapter 4 for definitions). No species of Trichilia is known to have trichomes on the inner surface of the pericarp but all species seem to have a brightly coloured aril. Having established character states and polarities, the data were put into a data-matrix, FIG. 7.2.

ANALYSIS

The computer program chosen to run the analysis was CAFCA-pc. vers. 1.9.6 (Zandee, 1989). This choice was partly because it seemed much easier to use (by a taxonomist with little knowledge of computing) than most other modern programs e.g. HENNIG 86 (Farris, 1988) or PAUP (Swofford, 1985), and partly

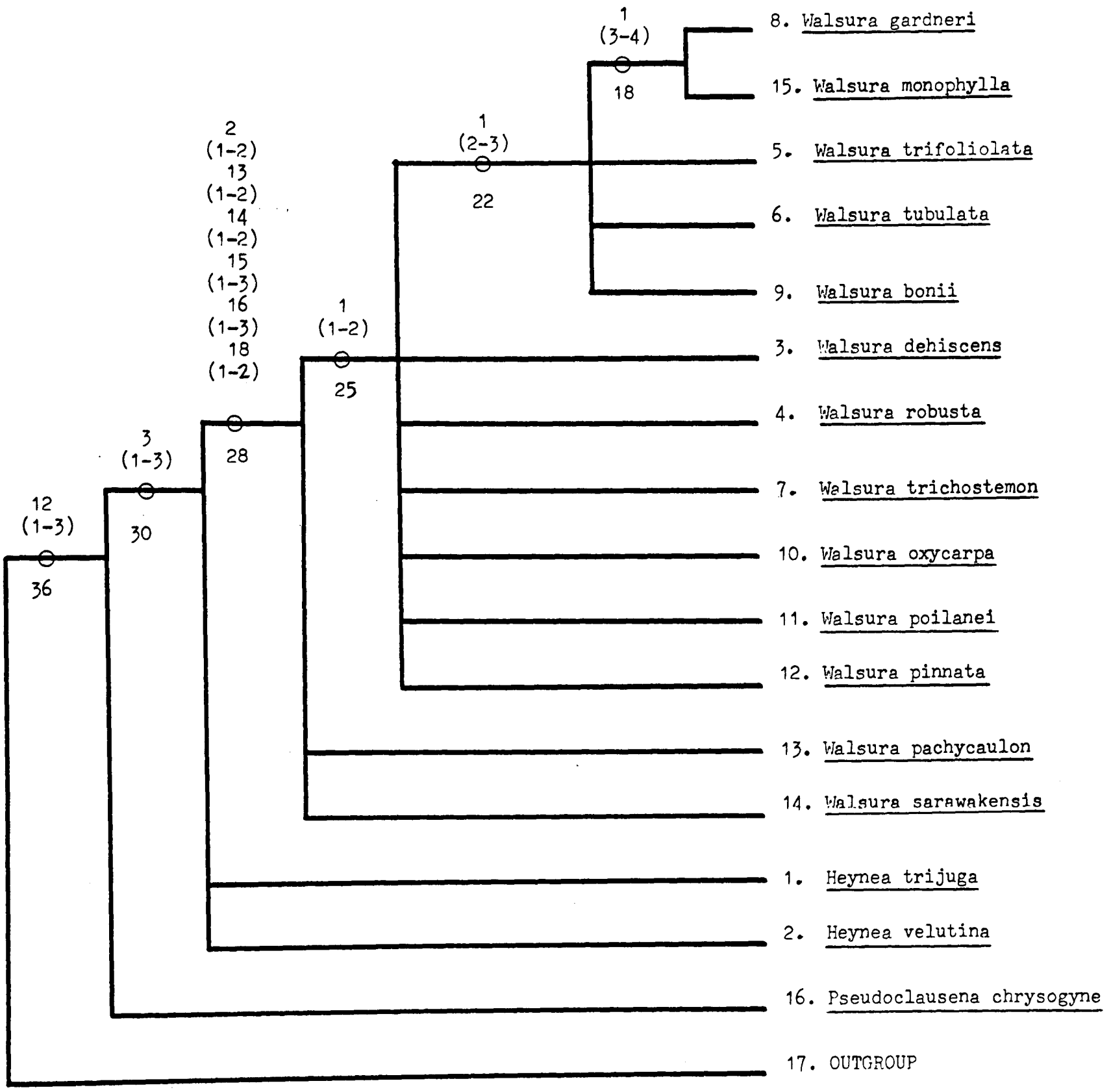

FIG. 7.3 Cladogram generated by cladistic analysis of the species of Heynea, Walsura and Pseudoclausena, using CAFCA program (Zandee, 1989). Each cladon (rooted at "o") is numbered (below the "o") as in the analysis and the characters and their state changes are given (above the "o").

because it was demonstrated to me (by Peter van Weltzen and Rob Geesink) at Leiden.

Characters were not weighted in this analysis and all columns were considered equal. However, prior to analysis, CAFCA converts all multi-state characters into binary series and these sub-columns are then considered co-equal. From the eighteen character matrix entered here, forty-six binary coded columns were generated. This effectively weights certain characters (see Discussion, below). Missing values, indicated by "-1" in the multi-state data matrix, are treated by CAFCA as if all possible outcomes are equally likely and it thus represents these in the calculations and resultant cladograms.

The building blocks for possible cladograms (clada; singular: cladon) were derived by the definition of partial monothetic sets of terminal taxa and their corresponding character states. Partial monothetic sets are defined by sets of unique character states. All clada in any one cladogram either exclude or include one another but they do not overlap, thus constituting a set of compatible clada or clique. The program only retains those cladograms constructed from the largest of these cliques. Six different options for cladogram selection criteria are available with CAFCA. "Maximum redundancy index" was chosen, which is an elaborate form of calculating parsimony.

From this analysis, only one cladogram was retained by the program (FIG. 7.3) and this has been labelled with cladon numbers and the character states defining each cladon.

DISCUSSION

After the outgroup, distinguished by its 3-locular ovary (character 12), the first branching is between *Pseudoclausena* and everything else, on the basis of its having the most primitive leaf epidermis type (character 3, state 1). This is particularly interesting since this genus exhibits completely advanced characters (N.B. not, strictly speaking, character states since the characters are completely absent from the genus) in the fruit. A study of the data matrix reveals, however, that in most other characters it is not especially advanced. Also most interesting is that it branches before the *Heynea* species. This seems to emphasise its difference from the *Walsura* species (see Chapter 6). The *Heynea* species come out as sister branches of the *Walsura* cladon branch. *Heynea* is the more primitive but this is to be expected given the nature of the complex described in Chapter 1. The most important things to note are that *Heynea* is segregated as distinct from *Walsura* by a number of characters (see below), but it is not so primitive (i.e. *Trichilia*-like) as *Pseudoclausena*.

The *Walsura* cladon is exceptional in having six defining character states, one foliar (i.e. 2, swollen rachis) and five fruit characters. This would suggest that not only is *Walsura* clearly segregated from both *Heynea* and *Pseudoclausena* but it is also a more tightly-knit genus, now that *W.chrysogyne* *et al.* have been removed to the new genus. Internal division of the genus seems to conflict, however, with the conclusions of the previous chapter. It is based entirely on leaflet number with the two 7-foliolate species branching first (as most primitive), then the six 5-foliolate, three 3-foliolate and two 1-foliolate species respectively.

Walsura Group 2 (see previous chapter) is drastically split up and W.gardneri is grouped with W.monophylla, even though they differ considerably in other characters and whilst the former has a very restricted distribution in Sri Lanka the latter is found only in the Philippines. W.dehiscens, peculiar with its dehiscent fruit and very short inflorescence, is included within the 5-foliolate group, as is W.robusta with its free filaments and pubescent inner pericarp surface. Failure to segregate even the very well defined sections of the genus is rather worrying.

Assuming, then, that the cladogram is giving a false picture of relationships within Walsura, how can this be explained ? Two reasons are suggested. Firstly, the leaflet number is the only character with four states, which in the binary data matrix gives four co-equal binary characters. Leaflet number is therefore effectively biased, perhaps rather more than it should be. Secondly, the program did not have sufficient data to produce natural groupings of species. Had time allowed, many more characters might have been included (with the associated problems of polarisation) and an analysis might have been run on the species of Walsura alone incorporating the data from the species descriptions in the previous chapter.

One has to constantly assess cladograms, however, against ones intuitive ideas of phylogeny having considered many characters from specimens across the ranges of each species. Unless massive quantities of data are put through the program, the analysis seems to be constantly at risk, e.g. from being 'fooled' by evolutionary convergence or parallelism as in grouping

the two unifoliolate Walsura species together. So, considering the time and effort involved in gathering such large quantities of data into a polarised data matrix, the question arises of whether the resultant cladogram(s) are worth it. A cladogram may be thought-provoking, especially in an analysis of a species complex, but it must be treated with care, and must not be considered a substitute for conventional methods of constructing phylogenies.

Abandoning the classification of Walsura species suggested by the cladogram does not mean that the classification at generic level must be similarly rejected since, by definition, differences between genera are going to be greater than those between species. Also, most of the eighteen characters in the data matrix can be individually employed to segregate the three genera. The segregation of the genera seems fairly sound, therefore, and the branching of Pseudoclausena before Heynea is a feature which must be considered further (see next chapter).

CHAPTER 8

DISCUSSION

Introduction

In Chapter 1, the problem of generic delimitation in the Trichilia - Heynea - Walsura complex was introduced. In the course of the present study, certain isoenzymes have been investigated in these three genera (Chapter 5); leaf surface (Chapter 2), pollen (Chapter 3) and fruit (Chapter 4) features have been investigated across the tribe and the species of Walsura have been taxonomically revised. Also, within Chapter 6, the new monotypic genus Pseudoclausena (based on Walsura chrysogyne) was described. These new data will now be used to augment the existing literature in a reconsideration of generic delimitation within the Trichilieae.

The status of Heynea, Walsura and Pseudoclausena

1. Bentvelzen's minor characters.

Bentvelzen (1962) refers to a "curious" wood anatomical character, i.e. the occurrence of vessel elements in the pith of the twigs of Walsura and their absence in Trichilia and Heynea. He says that Endert (1928), in his key to

vegetative material from Indonesia, also noted this feature in Walsura. However, Endert remarks not on the occurrence of vessel elements in the pith of the twig but on vascular bundles in the petioles. This casts some suspicion on this "curious" character. However, upon investigation of the twigs of T.emetica, T.dregeana, H.trijuga and W.tubulata (available as fresh material at Oxford) and of P.chrysogyne (dried herbarium material only: Wenzel 1621 and Prawiroatmodjo & Soewoko 1691), vessels were indeed found in the pith of the Walsura but not in the others. They were sparse and were scattered through the pith but were structurally very similar to those in the sapwood. Bentvelzen's character is therefore accepted, but tentatively due to the few species and specimens investigated. This curious feature deserves further investigation but time did not allow here.

He then states that Heynea has bitter substances throughout its tissues (leaf, bark and seed) and that he found bitter leaves in some species of Trichilia but in no species of Walsura. He does not specify whether he tasted dried or fresh leaf material. Dried leaves have not been sampled here, since many herbarium specimens have been treated with poisons at some stage, but fresh leaves of the above four species plus (in the field) leaves of W.trifoliolata, W.robusta, W.gardneri, W.dehiscens, W.pinnata ("pinnata" and "villamilii"), W. sp. A. and H.trijuga have been tasted by the author. All were bitter to some degree but Heynea could not be said to have been exceptionally so. It is interesting to turn back now to Roxburgh's Flora Indica (1832) account of Heynea, where he remarked, of H.trijuga:

"The bark, leaves and tender parts possess a considerable share of a peculiar bitter taste; and the cold infusion therof, with the addition of a little sulphate of iron, becomes black; two principles very generally found amongst the plants of this natural order, which grow in India".

Ferrous sulphate yielding a black precipitate is a standard test for the presence of tannin (Johansen, 1940), which would account for the bitter taste reported. Tannin occurs, in various tissues, across the family, and certainly in all species of Walsura. Therefore, even if tannin levels could be quantified scientifically, this would still be a poor character.

Bentvelzen's third and final character was the occurrence of glands on the undersurface of the leaf in Heynea and in one American species of Trichilia (un-named), but not at all in Walsura. Such glands in fact occur in most of the Walsura species (see Chapter 6) and it is unfortunate that Bentvelzen overlooked them when examining material at the Rijksherbarium. Leaf glands seem to be common in Walsura and Heynea and absent (or, at least, have not been seen in this study) in Trichilia.

2. Leaf rachis

One of the most obvious characters for distinguishing Heynea in the herbarium is that, in dried specimens, the nodes of the leaf rachis (i.e. points of insertion of the petiolules) are slightly collapsed transversely, giving a series of constrictions along the rachis. In Walsura, these nodes

are usually swollen slightly (see Chapter 6) and in Trichilia and Pseudoclausena there is no modification of rachis thickness.

3. Leaf surface

Papillae occur in all specimens of Heynea and Walsura species, but not at all in Pseudoclausena or Trichilia. Whereas trichomes in Heynea are very similar to those found in Trichilia, such hairs also occur in the 'pinnata' group species of Walsura (see Chapter 6) and so this is not a good character to distinguish Heynea. Pseudoclausena is unique within the tribe in having multicellular simple hairs. Subsidiary cell arrangement is probably linked to the presence or absence of papillae and emphasises the Walsura - Heynea affinity, Pseudoclausena being exceptional again.

Glandular bodies on the undersurface of the leaf (see '1' above) are common in Walsura and Heynea but rare in Trichilia and absent from Pseudoclausena. Overall therefore, in leaf surface characters, Heynea seems to show considerably greater affinity with Walsura than with Trichilia; Pseudoclausena is perhaps most similar to Trichilia.

4. Wood anatomy

Pennington (1965) and Pennington & Styles (1975) give brief descriptions of wood anatomy for each genus in the tribe but, since they maintain Bentvelzen's reduction, give no separate data for Heynea. It is not

possible to say how much of the variation in their descriptions of Trichilia is due to Heynea. Datta & Samanta (1983) examined wood anatomy of H.trijuga, W.trifoliolata, W.robusta, W.tubulata and P.chrysogyne, but of no species of Trichilia. They segregated Heynea since it has vessels of considerably greater diameter and fibres of greater length than any of the other species. They did not segregate P.chrysogyne but from their data it agrees with the other Walsura species in most characters except that it has a (vessel) pore density (per square millimetre) considerably greater than that of any of the other species (P.chrysogyne = 308; W.trifoliolata = 154; W.tubulata = 81; W.robusta = 62; H.trijuga = 25).

M. Claude Malassé (pers. comm.) of the Centre Technique Forestier Tropical (Nogent-Sur-Marne, France), has investigated the wood anatomy (particularly the pores, rays and fibres) of 24 species of Trichilia (New and Old world), two specimens of H.trijuga (from the Oxford Forestry Institute Wood Collection), four species of Walsura (W.trifoliolata, W.robusta, W.trichostemon & W.pinnata) and twig material of W.dehiscens (T.Clark 78, at FHO). He concluded that although both Trichilia and Walsura are very heterogenous genera in terms of wood anatomical characters, they and Heynea are all quite distinct.

5. Floral structure

The flower in Heynea (H.trijuga & H.velutina) has an annular disk and an androecium tubular for 1/4-1/3 of its length, each filament having a

shortly bifid apex. It could easily be accommodated within either the type section of Trichilia or that of Walsura. Only c.30% of Trichilia species possess a disk (see Chapter 7) but the structure does occur in other genera of the tribe and does not suggest any special affinity with Walsura, where all species possess an annular disk. Floral structure therefore seems of little use in segregating these genera.

Pseudoclausena differs from the other genera in possessing a 4- to 5-locular ovary and from Heynea and Walsura in lacking a disk.

N.B. Bentvelzen (1962) gives English descriptions of his newly reduced species and states that T.connaroides has 5 petals and sepals and 10 filaments and anthers. The plant of this species under cultivation at Oxford [= T.Clark 94 at FHO] has produced a small proportion of flowers with 4/8 parts amongst those with 5/10 parts, on the same inflorescence.

6. Palynology

Whilst there are few good characters available from pollen morphology in the Trichilieae, Heynea seems to show greatest affinity with the Trichilia species, even given the considerable variation within Walsura. Pseudoclausena is significantly different from Walsura, Heynea and Trichilia and indeed shows greater affinity with C. odessa.

7. Fruit anatomy

There is a strong similarity between the complex dehiscence apparatus of Heynea and that of Trichilia, particularly the African species. However, the thin layer of sclereid tissue enveloping the seed is unknown in Trichilia, as is the simple aperture of this layer. Some species of Walsura (W.trifoliolata, W.robusta & W.dehiscens) do have such a sclereid layer but here it is also overlying a fibrous layer. Other species of Walsura (in the 'pinnata' group) only have the fibrous layer. Only W.dehiscens has a suture in the sclerenchyma layers but this is above the point of attachment of the septum, not above the seed as in Heynea and Trichilia. In fruit anatomy then, Heynea seems intermediate between the other two genera, but all three are quite distinct. The trend away from Trichilia-type features is continued within Walsura with the complete loss of dehiscence and sclereids. In fruit structure, Pseudoclausena is significantly different from the rest of the tribe in completely lacking sclerenchyma.

8. Seed anatomy

Cheek (1989a) investigated seed anatomy across the Meliaceae, including that of T.emetica, T.monadelphia, T.capitata, H.trijuga, W.dehiscens (referred to as 'W.rhomboidea'), W.pinnata and P.chrysogyne. He concludes that Heynea and Walsura seem much more closely related to each other than to any other genus in the tribe. They are united by the possession of a pre-raphe,

funicular pre-raphe aril and an elongated hilum. None of these characters was observed in the Trichilia species. He went on to speculate that the common ancestor of Walsura/Heynea and Trichilia is very distant and that much parallel evolution has occurred. P. chrysogyne differs from the species of Walsura investigated in being unitegmic (possibly chalazal) and this character has almost certainly arisen independently of the same state in the African Trichilia species.

9. Cytology

The following chromosome counts have been published:

SPECIES	2n	REFERENCE
W.trifoliolata	28	Ghosh (1961 & 1968).
H.trijuga	28	Mehra & Sareen (1969); Rao (1969); Khosla & Styles (1975).
T.emetica	50	Styles & Vosa (1971); Khosla & Styles (1975).
T.dregeana	360	Styles & Vosa (1971).
T.havanensis	92	Khosla & Styles (1975).
T.heudelotii	50	Mangenot (1957).
T.lanata	50	Mangenot (1957).
T.odorata	92	Minfray (1963).
T.pieureana	50	Mangenot (1957).
T.rubescens	46	Styles & Vosa (1971).

Khosla & Styles (1975) observed that the karyomorphology of W.trifoliolata resembles that of H.trijuga in a number of characteristics i.e. basic chromosome number, centromeric position and occurrence of a long sub-median pair of chromosomes with secondary constrictions. They concluded that both have evolved from a similar stock and that structural alterations in chromosomes must have helped in the diversification of these genera; that

their close cytological similarity indicates wide separation from Trichilia; and that, on cytological grounds, Heynea should be maintained as a genus distinct from Trichilia.

10. Chemotaxonomy

Taylor (1981; 1984) has systematically investigated degraded triterpenes of the sort known as limonoids in most genera of the Meliaceae, using gas-liquid chromatography. Within the Trichilieae, species of Trichilia (many species but particularly those from Africa), Heynea, Walsura (only W.trifoliolata), Ekebergia (E.capensis, E.senegalensis & E.pterophylla) and Pseudobersama have been studied. Rather than suggesting affinity between Heynea and either Walsura or Trichilia, he concluded that the greatest similarities are with Ekebergia. W.trifoliolata has an unusual set of fairly simple limonoids of no particular affinity with that in any other genus.

The isoenzyme study made here seems to be the only other application of chemosystematics to the Heynea problem. Although there are certain similarities between Heynea and Trichilia, in some cases Walsura demonstrates greater affinity than Heynea with the larger genus. However, the two Trichilia species studied clearly belong to a group distinct from either Heynea or Walsura. The affinities shown by Heynea in those enzymes studied are more towards Walsura but the bias is not great and, if it shows

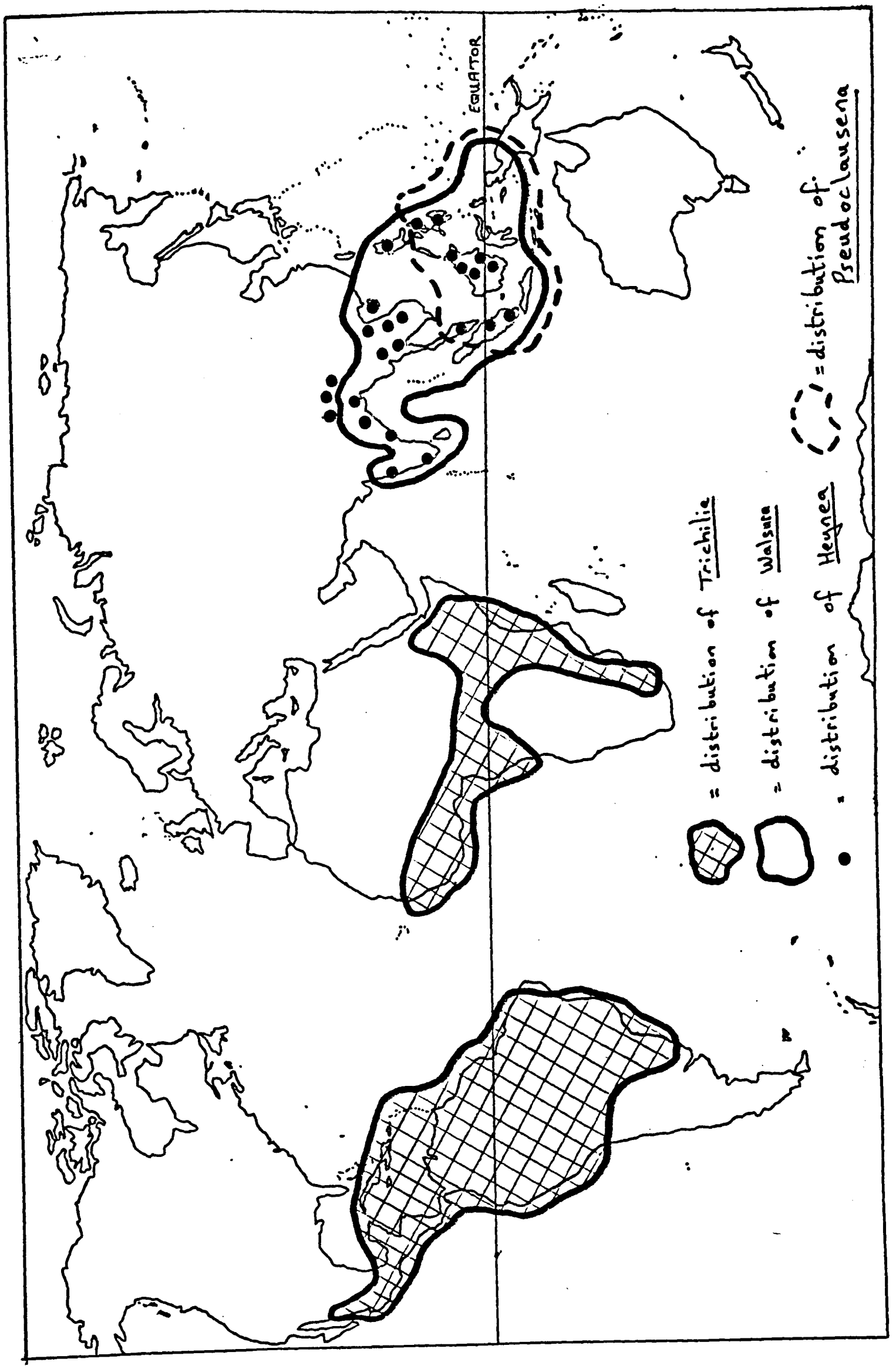

FIG. 8.1 Distributions of the genera Trichilia, Heynea, Walsura & Pseudoclausena.

anything, it emphasises just how phylogenetically close these three genera are to each other.

11. Geographical distribution

The modern distributions of Trichilia (taken from data in De Wilde, 1968 and Pennington & Styles, 1981), Heynea (taken from data on specimens at FHO and K) and Walsura and Pseudoclausena (taken from the revision in Chapter 6) are illustrated in FIG. 8.1. Trichilia occurs in Africa and America and Heynea and Walsura in the Indo-Malesian region. Pseudoclausena occurs at the eastern end of the distribution of Walsura, in the Malesian region. There is, therefore, a clear geographical separation between Trichilia and the three other genera.

CHARACTER	Trichilia	Heynea	Walsura	Pseudoclausena
1. LEAF RACHIS NODES SWOLLEN	NO	NO	YES	NO
2. VESSELS IN PITH OF TWIGS	NO	NO	YES	NO
3. WOOD VESSEL PORE DENSITY (/mm^2)	?	25	62 to 154	308
4. ABAXIAL LEAF SURFACE PAPILLATE	NO	YES	YES	NO
5. GLANDULAR BODIES ON ABAXIAL LEAF SURFACE	RARE	YES	YES	NO
6. MULTICELLULAR SIMPLE LEAF TRICHOMES	NO	NO	NO	YES
7. POLLEN SIZE (Polar axis, um)	20 to 56	30 to 45	30 to 50	22 to 26
8. DISK IN FLOWER	c. 30 % of species	YES	YES	NO
9. NUMBER OF LOCULES IN OVARY	(2) 3 (4)	2	2	4 or 5
10. TYPE OF FRUIT	Loculicidally dehiscent capsule.	Loculicidally dehiscent capsule.	Berry or (one species) septicidally dehisc. cap.	Berry
11. PERICARP SCLERENCHYMA	Sclereids only or sclereids & fibres in a few spp.	Sclereids only	Sclereids & fibres or fibres only.	Absent
12. CHROMOSOME No. (2n)	46 .....360 (T.rubescens) (T.dregeana)	28 (H.trijuga)	28 (W.trifoliolata)	?

FIG. 8.2 Summary of taxonomic characters (excluding seed and chemical characters) useful at generic level in Trichilia, Heynea, Walsura & Pseudoclausena.

12. Conclusions

The characters discussed above are summarised in FIG. 8.2, with the exception of the isoenzyme data and Martin Cheek's (1989) seed anatomy findings which are difficult to tabulate. Most of these characters suggest that Heynea has a far greater affinity with Walsura than with Trichilia, although these three genera clearly constitute a closely interrelated complex. In discussing the seed anatomical evidence, Cheek concluded that "Heynea trijuga Roxb. ex Sims is much more closely related to Walsura than to Trichilia yet quite distinct from the species of Walsura studied," He had studied W.pinnata in detail and W.dehiscens & W.chrysogyne (= P. chrysogyne) briefly. He further concluded that his findings suggested that Heynea be maintained as a distinct genus.

In the light of the evidence discussed in this thesis, to support Bentvelzen's (1962) reduction but maintain Walsura as a distinct genus would be quite unsatisfactory, and the geographic distributions of the genera (FIG. 8.1) seem to add weight to this conclusion.

If Walsura were reduced to Heynea then the augmented genus could easily be maintained against Trichilia on the basis of leaf surface, wood, cytological and chemical characters. However, even with the variation due to W.chrysogyne et al. removed (to Pseudoclausena), Walsura can still be segregated from Heynea on the basis of the former's swollen leaf nodes, its quite different fruit (a berry or septicidally dehiscent capsule) (see FIG. 8.2 & cladogram in FIG. 7.3), and a number of small pollen and chemical characters.

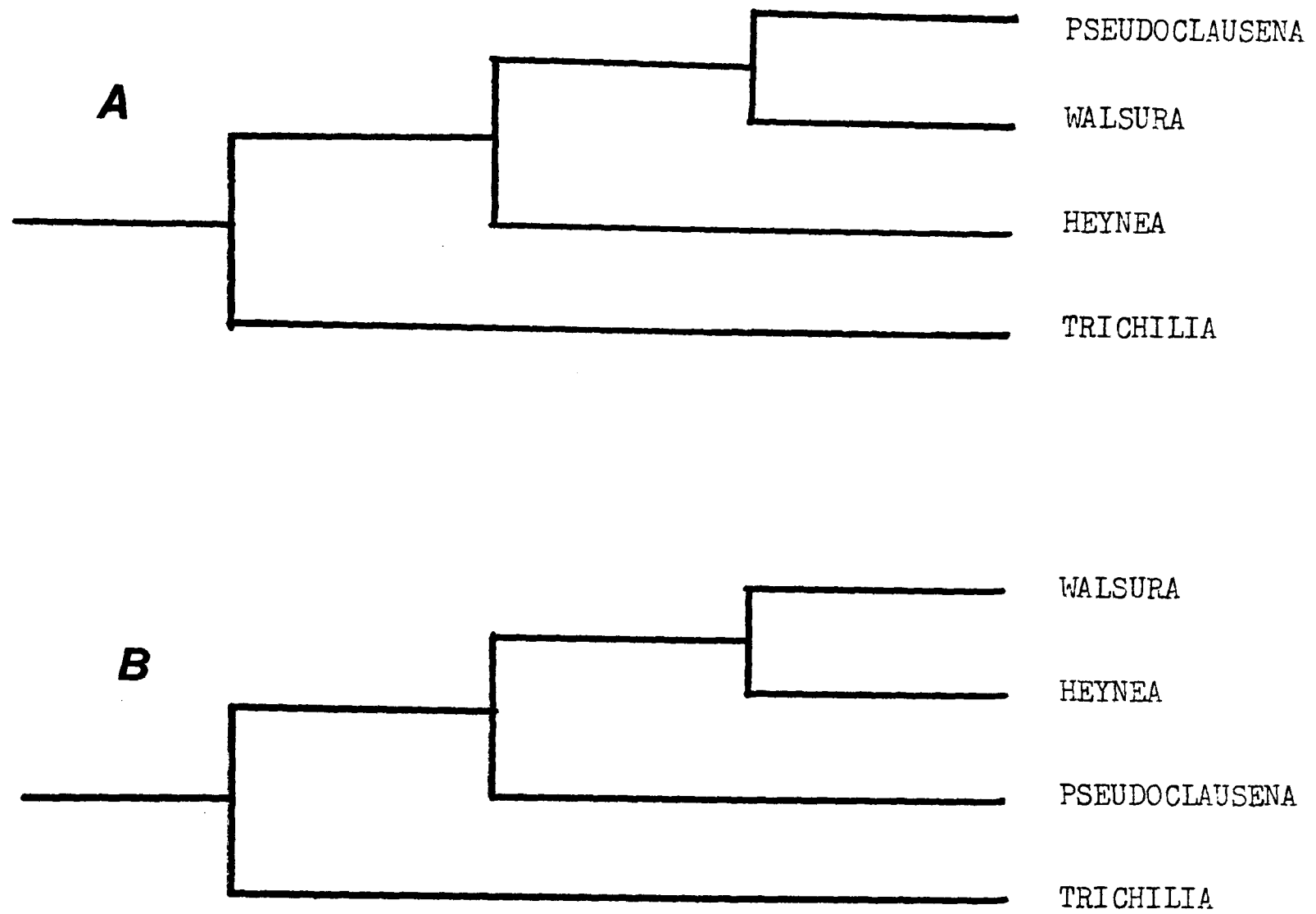

FIG. 8.3 Three possible phylogenies for the genera Trichilia, Heynea, Walsura and Pseudoclausena.

The similarity in morphology and anatomy between Heynea/Walsura and Trichilia is considered to be due largely to parallel evolution following a schism between the two in the distant past and this is supported by several small differences in isoenzyme banding patterns. It is therefore proposed to reinstate Heynea as a distinct genus in the alliance of Walsura with both of them more distantly related to Trichilia.

The case supporting Pseudoclausena as a distinct genus is, in comparison with that for Heynea, rather stronger. Multicellular leaf trichomes and a fruit completely lacking sclerenchyma (and an aril) segregate it from all the other three genera. The absence of a floral disk, the 4- to 5-locular ovary and the asymmetric fruit segregate it from Walsura and Heynea specifically (see Chapter 6). The absence of abaxial leaflet papillae in Pseudoclausena has not been employed as a generic character since both papillate and non-papillate occur within the genus Ekebergia. (N.B. The characters in FIG. 8.2 are not those proposed to define the genera.)

On the basis of these conclusions, three phylogenies are suggested (FIG. 8.3: A, B & C). Pseudoclausena could be considered a highly advanced branch from Walsura but the differences between the two genera are considerable. Also, there are several similarities with Trichilia which are not easily explained away by evolutionary convergence e.g. a large leaflet number but absence of leaf rachis node swellings, absence of leaf papillae and absence of a floral disk. Phylogeny "A" is, therefore, rejected.

Walsura and Heynea have much in common but demonstrate transition series in certain characters starting in Trichilia, e.g. the transition of the endocarp and dehiscence apparatus from Trichilia, through Heynea to Walsura. This further supports the "B" or "C" phylogenies but to choose between them is extremely difficult. "B" was the one generated by the cladistic analysis (FIG. 7.3) but, since Pseudoclausena is so different from both Walsura and Heynea, it is perhaps the product of a much earlier (or at least a separate) schism from Trichilia, as in phylogeny "C". If fresh material from a wide range of species could be gathered together, further chemotaxonomic investigation would probably throw much more light on this problem.

There is also a glaring paucity of cytological data for Walsura species, there being chromosome counts (and other basic cytological observations) for W.trifoliolata only (see above). Alas, it has not yet been possible to make chromosome counts for the two plants of W.tubulata in cultivation in Oxford. Counts for sect. Walsura Group 2 species would be most useful and if W.dehiscens (sect. Ruswala) were found to be different from the other species of the genus, this would add weight to its being placed in sect. III, i.e. furthest from Heynea (see FIG. 4.34 & Chapter 6, "Variation within the genera"). On the basis of its morphology and anatomy, the chromosome count of Pseudoclausena chrysogyne is extremely difficult to predict and, perhaps, should be given priority in cytological investigations, especially as it is such a widely occuring species.

A key is given (FIG. 8.4) for the identification of these four genera.

1. Leaf with multicellular simple trichomes;
fruit completely lacking sclerenchyma.....PSEUDOCLAUSENA

Leaf with unicellular simple or multicellular
2 to many-armed trichomes;
fruit with a sclerenchymatous endocarp.....2

2. Leaf rachis nodes slightly swollen (*in vivo* & *in sicco*);
fruit a berry or septicidally dehiscent capsule.....WALSURA

Leaf rachis nodes not swollen (*in vivo* or *in sicco*);
fruit a loculicidally dehiscent capsule.....3

3. Leaf rachis nodes transversally compressed (*in sicco*);
ovary 2-locular; capsule with at least one simple
dehiscence apparatus (see Chapter 4 for definition);
Indo-Malesia.....HEYNEA

Leaf rachis nodes not compressed (*in sicco*);
ovary (2-)3(-4)-locular; capsule with complex dehiscence
apparatus only (see Chapter 4 for definition);
Africa & America.....TRICHILIA

FIG. 8.4 Key to the genera Pseudoclausena, Walsura, Heynea and Trichilia.

The status of the other genera of Trichilieae.

The other satellite genera of Trichilia, with the possible exception of Pseudobersama (see below), are well-defined by the characters given by Pennington & Styles (1975) and, on the basis of these characters, there is little or no controversy over the status of any genus. The present study, far from casting doubt on these generic concepts, supports them (particularly in fruit characters) and also (particularly in leaf surface characters) suggests possible affinities between the genera. These affinities can then be used as the basis of phylogenetic speculation but they do not provide a sufficient basis for the reduction of any of the genera.

Cipadessa is similar in floral structure, pollen morphology (see Chapter 3) and leaf surface features (see Chapter 2) to Pseudoclausena but the fruit is significantly different to maintain the genus. Ekebergia and the Walsura-Heynea complex have certain common features. Leaf papillae are found only in these genera and Taylor (1984) remarks on the similarities between Heynea and Ekebergia in limonoid composition. Ekebergia differs considerably from both Heynea and Walsura, however, in fruit structure. Of the other genera of the Trichilieae, the only one about which there is some doubt as to its status is Pseudobersama. It seems to show most affinity with the closely related species-pair Trichilia capitata Klotzsch and T.lovettii Cheek (see Cheek, 1989b) and Cheek points out several shared characters, mainly in seed anatomy. The fruit of the smaller genus, whilst possessing the same basic layers and sclerenchyma 'wings', is different,

however, in many ways from anything observed in Trichilia. The sclerenchyma wings are much thicker (proportional to the pericarp as a whole), and the entire mesocarp and exocarp tissue is heavily laden with tannin to give a very thick and tough capsule, both of which are conditions unknown in Trichilia. This, together with the possession of superposed seeds and a normally 5-locular capsule (compared with collateral seeds and a normally 3-locular state in Trichilia), and in the absence of any other intermediates, are considered to be sufficient grounds to maintain Pseudobersama as a genus distinct from Trichilia.

The way forward

Comment has been made, above, on the paucity of cytological data for the Asian Trichilieae species. This state of affairs is, alas, not limited to this tribe. Chromosome counts for Aglaia spp. (Aglaieae) and Chisocheton and Dysoxylum spp. (Guareeae) are also few (Mabberley, 1979; B.T. Styles pers. comm.; Simon Bennett pers. comm.). The principal reasons for this seem to be a lack of cytological work in the countries where the species actually occur and the short viability of the seeds of many of these species. Seeds of various Walsura species were brought (in hand lugguage) or sent (air mail) back to Oxford (in 1987) for isoenzyme extraction but most were dead within two weeks of harvesting. Many chromosome counts have been made for Meliaceae species occurring in India because of the long established cytological interests in that country, but counts from other countries of south and south-east Asia are very sparse. There is then a

great need for cytological work actually within the countries where the species are growing, perhaps at botanic gardens or other centres where living collections could be built up. In Malaysia, for instance, there are well-equipped research laboratories and germination beds within the Forestry Department institutes at Kepong (Malay Peninsula), Kuching (Sarawak) and Sandakan (Sabah), and directors of research at these places seem keen to co-operate in joint projects with British workers.

Leaf surface studies (Chapter 2) have proven most interesting and useful from a taxonomic viewpoint, and obviously there is also great potential here for a widening of the study to consider ecological factors such as micro-climates and plant-animal interactions at the leaf surface. Investigations of leaf surfaces might profitably be applied to other tribes of the Meliaceae as well, especially since an SEM study of herbarium material is a fairly straightforward study to make.

Pollen morphology does not seem to be of great use, taxonomically, in the Trichilieae and this bears out Pennington's (1965) findings for the family as a whole.

Fruit anatomy in the Trichilieae is, clearly, extremely diverse and has provided many useful taxonomic characters, at the generic and species level. A similar study across a different tribe might prove equally useful. The disposition of sclerenchyma tissue surely merits further investigations in other groups of the family.

Like the cytology, isoenzyme investigations are limited by the availability of fresh material. Limonoids, however, (see Taylor 1981 & 1984), which seem to occur throughout the family, can be extracted from dried material and this is clearly a line of evidence which deserves further investigation.

In addition to tackling particular taxonomic problems, it has been, from the outset, an aim of this thesis to evaluate potential taxonomic characters which have been little or not at all previously studied. Hopefully, the comments made above and in preceeding chapters will suggest lines of investigation which other workers may wish to follow when they are faced with knotty taxonomic problems in this fascinating and important family.

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APPENDIX 1

List of specimens used in the study of leaf surface features.

With the exception of those Ekebergia specimens marked with an asterisk (see Chapter 2), all of the following were studied under SEM and many were studied by light-microscopy, after epidermis isolation, also. c.97% of the specimens are at FHO.

1. TRICHILIA

T.americana	Pennington et al. 10011.
T.bullata	Silva & Rosarió 3845. Amazon.
T.capitata	Chapman 6338. Malawi.
T.capitata	Reach & Smith 10939. Mozambique.
T.catigua	Heringer et al. 4568. Brasil.
T.cipo	Pennington et al. 9971. Amazon.
T.cipo	Prance et al. 24162. Amazon.
T.dregeana	Hoyle 1102. N.Zimbabwe.
T.dregeana	Ross 1270. Natal.
T.dregeana	Styles 206. Uganda.
T.dregeana	Styles 210. Uganda.
T.dregeana	Taloy 306. S.Africa.
T.dregeana	Watkins 297. Tanzania.
T.emetica	Greenway 4695.
T.emetica	Styles 254. Uganda.
T.emetica	Styles 286. Uganda.
T.emetica	Taylor 302. S.Africa.
T.emetica	Thompson 197. Zambia.
T.emetica	White 10415. Natal.
T.gilgiana	Binuyo 41415. Nigeria.
T.gilgiana	Leonard 185. Congo.
T.gilletii	Carlier 244. Congo.
T.glabra	Hartshorn 1395. Costa Rica.
T.havanensis	Steyermark 11054. Venezuela.
T.heudelottii	deWilde. Ivory Coast.
T.lepidota	Steyermark 88275. Venezuela.
T.magnifolia	Santos 912.
T.martineaui	Hall & Abbiw 44172. Ghana.
T.martineaui	Oldeman 719. Ivory Coast.
T.megalantha	Latilo 45948. Nigeria.
T.megalantha	Onochie 38331. Nigeria.
T.micrantha	Rodrigues 6919. Amazon.
T.monadelpha	De Wilde 751. Ivory Coast.
T.ornithothera	Enti 71. Ghana.
T.ornithothera	Enti 487. Ghana.
T.pallida	Jimenez Saa 1269. Venezuela.
T.pallida	Pennington et al. 9970. Brazil.
T.pallida	Pennington & Sarukhan 9434. Mexico.
T.pallida	Prance & Silva 58256. Brazil.
T.pleeana	Steyermark 99843. Venezuela.
T.poeppigii	Gentry 9797. Ecuador.
T.prieureana	Kennedy 2114. Nigeria.
T.prieureana	Latilo & Daramola 28899. Cameroons.
T.priuereana	Styles 14. Uganda.
T.prieureana	Styles 219. Uganda.
T.quadrivalvis	White 3451. N.Zimbabwe.
T.retusa	Hoyle 362. Sudan.
T.retusa	Leonard 762. Congo.

T.retusa	Taylor L9. Nigeria.
T.rubescens	Styles 330. Uganda.
T.rubescens	Testu 4.447.
T.rubra	Schunke 3857. Peru.
T.shrombergkii	Pennington et al. 9988. Brazil.
T.singularis	Silva & Rosarió 3655. Amazon.
T.solitudinis	Berg et al. P18585. Amazon.
T.tessmannii	Evrard 4877. Congo.
T.tessmannii	Leonard 1785. Congo.
T.welwitschii	Liben 3343. Congo.
T.welwitschii	Testu 7318. Gabon.
T.welwitschii	Toka 27. Congo.
T.welwitschii	Vermoesen 2288. Zaire.

2. PSEUDOBERSAMA

P.mossambicensis	Sem Sei S1387. Tanzania.

3. PTERORHACHIS

P.zenkeri	Oxford Botanic Garden cult. Congo origin.

4. WALSURA

W.chrysogyne	SAR 24268. Sarawak.
W.chrysogyne	SAR 26985. Sarawak.
W.chrysogyne	Sundaling 84007. Sabah.
W.chrysogyne	Tan & Wright 27267.
W.dehiscens	SAR 32293. Sarawak.
W.monophylla	Elmer 12903. Palawan.
W.pachycaulon	SAN 30573. Sabah.
W.pinnata	Clark 82. Sabah.
W.pinnata	Elmer 21487. Sabah.
W.pinnata	Frana 79334. Philippines.
W.pinnata	Griffiths s.n.
W.pinnata	Hey et al. 61654. Sabah.
W.pinnata	Kerr 498.
W.pinnata	Luang 21733.
W.pinnata	Mabberley 1660. Sabah.
W.pinnata	Parkinson 1686. Burma.
W.pinnata	Pennington 7815. Selangor.
W.pinnata	SAR 19220. Sarawak.
W.robusta	Sangkhachand 365. Thailand.
W.sarawakensis	Purseglove 5143. Sarawak.
W.sarawakensis	Purseglove 5204. Sarawak.
W.trichostemon	Burma Forest School 10. Burma.
W.trichostemon	Burma Forest School 32. Burma.
W.trichostemon	Helfer 89 Calcutta.
W.trichostemon	Ohn Shwe 5037.
W.trifoliolata	Simpson 9223. Sri Lanka.

5. HEYNEA

H.trijuga	Fedelis 88314. Sabah.
H.trijuga	Saradet 427. Thailand.
H.trijuga	Abas 85695. Sabah.

H.trijuga	Binideh 55798. Sabah.
H.trijuga	Goklin 3404. Sabah.
H.trijuga	Kostermans 5126. Kalimantan.
H.trijuga	Mabberley 1677. Sabah.
H.trijuga	Pennington 7877. Sabah.
H.trijuga	Pennington 7948. Sabah.

6. LEPIDOTRICHILIA

L.volkensii	Hughes 84. Kenya.
L.volkensii	Styles 179. Uganda.

7. MALLEASTRUM

M.obtusifolium	SF 8878.
M.sp.	Hnatiuk s.n.. Aldabra.
M.sp.	Woodell 7403. Aldabra.

8. EKEBERGIA

E.benguelensis	Clements 88. Nyasaland.
"	*Denning 20. Zambia.
"	*Duff 225/37. Zambia.
"	*N.R.G.Herb. 1251. Zambia.
"	*Angus 446. Zambia.
"	*White 2343. Zambia.
"	*Martin 873. Zambia.
"	*Hoyle 111. Zambia.
"	* " 112. Zambia.
"	*White 2114. Zambia.
"	*Holmes H204. Zambia.
"	* " H205. Zambia.
"	*Miller 5659. Zambia.
"	*Fanshawe 1451. Zambia.
"	*Miller D.153. Zambia.
"	*White 3663. Zambia.
"	*Pardy P203/33. Zimbabwe.
"	*White 2946. Zimbabwe.
"	*Palgrave M/23/37. Zimbabwe.
"	*McGregor M/110/37. Zimbabwe.
"	*Pardy P51. Zimbabwe.
"	*de Silva 3339. Angola.
"	*Finlay A141/37. Zimbabwe.
"	*Chapman 888. Malawi.
"	*Banda 875. Malawi.
"	*Chapman 1740. Malawi.
"	*Adlard 43. Malawi.
"	*White 2862. Malawi.
"	*Chapman 2282. Malawi.
"	*Clements 818. Malawi.
"	*Adlard 486. Malawi.
"	*Topham 213. Malawi.
"	*Clements 125. Malawi.
"	*Topham 910. Malawi.
"	*Burtt Davy 21098. Zambia.
"	*Brenan 7854. Zambia.
"	*Miller D153. Zambia.

"	*Holmes 861. Zambia.
"	*Trapnell 7900. Zambia.
E.capensis	Clements 656. Nyasaland.
"	Styles 290. Uganda.
"	Styles 294. Uganda.
"	White 8212. Nigeria.
"	*Chapman 1471. Malawi.
"	*McGregor 32/38. Rhodesia.
"	*Gillibrand 976. Rhodesia.
"	*Greenhow 74/51. Rhodesia.
"	*Goldsmith 83/61. Rhodesia.
"	*Kelly Edwards E47/33. Rhodesia.
"	*Loveridge 1425. Rhodesia.
"	*Angus 3832. Rhodesia.
"	* " 3721. Rhodesia.
"	*Mutimushi JMM178. Mozambique.
"	*Chapman 1215. Mozambique.
"	*White 3399. Mozambique.
"	*Lawton 1459. Zambia.
"	*White 3024. Zambia.
"	*Brenan 7735. Zambia.
"	*Angus 1673. Zambia.
"	*Lawton 1475. Zambia.
"	*Fanshaw 4184. Zambia.
"	*Robson 636. Zambia.
"	*Stevenson 86/30. Zambia.
"	*White 3133. Zambia.
"	*Guy 98851. Zambia.
"	*Lawton 1459. Zambia.
"	*Angus 471. Zambia.
"	*Lawton 779. Zambia.
"	*Brenan 8079. Zambia.
"	*Angus 1774. Zambia.
"	*Burtt Davy 20823. Zambia.
"	*Greenway & Trapnell 5730. Zambia.
"	*Rosevear s.n. Gambia.
"	*Letouzey 3546. Cameroun.
"	*White 8327. Nigeria.
"	*White 8146. Nigeria.
"	*Mitchell A98/29. Nigeria.
"	*Kennedy 2973. Nigeria.
"	*White 8212. Nigeria.
"	*FHI 57539. Nigeria.
"	*White 8146. Nigeria.
"	*Uzoching 18/71. Nigeria.
"	*UNH A29/71. Nigeria.
"	*Fairbairn 728T. Kenya.
"	*Wimbush 1116. Kenya.
"	*Hockliffe 34. Kenya.
"	*Gardner 380. Kenya
"	*Sem Sei S945. Kenya.
"	*F.H. 2048. Tanzania.
"	*Pitt 537. Tanzania.
"	*Greenway 5801. Tanzania.
"	*Pitt-Schenkel 352. Tanzania.
"	*Smith 925. Tanzania.
"	*Sem Sei 1955. Tanzania.
"	*F.H. 709. Tanzania.
"	*Pitt-Schenkel 261. Tanzania.
"	*Ross 590. Tanzania.

" *Stolz 1582. Tanzania.
" *Greenway 7293. Uganda.
" *Thomas Th.4134. Uganda.
" *Eggeling 1959. Uganda.
" *Eggeling 284. Uganda.
" *S.Paulo 586. Uganda.
" *St.Clair Thompson E5244. Uganda.
" *Chandler NE0133. Uganda.
" *Eggeling FD 1565. Uganda.
" *Gibson 2/HA. Kenya.
" *Jarrett 151. Kenya.
" *White 8291. Nigeria.
" *White 8272. Nigeria.
" *White 8146. Nigeria.
" *FHI 36904. Nigeria.
" *White 8212. Nigeria.
" *White 8327. Nigeria.
" *Chapman 2882. Nigeria.
" *McGregor 392. Nigeria.
" *Fox 78. Sierra Leone.
" *White 8853. Nigeria.
" *White 8146. Nigeria.
" *FHI 55688. Nigeria.
" *Pierlot 534. Zaire.
" *Stevens 8379. Cape.
" *Stevens 8380. Cape.
" *White 10527. Natal.
" *Edwards 1531. Natal.
" *Edwards 1339. Natal.
" *Miller 8/73. Swaziland.
" *White 10188. Transvaal.
" *White 10156. Transvaal.
" *Codd 4298. Transvaal.
" *Thorncroft 429. Transvaal.
" *Codd 4471. Transvaal.
" *Taylor 303. Transvaal.
" * " 304. Transvaal.
" *Matthews 91. Transvaal.
" *Matthews 92. Transvaal.
" * " 93. Transvaal.
" *Codd 6690. Transvaal.
" *Thorncroft 1066. Transvaal.
" *Scheepers 139. Transvaal.
" *Renny 64. Transvaal.
" *Chapman 1788. Malawi.
" *Aslard 529. Malawi.
" *Chapman 1713. Malawi.
" *Marner 40. Malawi.
" *Patel & Tawakali 1017. Malawi.
" *Chapman 6290. Malawi.
" *Chapman 5913. Malawi.
" * " 6086. Malawi.
" * " 6178. Malawi.
" * " 6156. Malawi.
" * " 1792. Malawi.
" * " 159. Malawi.
" * " 279. Malawi.
" * " 2209. Malawi.
" * " 2304. Malawi.
" * " 1471. Malawi.

"	* " 965. Malawi.
"	*Topham 137. Malawi
"	*Patel & Tawakali 6221. Malawi.
"	*Clements 656. Malawi.
"	*Robson 542. Malawi.
"	*Townsend 66. Malawi.
"	*Burtt Davy 2107. Malawi.
"	*Clements 85. Malawi.
"	* " 662. Malawi.
"	*Jeke 75. Malawi.
"	*Lewis 13. Malawi.
"	*Chapman 6156. Malawi.
E.senegalensis	Eggeling 3504. Uganda.
"	*Dawkins D525. Uganda.
"	*Chandler 556. Uganda.
"	*Hoyle 589. Sudan.
"	*Zarvia 2895. Nigeria.
"	*Taylor A119/37. Nigeria.
"	*Costello A48/30. Nigeria.
"	*White 8341. Nigeria.
"	*McGregor 392. Nigeria.
"	*UNH A29/71. Nigeria.
"	*Jean Louis 6700. Zaire.
"	*Taylor 319. Natal.
"	*Edwards 2204. Natal.
"	*Wells & Edwards 134. Natal.
"	*Miller S/25. Swaziland.
"	*Miller S/164. Swaziland.
"	*White 10255. Transvaal.
"	*Renny DB58. Transvaal.
"	*Burtt Davy 5217. Transvaal.
"	*Robertson s.n. Transvaal.
"	*Acocks 12860. Transvaal.
"	*Codd 2949. Transvaal.
"	* " 3030. Transvaal.
"	* " 1566. Transvaal.
"	* " 2949. Transvaal.

9. ASTROTRICHILIA

A.asterotricha	Mabberley 825. Madagascar.

10. OWENIA

O.acidula	Mc Whirter 10. Queensland.
O.reticulata	Symon 6898. Northern Territory.
O.venosa	Mc Whirter 7. Queensland.
O.vernicosa	Symon 7121. W.Australia.

11. CIPADESSA

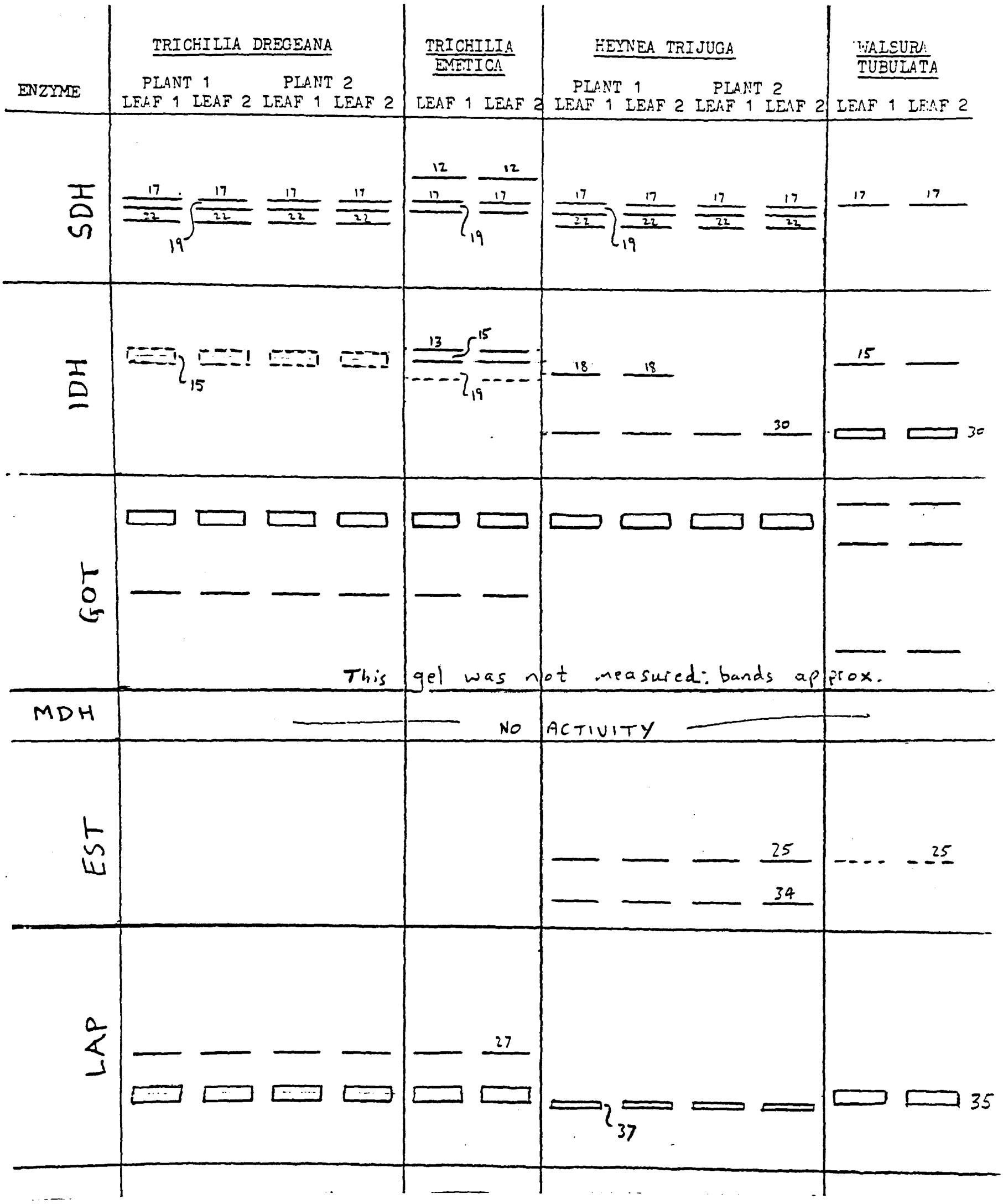
C.baccifera	Forrest 9884. Yunnan
C.baccifera	Iowa Univ. (cult.) 50011.

APPENDIX 2

List of specimens used in the study of pollen morphology
(with mean dimensions of grain, where measured).

SPECIES	COLLECTION	P(microns)	E(microns)
Trichilia			
T.capitata	Torre 776. Mozambique.	29.9	28.3
T.cipo	Nascimento 783. Amazon.	25.6	20.8
T.cipo	Prance et al. 24162.		
T.dregeana	Styles 321. Uganda.	56.8	51.7
T.dregeana	Styles 333. Uganda.		
T.emetica	Davy 21710. Malawi.		
T.emetica	Styles 265. Uganda.	33.9	33.0
T.emetica	Styles 286. Uganda.	39.0	39.0
T.gilgiana	Breteler 2126. Cameroon.	37.6	32.8
T.havanensis	Stead & Styles 118. Guatamala.	32.0	30.7 #
T.heudelotii	FHI 35544. Cameroon.		
T.hirta	German 775. Guatamala.	39.0	36.8
T.megalantha	Hambler 15. Nigeria.	42.7	39.5
T.ornithothera	De Wilde 4888. Liberia.	32.0	30.4
T.pallida	Brit.Guiana F.D. D176.	27.2	21.6
T.prieureana	Kennedy 301. Nigeria.		
T.prieureana	Styles 219. Uganda.	24.8	26.0
T.quadrijuga	Bahia 60. Amazon.	21.6	19.6
T.rubescens	Latilo 34. Nigeria.	28.3	24.5
T.schomburgkii	Maguire 47099. Brazil.	34.0	31.0
T.solitudinis	Berg P18585. Amazon.	24.5	22.4
T.surinamensis	Brit.Guiana F.D. D198.	38.4	36.8
T.tessmannii	Noel 88. Zaire.		
T.tessmannii	De Wilde 3419. Liberia.	32.0	28.8
T.tuberculata	Stem & Chambers 146. Panama.	33.6	26.2
T.welwitschii	Jean Louis 1078. Congo.	32.0	31.5
Pseudobersama			
P.mossambicensis	Torre 6328. P.E.A.	49.6	46.1
Pterorhachis			
P.zenkeri	Oxford Botanic Garden Cult. (Origin: Cameroon).	32.0	32.4
Walsura			
W.brachybotrys	Wenzel 295. Philippines	28.8	19.2
W.chysogyne	Pennington 7907. Sabah.	25.6	19.7
W.pinnata	Poilane 13229. Laos.		
W.pinnata	SAN 61654. Sabah.	34.0	28.0
W.pinnata	Sangkhachad 373. Thailand.	30.0	24.0
W.pinnata	Sinclair 9334. Sabah.	53.6	41.6
W.trichostemon	Bertal 11069. Thailand.	36.0	30.0
W.trichostemon	Burma F.S. 6. Burma.	34.0	29.0
W.trifoliolata	Haines 18541. India.	49.6	40.8
W.trifoliolata	O.B.G.(cult.), India.	36.8	36.8
W.trifoliolata	Worthington 2616. India.	48.4	40.4
W.tubulata	O.B.G.(cult.), Darjeeling.		

Heynea			
H.trijuga	Poilane 25832. Indochina.	41.5	37.8
H.trijuga	Pennington 7948. Sabah.	38.0	36.0
H.trijuga	Soradet 427. Thailand.		
Lepidotrichilia			
L.volkensii	Eggeling 1678. Uganda.	28.0	28.4
L.volkensii	Gutzwiller 3629. Zaire.		
Malleastrum			
M.excelsum	Humbert 2494.	30.4	28.0
M.obtusifolium	SF 8878.	26.4	24.8
Ekebergia			
E.capensis	Styles 290. Uganda.	28.3	26.7
E.capensis	White 8212. Nigeria.		
E.senegalensis	Collection unknown.	25.2	23.6
Astrotrichilia			
A.valiandra	Humbert 29663. Madagascar.	36.0	36.0
Owenia			
O.venosa	Helms 136. Queensland.	21.6	21.1
Cipadessa			
C.baccifera	Forrest 9884. Yunnan.	23.6	23.8



APPENDIX 3

Scale diagrams of banding patterns after electrophoresis and enzyme-specific staining of extracts from four species.
Bars indicate discrete bands; boxes, diffuse bands; dotted lines, weak bands. The distance (in mm) from the reservoir of each band is given and for a diffuse band, the measurement is taken at its middle point.

contd.....

ENZYME	TRICHILIA DREGEANA PLANT 1 LEAF 1	TRICHILIA DREGEANA PLANT 1 LEAF 2	TRICHILIA DREGEANA PLANT 2 LEAF 1	TRICHILIA DREGEANA PLANT 2 LEAF 2	TRICHILIA EMETICA LEAF 1	TRICHILIA EMETICA LEAF 2	HEYNEA TRIJUGA PLANT 1 LEAF 1	HEYNEA TRIJUGA PLANT 1 LEAF 2	HEYNEA TRIJUGA PLANT 2 LEAF 1	HEYNEA TRIJUGA PLANT 2 LEAF 2	WALSURA TUBULATA LEAF 1	WALSURA TUBULATA LEAF 2
G6PD				27	18	15 27				18 30 32		15 30
6PGD				15 23		12 20 28				15 23 32		15 20 23 28 32
PER				23 35		23 35 39				23 35 39		17 20 35
ACP				12	12 9 17				12 9 15		12 9 15	
AAP	79				79		79					

NO ACTIVITY

APPENDIX 4

List of specimens studied in preparing the taxonomic revision in Chapter 6.

Numbers in brackets correspond to numbers given to species in the above account.
(2)= ssp. trifoliolata and (2')= ssp. acuminata.
(16)= forma chrysogyne and (16') = forma velutina.

Adduru 183(9); Agama 10222(16); Ahern 264(9); Alfred 43/22(1); Alston 2227(5), 17211(16); Alzell s.n.(2); Amherst 1266(1), 8112(1); Amiruddin 24(16); Balgooy 4977(16); bb 24892(16); Beccari 5/1888(9); Beddome 298(2); Bernadi 14231(2); Beusekom & Charoenpol 1900(9); Biswas 1783(3), 2070(3); BKF 2812(4), 11069(4), 12500(9), 13004(9), 18203(1), 34647(9), 35958(9), 37456(9), 37511(1), 38134(4), 40246(1), 45581(16), 46507(1), 47619(9), 51943(16'), 52047(16'), 52143(9); BNB A823(9), 1952(16); 3995(16'), 10142(9); Bon 5217(6); Bourdillon 159(2'), 395(2'); Bourne 822(2), 2281(2), 2282(2), s.n.(2); Brandis 718(4); B.S. 257(9), 1257(9), 1613(9), 3110(9), 13600(9), 21463(9), 24140(16), 2438(16), 27052(16), 28223(16), 26087(9), 29053(9), 29126(16), 39167(16), 49321(9), 79334(9); Bunchuai 1555(1), 1822(1); Burma F.S.H. s.n. X 40(4); Castro & Melegrito 1366(9); CF 2265(16); Chatterjee s.n.(1); T.Clark 76(14), 77(9), 78&79(13), 80(9), 81&82(9), 89(1), 90(5), 91(2); Clemens 3397(16), 4449(16); Collins 386(9); Comanor 850(2); Cooray 70031903R(2); Cowan 51; Deschamps.s.n.(2); Dickason 5503(1), 5524(4), 6952(4), 6989(4), 7046(4), 7887(1); Ebalo 165(9); Elbert 3188(16), 3225(16); Ellis 11791(2); Elmer 2847(9), 12903(12), 12907(12), 13138(16), 13158(16), 15628(9), 20167(16), 21487(9), 21574(9); Falconer 643(4); FB 3110(9), 3463(9), 17933(16), 27052(16); Fernandes 1965(2'); Forbes 1154(16), 1216(16); Fosberg 50303(2);

FRI 2986(16), 3497(16), 6713(16), 6772(9), 6788(16), 11145(16), 11224(9), 11250(16), 11684(16), 11873(16), 13007(16), 13198(16), 13206(16), 13224(16), 13770(16), 14017(9), 14269(16), 14371(9), 14413(16), 15756(16), 16145(9), 16649(16), 16658(16), 17320(16), 17703(9), 19273(9), 19980(9), 20163(1), 20711(9), 23380(16), 26068(16), 27278(9), 29155(16), 29370(9), 32646(9), 60163(1), 64747(16), 66524(16), 73759(16), 76521(16), 94087(16), 98187(16), 99474(16), 100120 (9), 104269(16);

Fung 20089(9), 20154(9); Gamble 7828(1), 7937(1), 14016(2), 18180(2); Gardner 136(5); Garrett 16(4), 1237(9); Garston 2227(5); Geesink & Hiepko 7842(1); Geesink, Phanichapol & Santisuk 5611(9); Griffith s.n.(3), 155(4), 335(1), 1057(9), 1058(3), 1059(1), 1060(1), 1089(1), 1091(1); Groff 5676(9); Hainan 20089(9), 20154(9), 65053(9), 70644(9), 70695(9); Haines 2350(2), 5533(2), 5534(2), 5535(2); Hallier 312(13), 355(13), 715(16); Harmand 335(4), 713(1); Haviland 1635(9); Helfer 34(1); 89(4), 1056(4), 1059(1); Henry 10849(9), 12929(9); Hort.Bog. III-B-20(9), III-D-20, III-F-23(16), VIII-B-92(3); Hose 394(16), 629(16'), 643(16'); How 70544(9), 70695(9); Jayasuriya 1682(2), 1938(2), 2000(2), 2208(5); Kanehira & Hatusima 11417; KEP 64310(9), 64423(9), 77866(9), 94022(9), 98187(16), 100120(9);

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8552(1), 8594(1), 8764(1), 9801(4), 9866(1), 10447(1), 11648(1), 12606(1), 12980(1), 12983(1), 17055(1), 17140(9), 17636(1), 17890(1), 17974(9), 19897(4), 20048(9), 20243(9), 20296(1), 21208(9);

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Kostermans S.133(16), 2885(9), 4348(16), 4385(16), 4421(10), 4844(16'), 4890(16'), 7156(16'), 7275(16'), 7454(16), 7475(16), 7477(16), 8106(9), 8206(9), 10064(16), 10324(13), 12323(16), 12553(13), 12630A(10), 24022(9), 24197(2'), 24314(2), 24586(5), 24814(2), 25161(2), 25258(2), 25291(2), 25557(2'), 27398(2), 27795(5), 27956(5), 28066(5), 28140(2), 28603(2), 77866(9); Koyama 13322(2); Kuriakose s.n.(2); Kurz 2052(4), s.n.(1), s.n.(3), s.n.(7), s.n.(9), last collection s.n.(1); Kuswata & Soepadmo 12(16), 77(16), 184(16); Lace 2757(4), 2802(4), 3015(1), 4567(4), 4695(4), 5211(4); Lakshnakara 561(1), 997(16), 1312(4), 1313(4); Lau 291(9), 3852(9), 25975(9); Le février 106(9), 551(9); Lei 253(9), 597(9); Liang 65053(9), 65324(9); Loher 6819(9); Mabberley 1660(9), 1664(9); MADW 24507(1); Maingay 344(9), 345(9), 1638(9), 2571(16); Marcan 635(4); Maung Ba Pe 13022(4); Maxwell 75-176(9), 81-199(16); Meijer 200(2), 2099(16'); Merrill 715(16), 2534(9), 2847(9); Minjulu 79224(16); Mogea 3711(9), 4163(9); Mooney 2120(2), 2215(2); Mueller-Dombois 69030805(2), 69030805(2), 69042609(2); Nooteboom 1638(16); Oxf.B.G. s.n.(2); Parker 2285(1); Parkinson 56(7), 283(1), 1686(9), 5242(9), 14478(1); Parry 1161(1); Pennington 7815(9), 7831(16), 7899(16), 7907(16), 7921(16), 7983(16), 8000(9); Perry 11068(1); Pételot 1272(9), 2007(9), 4326(9), 7857(9); Phua 509(1); Pierre 517(4), 1280(9), 1534(1), 4219(9), 4244(1), 4256(4), 4299(1); Pleyte s.n.(1), 233(16); PNH 252(12), 4134(16), 4715(16), 12339(12), 13660(16'), 14103(12), 17046(9), 38022(16), 38058(16), 41949(16), 78185(9); Poilane 1186(8), 3219(1), 3221(1), 9405(1), 15258(4), 13229(9), 19232(1); Prawiroatmodjo & Soewoko 1691(16), 1962(16); Purseglove 5143(11), 5204(11), 5219(11); Put 558(1), 652(4), 1288(1), 2812(4), 3506(4); Rastini 152(9); RHT 26244(2, 27043(2); Richards 2304(9); Ridley s.n.(9), s.n.(16); Roxburgh s.n.(2), s.n.(2);

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100304(9), 107255(16), 108771(9), 109629(16), 110193(9), 114101(9); San Carlos 809(16);

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