# THE SYSTEMATIC SEED ANATOMY OF THE MELIACEAE

## - with particular reference to the seed-coat of the Melioideae

BY

MARTIN ROY CHEEK

WADHAM COLLEGE

OXFORD




A thesis submitted for the degree of Doctor of Philosophy

in the University of Oxford

January 1989

# ABSTRACT

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Detailed and original descriptions & illostrations of the seed anatomy (especially that of the seed-coat) are presented of the tribes Turraeeae, Melieae, Trichilieae, Guareeae and Sandoriceae. Homologies of the seed-coat strata are established as far as possible, the taxonomic utility of each of the many characters assessed for each tribe and the taxonomic implications gauged using Pennington and Styles' (1975) generic monograph of the Meliaceae as a basis.

Seed-coat characters seem particularly useful in several cases of generic delimitation and show great promise at the infra-generic level, their characters being relatively constant at the species level, but

showing great variation between species. At the tribal level, they seem to be of less use in delimitation than do morphological characters but, nevertheless, do give an indication of affinities.

Particular attention is paid to the systematic anatomy of 'arillate' and 'sarcotestal' seeds in the Meliaceae and an attempt is made to establish a nomenclatural basis for fleshy seed types in the family. The phylogenetic implications of seed-coat characters are discussed at length on a generic and tribal basis and the functional significance of fruit and seed anatomical characters examined as far as is possible.

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# CHAPTER ONE

## MELIACEAE TAXONOMY AND ECOLOGY. IMPORTANCE OF SEEDS.

The Meliaceae is a medium sized family of pan-tropical trees and shrubs numbering about 51 genera and 575 species (Mabberley, 1987). Although some are plants of bush or savannah, most species are found in tropical rain forest either as emergents, or, more usually as medium to small understorey trees and sometimes shrubs.

The family is characterized by its usually spirally arranged, pinnate, exstipulate leaves, usually with entire leaflets, simple and unbranched indumentum, absence of gland dots and by its flowers with five free petals and a superior syncarpous ovary. The androecium nearly always comprises a staminal tube, usually as prominent as the petals, the anthers, normally 8-10, inserted at the rim or just inside it, often alternating with variously formed appendages. A nectariferous 'disk', often cup-shaped, is frequently present within the staminal tube. Sometimes this is absent or the ovary tops a nectariferous stipe. The ovary is (1-)3-5(-10)-locular, with axile placentation, surmounted by a single style and stigma, the latter variable, but rarely lobed.

Recently it has been discovered that many, possibly most, species are dioecious (Styles, 1972), male flowers having non-functional but often only slightly reduced gynoecia and female flowers with indehiscent but often almost fully-formed anthers.

Economically, the Meliaceae are best known for high quality hard wood timbers of importance to the international market. These are largely produced by the Swietenioideae (see below). Swietenia mahagoni produced the Bermudan Mahogany favoured by Chippendale whilst, in Africa, Khaya produces 'African Mahogany' and Entandophragma 'Utile' and 'Sapele'. Cedrela and Toona are faster-growing trees producing lighter woods and used in plantations, the former traditionally for cigar boxes. Lovoa and Carapa are less important. Of the Melioideae (see below), Turraeanthus ('Avodire'), Dysoxylum, Guarea and Melia have also been used in international commerce. Vegetable oils are produced from seeds of Carapa and Trichilia. Lansium and Sandoricum are important sources of edible fruit in S.E.Asia. Azadirachta is a source of insecticide and medicines. Many Meliaceae are locally medicinal, particularly in Madagascar (Neobeguea, Capuronianthus, Turraea and Malleastrum). Species of Melia, Turraea, Toona and Azadirachta are grown as ornamentals.

This natural family was first recognized (as the Melieae, taking its name from Melia azedarach L., now considered the type species) by A.-L. de Jussieu in his Genera Plantarum of 1789. Subsequent major accounts were published by A. De Candolle in his Prodromus in 1824, A. de Jussieu in 1832, by J.D.Hooker in 1862 in his and G.Bentham's Genera Plantarum, Casimir De Candolle in 1878, H.Harms in 1896 and 1940 in Engler and Prantl's Die Natürlichen Pflanzenfamilien, culminating in that of Pennington and Styles'(1975) Generic Monograph of the Meliaceae in which a full taxonomic history is given, and where many questions of family , subfamilial and tribal delimitation are finally resolved and in which framework this thesis is largely set.

There are two major subfamilies and these are very distinct:

Swieteniodeae are usually tall trees, often forest emergents, with paripinnate leaves and bud scales, and have woody, septifragally dehiscent fruits with a large, woody , central placental columella and dry, winged, wind dispersed seeds derived from multi-ovulate locules.

Pennington and Styles (1975) recognize three tribes,

1. Swietenieae (9 genera) with or without an androgynophore and without free stamens.

2. Cedreleae (2 genera) with an androgynophore and free stamens.

3. Xylocarpeae (2 genera) of river margins , marsh and mangrove; seeds unwinged with corky seed-coat, cotyledons united, fruits without a large woody central placental columella.

Melioideae are generally understorey trees or shrubs with imparipinnate leaves, no bud scales and fleshy-leathery loculicidally dehiscent fruits with fleshy ('arillate'/'sarcotestal') seeds derived from locules with one or two (very rarely more) ovules.

Pennington and Styles recognize 7 tribes:

1. Turraeeae (6 genera) often shrubs with simple leaves, hermaphrodite flowers and seeds slightly curved, embryo with exserted radicle and endosperm. Wood with non-septate fibres.

2. Melieae (2 genera) with leaves often bipinnate(-fid), petiole with paired glands, fruits drupaceous.

3. Vavaeeae (1 genus) are trees with 'Terminalia' branching, flowers hermaphrodite, loculi 1-many ovulate. Fruit a berry.

4. Trichilieae (10 genera) with leaves pinnate, anthers inserted apically on the staminal tube or filaments, disk poorly developed.

5. Aglaieae (5 genera) with pinnate leaves, staminal tube globular to cup shaped, appendages absent, disk absent. Cotyledons superposed, radicle included. Fruit a berry.

6. Guareeae (10 genera) with pinnate leaves, anthers inserted inside the staminal tube, disk well developed, style-head discoid.
7. Sandoriceae (1 genus) leaves trifoliolate, staminal tube ribbed above, stamens inserted within the tube, disk tubular, style-head deeply 4 to 5 lobed.

Intermediate between the two major subfamilies, Pennington and Styles (1975) described two new subfamilies from Madagascar:

Quivisianthoideae (1 genus) without bud scales, leathery-woody capsules with loculicidal dehiscence and dry, winged seeds from bi-ovulate locules.

Capuronianthoideae (1 genus) with naked buds, opposite leaves, fruit dry with partial septifragal dehiscence; seeds with a corky sarcotesta from 2-4 ovulate loculi.

A further sub-family from Madagascar has been proposed by Leroy (1981) based on (and still known only from) a single fragmentary collection:

Neomangenotioideae (1 genus) has perigynous flowers without a disk, fruit a septicidal drupe (Leroy, 1981).

Few monogaphs of complete genera have been published, apart from those of Chisocheton (Mabberley, 1979), Vavaea (Pennington, 1969) and Cedrela (Earle Smith, 1960, but superseded by Styles in Pennington and Styles, 1981). For the most part treatments have been regional monographs, e.g. African Guarea (Pellegrin, 1939), African Trichilia (de Wilde, 1968) or the neotropical genera (Pennington and Styles, 1981) and naturally, these have not been able to do full justice to infra-generic classification and phylogeny.

## IMPORTANCE OF MICROCHARACTERS

With few exceptions, studies of Meliaceae taxonomy have been based entirely on traditional morphological characters. The main exception is that of Pennington and Styles (1975) which included a detailed review and survey of wood structure and palynology.

Wood anatomy, has been implied by Kribs (1930) to provide a basis for generic delimitation. However, Pennington and Styles have shown, on the evidence of a much wider survey and more exhaustive examination of the variability of characters, that few genera can be distinguished on their wood anatomy alone and that those are mostly already distinct on morphological grounds. However, sub-families can be distinguished, and within the Melioideae, the tribes fall cleanly into two groups, those with non-septate fibres, usually with terminal bands of apotracheal parenchyma and those with septate fibres, usually without terminal bands of apotracheal parenchyma.

Palynology, whilst of use in delimiting the family, is of no use at the sub-family level and is rarely useful at the tribal level, the exception being Turraeeae with oblate-spheroidal, 3-colporate, prominently scabrous or verrucose exine. 'Pollen characteristics are of limited value in identifying genera'. 'Occasionally pairs or groups of genera are characterized by distinctive grains, e.g Aglaia, Lansium, Reinwardtiodendron with very small, usually 3-colporate prolate grains'. (Pennington and Styles, 1975).

Limonoid chemistry, extensively investigated by Taylor et al. (summarized in Waterman and Grundon, 1983), has shown these structures to be useful at delimiting families and sub-families, but of limited use at the tribal and generic level.

None of these character suites appears to have been studied fully at the infra-generic level.

## IMPORTANCE OF SEEDS

Seeds, especially their micro-anatomy, have been generally neglected as a source of taxonomic characters. Harms (1896, 1940) did, it is true, delimit Turraeeae largely on the evidence of gross seed structure: endospermous seeds with foliaceous cotyledons and long exserted radicles, but did not consider anatomy. De Wilde (1968) rightly places great importance on the internal seed structure of Trichilia in determining species alliances, but does not investigate the anatomical basis. Pennington and Styles (1975, 1981) use gross morphological aspects of fruit structure at the sub-familial level and, in neotropical Guarea, these are crucial at the specific level. In the Melioideae, fruit indehiscence/dehiscence has been seen as important in generic delimitation. However, seed characters are less widely employed apart from the obvious distinction between the dry, winged, wind-dispersed seeds of the Swietenioideae and the fleshier, ex-alate seeds of the Melioideae. In the Melioideae, a wide range of fleshy seed types (possibly associated with different animal dispersal syndromes: see later chapters ) from 'sarcotestal' to 'arillate' occur, often in the same genus. Not surprising, then, is it that these seed characters are only 'sometimes sufficiently modified to be useful as a diagnostic generic character'(Pennington and Styles, 1975). Whilst Pennington and Styles do define and justify their descriptive terms, 'arillode' and 'sarcotestal' (see chapter 3), they do not go beyond this and investigate the anatomy in order to establish homologies.

Substantially then, seed characters have been passed over by monographers of the Meliaceae. This despite the fact that, as Corner (1976) so perceptively points out: 'This is a family in which the variety in fruit and seeds far outweighs 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...' and 'There is great need to overhaul fruit and seed structure in order to understand specific alliances within genera, and generic alliances.'

The purpose of this thesis is to :

1. Assess the value of seeds as a source of taxonomic characters at the familial, tribal, generic and species level, using Pennington and Styles (1975) and monographs of individual genera as a framework for evaluation.

2. Establish the anatomical basis of 'sarcotestal' and 'arillate' seeds in the Meliaceae.

3. Formulate a nomenclature for fleshy seed types in the Meliaceae.

4. Investigate the possibility of drawing evolutionary conclusions from seed characters.

5. Examine the functional significance of fruit and seed anatomical characters in the ecology (particularly dispersal) of the Meliaceae.

# CHAPTER TWO

## MATERIALS, METHODS AND CHRONOLOGY

### MATERIALS

Materials used in this study were obtained mainly from the large spirit collection of Meliaceae fruits and flowers collected over the last 25 years at the Department of Plant Sciences, Oxford by successive Oxford workers on the family, particularly by T.D.Pennington and D.J.Mabberley, mainly from S.E.Asia, but with additions of other genera from around the world, largely obtained at the behest of B.T.Styles. The spirit collection at Kew, particularly strong in South American Meliaceae, was also employed. It was found necessary to collect other materials from equatorial Africa and Madagascar.

Dried fruits and seeds from herbarium material (FHO, K and TAN) were used in the absence of spirit material or to obtain data on variation. Its limitations are discussed under 'variation'.

Fresh fruit and seed material were used of Nymania capensis (Thunb.)Lindb. and Turraea heterophylla Sm. grown at Oxford.

A list of specimens, with provenance data, inspected during the course of this investigation is given in Appendix One.

### AUTHENTICATION

Recent floristic work for Flora Malesiana (Mabberley and Pannell, in prep.) and the neotropics (Pennington and Styles, 1981) has ensured that

specimens from these regions at Oxford are authoritatively named. In Africa, floristic accounts are more fragmented. The Flora of West Tropical Africa (Keay, 1958), Flore du Congo Belge (Staner and Gilbert, 1958), and Flora Zambesiaca (White and Styles, 1963) have been followed, except where Pennington and Styles (1975) have indicated otherwise. The nomenclature for African Trichilia follows de Wilde (1968). For Madagascar, the literature is even more ramified and incomplete. The works of Leroy on individual genera ( Capuronianthus, 1958b; Lepidotrichilia, 1958a; Astrotrichilia, 1958c; Calodecaryia, 1960; Malleastrum, 1964; Humbertioturraea, 1969) have been followed in conjunction with a study of herbarium specimens and protologues. In some cases, nomenclatural adjustments (Cheek, 1989a) have been found necessary.

## COLLECTING METHODS

Small fruits, (e.g. those of Turraea spp.) and flowers were collected into screw-top 'Wellcome' plastic bottles or 'whirl-paks' (thick plastic collecting bags with included wire sealer, relatively easily sealed and unsealed). Larger fruits were collected into plastic 'freezer-bags', adding a jeweller's tag and preservative before sealing with wire and then placing the whole in a series of three or four other bags to reduce the risk of leakage and to aid padding and protection. The outer bag was usually marked to aid subsequent sorting. Smaller fruits, such as those of Turraea species, were preserved in 50% methylated spirit. Larger, fleshy fruits, pre-eminently those of Leplaea, with larger volumes of water in the tissues, were preserved with much higher concentrations, sometimes undiluted, of ethanol. Before air-freighting collections to Oxford, most of the preserving fluid was decanted to reduce weight.

Often, fruits would be collected in an immature state from trees (e.g. Turraea, Astrotrichilia and Humbertioturraea.). In this case, several fruits would be placed in plastic bags without alcohol for several days, to study and promote ripening, before eventually preserving.

MACRO-METHODS

The fruits and seeds described and depicted were chosen as representative of their sample. Spirit materials preserved in formalin mixtures were leached in 50% alcohol to remove it. Dried herbarium material was boiled, then simmered over a bunsen burner to rehydrate and soften for from 10 minutes to 2 hours depending on the nature of the material.

Coarse sections were made in Petri dishes with a single-edged razor blade in transverse and median planes. Measurements and observations, from which drawings were made, entailed using a Nikon dissecting microscope. Having coarsely dissected and sectioned fruit and seed, portions were selected for the microtome.

Dissected and sectioned materials were placed in small plastic bags before replacing in the original bottles to facilitate subsequent retrieval.

MICRO-METHODS

Materials were sectioned using a Reichert OM sliding microtome, orientating and sectioning in cork, at a knife angle of 15 degrees, and a sectioning thickness of 18-20um (see Cutler, 1978). Densely tanninized and vascular seed-coats were sectioned as thin as 14um and membranous 'arillar' tissue at up to 35um, constantly irrigating with 70% alcohol. Sections were 'lifted' directly from blade to slide with a brush,

cleaning, clearing and staining (see below) where necessary, on the slide. In an earlier, preparatory project (Cheek, 1983) this was found vital to reduce disintegration (incurred during conventional staining treatments) of the large, often histologically heterogeneous and hence fragile sections usually derived from fleshy seed-coats.

Longitudinal and transverse sections were taken from different parts of the seed coat in order to discover the extent of variation and to determine seed-coat structure fully, generally from:

A. The chalaza: integument boundary. Usually dorsal and median parts of seed.

B. The micropyle. Normally median, dorsal.

C. The raphe. Ventral, usually midway, T.S.

Paradermal sections, particularly testal O.E. (to examine anticlinal wall shape and thickening, and to search for stomata), but also of exotegmen and testal I.E., (where elusive or non-crystalline), were made by mounting whole seeds in the specimen clamp, or, by hand, with a single-edged razor blade.

Macerations, usually of exotegmic fibres, were made with the aid of 10% solution in water of chromic acid (see Peacock, 1975). Thick and tanninized sections were 'cleared' using a 10% solution of household bleach (largely sodium hypochlorite) for 1-10 minutes, depending on the intransigence of the material. The clearing agent helped to 'relax' those tissues compressed during preparation or during the formation of the seed-see Cutler (1978:6), who applied this technique to wood sections.

Sections were mounted in 95% glycerol, to be made permanent by sealing with 'Glyceel'. Staining was used rarely, the tissues themselves being

sufficiently pigmented (especially spirit material) to provide contrast.

Acidified phloroglucinol was used from time to time to test for lignification and Sudan IV for lipid (see Peacock, 1975)

Observations, measurements and drawings at standard magnifications on squared paper were made with the aid of a Watson 'Barnet' binocular compound microsope fitted with an eyepiece graticule.

S.E.M. METHODS

Small slivers (1-4mm across) of seed or fruit surfaces were cut freehand with a single-edged razor blade, and mounted on a standard 'Cambridge' stub using 'Araldite'. Stubs were coated in a thin film of gold using a Polaron sputter coating unit.

Observations were made with a Cambridge Stereoscan 150 scanning microscope at an AKV of 10-15KV. For a full explanation of the operation of this instrument, see Oatley (1972). Photographic exposures were made using a Pentax K1000 35mm roll film camera.

PRESENTATION OF DATA

One example from at least one species in each of the genera surveyed is represented by a lengthy (one- to two-page) description of fruit and seed, commencing with name, authority and collection number and including collectors' notes (colour, dispersal and state of maturity) and references to other significant descriptions of fruit and seed.

A description of the macro-morphology, commencing with the outer dimensions of the fruit and working inwards to its internal structure, followed by the same for the seeds, prefaces a description of the microscopic anatomy of the seed-coat. In Chisocheton the testa, tegmen

and chalaza, together with perisperm, endosperm and cotyledonary structures are described. In the remaining genera, in order to save time, descriptions were usually confined to the testa and tegmen only (except in completely pachychalazal seeds) and the perisperm and endosperm are described if they appear.

Descriptions are usually based on transverse, longitudinal and paradermal planes of section. They are heavily illustrated in order to facilitate comprehension and interpretation of the data, which is not made easy due to the complicated and strongly three-dimensional aspect of the subjects.

Each species is usually represented by two plates, the first showing gross morphology of the fruit and seed, the second showing micrographs of the various planes of section, often cross-referenced to a tissue diagram. Standard magnifications were used throughout in order to aid comparison and illustrated by linear scales. Drawings were made using pencil on paper with blue squares, then photographed using a blue filter to reduce this feature in the finished plates. Captions to each plate are placed on the facing page. Photographic plates of living fruits are included where possible to illustrate fruit and seed colour and disposition.

## ACCOUNTING FOR VARIATION

Due to the limitation of available material, many genera are regrettably represented here by only a single species and often only a single collection. Every attempt was made to look at more than one seed per collection. Most descriptions are composite, taken from several seeds. Measurements of each parameter are expressed as a range, e.g. 30-40um, or, when the range is considered small, as an average. Where

exceptional values occur sporadically, they are expressed in brackets on either side of the range, e.g. (19-) 30-40um. Measurements were usually based on longitudinal and transverse sections. Where macerations were the basis, this is specified.

Where a second spirit collection was available, this was sectioned and any significant differences noted after the main description under the heading 'variation'. In some cases two or three collections were examined in detail to obtain an accurate idea of the variability within species of the characters described. This was considered especially important in monotypic genera which might otherwise be represented by data from only a single, possibly aberrant, seed . In genera where several species were being examined and described in full (e.g. Dysoxylum, Trichilia and Chisocheton) at least one species was investigated exhaustively for the same reason.

In some genera, e.g. Walsura where time was limited, only a single, representative species was described in full and variation considered, the other species being examined briefly and only abbreviated descriptions based on single collections were made.

Dried material, after revival by boiling (see above) when used in examining intra-specific variation, was treated warily. Desiccation, even for a few hours, can have an irreversibly disruptive effect on delicate tissues and leave them of only limited value in comparing variation and can render them quite misleading if used as the sole basis for a generic description. Revival of desiccated tissues is possible (see methods) to a varying extent (probably correlated with extent and duration of desiccation) but this appears to stretch cell walls, enlarging cells and narrowing walls artificially.

CHRONOLOGY

Being aware of the need to work with spirit material, it was deemed necessary to determine what was available at Oxford before commencing anatomical work. The spirit collection at Oxford was highly fragmented, being then split into eight localities. Moreover, many bottles bear only collector's numbers and lack names. or are named only to genus. In order to determine what was available and where, the first term was spent cataloguing all the collections by storage site, assessing whether flower or fruit were present, the state of maturity (dehisced or not), quality (whether it, had been visibly desiccated at any point) and noting names, where given. Then, to correlate with names and collectors notes, it was necessary to go through the entire Meliaceae herbarium (FHO), scanning the herbarium specimens for references to 'fruits in spirit' and then checking the collector's number on the sheet with those listed in the bottle catalogue. If a match was made, the herbarium collection data, notes on fruit characters ( indications of maturity, colours, dehiscence or dispersal notes) and name noted for future use. This work considerably helped familiarization with the genera of Meliaceae.

By the second term, a literature review had been substantially completed and sectioning equipment obtained and set up.

It was decided to start work with Chisocheton since this has large, orthotropous seeds, uncomplicated by a raphe and has species with both sarcotestal, arillate and intermediate conditions. Moreover, this genus is one of the few revised recently (Mabberley, 1979) hence with a newly overhauled taxonomic framework, and most importantly was comparatively

very well represented by fruit in spirit (c.30% of species) with ample material with which to experiment in technique.

Pericarp anatomy was investigated at the outset. Sections were taken from a wide range of species for microscopic examination but characters found were variable within species, the anatomy relatively unorganized and difficult to quantify or interpret.

Secondly, surface characters, using S.E.M. techniques were investigated. The hairs of the outer pericarp were of the same basic structure, differing significantly only in quantitative characters (e.g. degree of cuticular sculpturing, density and length) and were obviously of relatively little taxonomic importance (see plate 66B).

The seed-coat surface was generally featureless, except where the outer periclinal walls of the outer testal epidermis were concave in which case the anticlinal walls were prominent and cell shape could be determined. Unfortunately, with few exceptions (see plate 1) these characters ( anticlinal wall thickness and shape, testa cell shape and size) were uniform. Cuticular sculpturing was entirely absent.

Although complicated, seed-coat anatomy proved, by comparison, of far greater worth as a source of taxonomic characters. The homologies of the seed-coat tissues were readily ascertained (though this took some months to establish) and many, previously unsuspected, characters proved useful at the species level. It was possible to establish the distinction between pachychalazal and conventional, bitegmic seeds, to determine the anatomical basis of arillate and sarcotestal seeds and to draw conclusions on the phylogeny of these different seed types in this genus.

Towards the end of the first year, anatomical work on the genus Dysoxylum was started. It soon became clear that, although sharing the

same tribe with and being perhaps nearly related to Chisocheton, its seed anatomy was quite different in a number of constant characters as well as in the ovule/seed tropism.

At the outset of the project, the second year had been scheduled for fieldwork. Two choices for fieldwork presented themselves: to continue with Chisocheton, and work in S.E.Asia to fill in the gaps, i.e. to obtain material of the missing 70% of species and to obtain series of developmental stages of selected species, or to continue the work as a generic survey of seed anatomy in the Meliaceae and to obtain material of genera unrepresented in spirit.

In the context of systematics, the greatest value of developmental studies is often in determining homologies of structures in the mature state. Since these homologies had been firmly established in Chisocheton, it was decided that the generic survey would be the more profitable option. The areas in which unrepresented genera were most concentrated were equatorial Africa ( Leplaea (i.e. Guarea in Pennington & Styles, 1975), Turraeanthus, Heckeldora, Lepidotrichilia and Pseudobersama) and Madagascar (Humbertioturraea, Malleastrum, Astrotrichilia, Quivisianthe, Capuronianthus, Neobeguea and Neomangenotia).

An expedition to secure these materials was planned; itineraries were based on a study of fruiting times and localities from herbarium material (primarily FHO and P) which were also studied to familiarize the author with vegetative characters to aid identification in the field.

After two months of planning and preparation, fieldwork started at the end of December 1984.

In Cameroun, ripe Turraeanthus fruits were obtained and Heckeldora discovered in flower (fruits were sent on later). In West Uganda, perfect fruits of Leplaea were collected. In Madagascar material from species of all but one of the aforementioned requisite genera were obtained in fruit before returning to East Africa in mid-April when immature and ripe fruit of Pseudobersama and Lepidotrichilia were obtained before returning to England. In addition, materials representing six other genera of Meliaceae often of species hitherto unrepresented in spirit in Oxford and Kew were obtained to supplement collections at FHO and K. In all twenty-five genera (though not all fertile) were studied in the field. The single largest failure was to obtain material of the mysterious Neomangenotia: described as a fifth sub-family, but only known from a single fragmentary collection and perhaps not meliaceous at all.

The remaining time was spent investigating this material (and that representing other genera already available), as far as possible.

# CHAPTER THREE

## LITERATURE REVIEW

History of Systematic Fruit and Seed Anatomy.

As far as I can trace, systematic studies of fruit anatomy started with Nehemiah Grew (1671, 1682) who, in his 'Anatomy of Plants' included a chapter on fruits in which he contrasted, amongst others, apple and pear pome anatomy. He (and Malpighi, 1675) also investigated seed structure in legumes.

A century or so seems to have elapsed before systematic anatomical studies in the strict sense (Gaertner, 1788, catalogued the morphology of vast numbers of fruits and seeds but seems to have ignored anatomical considerations) were pioneered by Hoffman (1814) working with Umbelliferae and investigating the taxonomic use of numbers and positions of vittae: still important today in the classification of the family.

Brown is credited (Bouman, 1984) with being the first to proclaim the knowledge of the bitegmic nature of the ovule (fundamental to the understanding of the angiospermous seed-coat) in a paper on Kingia (Brown, 1826). Though he hints at this even earlier (Brown, 1818) in an aside from a paper on the structure of fruits and seeds in which he far-sightedly pleads for the establishment of homologies in such studies if the affinities of plants are to be determined.

Seed anatomical investigations continued piecemeal (rarely systematic in that usually only a single species was considered on each occasion), largely in the latter half of the nineteenth century, all being reviewed by Netolitzky (1926).

## Modern Systematic Studies

For the Meliaceae, Netolitzky devotes less than two pages, but gives very brief accounts (and barely any illustration), based on his predecessors and his own work, in which representatives of nine genera (Melia, Carapa [probably Xylocarpus], Aglaia, Dysoxylum, Trichilia, Swietenia, Sandoricum, Turraea and Chisocheton), had been investigated, though apparently always by only a single species and these usually incompletely. Nevertheless, as Corner (1976) states, his work is profoundly erudite and shows an appreciation of integumentary interpretation usually lacking in earlier accounts, though most important to comparative anatomy. It is apparently Netolitzky for example, who is first to draw attention to the simultaneous occurrence of the prismatic crystals in the inner epidermis of the testa of several families. Vaughan (1970), in the course of investigating the structure of oil seeds, investigates an oleaginous representative from each of five genera of Meliaceae: Aphanamixis (as Amoora), Carapa, Melia, Azadirachta and Trichilia. Unfortunately, though his work is copiously illustrated, he does not attempt to discriminate between testa and tegmen or, integuments and pachychalaza and all the taxa he has chosen seem to have been investigated already. In mitigation, it must be said that his work is not primarily taxonomic.

The most comprehensive and far-reaching work on systematic seed anatomy is unquestionably that of Corner (1976). For the Meliaceae, he presented

descriptions (mostly based on his own observations), for 19 genera, many of the larger being represented by studies of several species, the whole being illustrated by 16 pages of plates. He is the first to analyse the range of variation in the meliaceous seed both between and within genera and to establish its basic structure. Although when first published apparently ignored, or roundly criticised (Anon., 1978) it is only now, rather belatedly, attracting more enthusiastic support (Schmid, 1986 and, more importantly, Boesewinkel and Bouman, 1984). It is difficult to understand this behaviour. Perhaps it was an expression of indigestion by a public unprepared to receive such a vast quantity of novel data, complexly organized, from such an unregarded field, leading to such unorthodox conclusions.

Precursors to Corner's Magnum Opus were his treatises on leguminous seeds (Corner, 1951) and the incredibly complicated annonaceous seeds (Corner, 1949). Contemporary works on systematic seed anatomy are very sparse. Generally, such studies are either confined to temperate groups with small seeds and thin walled seed-coats, reflecting the long prevalent temperate bias of botanical science (Mabberley, 1983) or pay scant regard for the need to establish homologies, e.g Vaughan and Whitehouse (1971). A rare exception is the work of Robbrecht and Puff (1986) working on a thick seed-coated tropical group in their study of the Gardenieae (Rubiaceae), who do make some effort to establish homologies. The important works of Boesewinkel and Bouman are dealt with below.

The reasons for the current neglect of systematic fruit and seed anatomy, particularly of tropical groups, especially in the light of Corner's works, are hard to comprehend. As Davis and Heywood, (1963) state, seeds in particular are of "potential importance in producing

characters of value for comparative or interpretive purposes", and that "internal anatomical features of the seed, although more difficult to observe, are even more valuable than external characters". According to Stace (1980), it is widely held that anatomical characters are as good, if not better than morphological ones. Despite this, as Carlquist (1962) points out, the anatomy of the seed in relationship to taxonomy has rarely been investigated in comparison with anatomical studies of other plant organs. One has only to consult the monumental Metcalfe and Chalk (1950) to see this truth. Indeed, in some major taxonomic texts, such as the compendious Radford et al. (1979), the subject is omitted altogether.

Developmental Studies

A number of developmental investigations of Meliaceae seeds, have been made, largely by Indian authors: the first, of Sandoricum koetjape by Juliano (1934); Narayana (1958) working on Cipadessa fruticosa (i.e. C. baccifera), Nair (1958) on Sandoricum indicum (i.e. S. koetjape), Naregamia (Nair, 1959a), Melia azedarach (Nair, 1959b) and Azadirachta indica (Nair and Kanta, 1961). These were followed by investigations of Aphanamixis polystachya (Ghosh, 1972) and Lansium domesticum (Prakash, Lim, and Manurung, 1977). Unfortunately, these investigations all lean heavily towards the embryological and pay scant regard to the development and anatomy of the mature seed-coat. As pointed out by Corner (1976), many structures, important in characterizing the seed-coat, only occur in the final stages of development when the seed-coat is becoming hard and not suitable for the Paraffin Wax-Rotary Microtome technique used in most developmental research.

The most outstanding developmental study (in the field of Meliaceae seed anatomy), is that of the seed development of Trichilia grandifolia by Boesewinkel (1981). Here, attention is concentrated on the development of the SEED-COAT (as opposed to the embryology) and much space devoted to an investigation of the mature seed structure. This paper is invaluable in that it confirms the homologies attributed to Meliaceae seed-coat structures by Corner and in that it investigates a relatively advanced and complicated seed. It will be referred to again in the discussion. Regrettably, Boesewinkel did not go on to investigate and compare the anatomy of other Trichilia species.

Boesewinkel has continued his work in this field but along more comparative lines, investigating the affinities of ambiguously placed genera and small families: the Oxalidaceae (Boesewinkel, 1985), Trigoniaceae (Boesewinkel, 1987) and Hypseocharis (Boesewinkel, 1988). He is currently unique in studying seed-coat development from inception in the ovule primordium through to the mature seed-coat and in comparing related taxa. Unfortunately, the time evidently needed to pursue such studies and the great difficulty in obtaining series of developmental stages of tropical seeds appears to have restricted his scope to some excellent comparisons of a few genera within smaller families, and the affinities of these families. He has not looked at the systematic and evolutionary significance of mature seed characters within large genera and of generic affinities within a larger family as I shall try to do in the following chapters.

S.E.M. Studies

The ease with which scanning electron microscopy can be applied in plant taxonomic studies, and the large variety of micro-morphological

characters, previously difficult to observe, rendered, at a stroke easily discerned and recorded, has led to an explosion of publications of SEM studies in the past two decades.

Heywood, in 1968, enthusiastically records the first employment of this instrument and estimates its potential. Only seven years later (Heywood, 1976), it had become a standard and popular taxonomic tool, the only restrictive element to its use being its relatively high capital and maintenance costs.

Fruits and seeds in particular have proved rewarding subjects for systematic study by SEM, often providing the most diverse assemblages of characters of any organ. They have been extensively used in monographic studies and have proved especially useful at establishing species alliances, also in diagnosing species limits and in indicating generic affinities in Umbelliferae (Heywood, 1968), Cruciferae (Stork and Wuest, 1978), Scrophulariaceae (Chuang and Heckard, 1983), Acanthaceae (Balkwill et al., 1986), Lentibulariaceae (Taylor, 1989) and Lythraceae (Panigrahi, 1986). Only lately (and even now, all too rarely) have these studies been complemented by anatomical investigations to establish the basis for these sculptures.

The nomenclature of seed and other plant epidermal micromorphological characters is largely unstandardized. Earlier studies (e.g. Stork and Wuest, 1978) generally try to apply palynological nomenclature to describe seed sculpturing. Often, however, the terms depend on the whim of the author and are undefined. The most comprehensive essay at standardization of nomenclature in this area is that of Barthlott and Ehler (1977), based on a logical categorization of testa cell shape. Although eminently practicable, this work has been largely ignored, especially in the United States where so many SEM studies are carried

out, apparently due to its being published in German. The nomenclature advocated by Barthlott & Ehler is used in this study for those few members of the Meliaceae with significantly sculptured seed surfaces.

It is rarely perceived that SEM micromorphological studies are almost always only useful in small, dry seeded (predominantly temperate) plant groups. In most tropical plants, with large seeds often derived from fleshy fruits, seed micromorphology is almost valueless (Cheek, 1983).

The nomenclature of fleshy seed appendages.

In most species of the Melioideae, part of the exterior of the seed or its stalk is fleshy, i.e. the tissue is succulent, the cells thin walled, the epidermis thin and often brightly coloured. The origin and distribution of this tissue varies widely with regard to the seed-coat, often markedly between species of a single genus in the Meliaceae so that the nomenclature is of some moment to this work. The vocabulary of terms associated with this subject is suprisingly large. Aril, caruncle, arillode, strophiole, sarcotesta, elaiosome and arilloid have all had a wide currency.

An extensive literature exists on the terminology of these appendages and is reviewed by de Lanesson (1876), Kapil et al. (1980) and Boesewinkel and Bouman (1984). However, owing to the importance of this subject in the Meliaceae, a short history of the application of these terms is given below.

According to Corner (1976), Linnaeus was first to use the term aril in relation to seed structure, using it to mean the seed-coat. Gaertner (1788) redefined it to mean an accessory integument attatched to the hilum and enveloping the seed completely or incompletely. Small outgrowths from other parts of the seed-coat he termed strophiole,

epiphysis or spermatotylium. Planchon (1845) divided the fleshy structures up into 3 strict categories based on their exact site of origin:

1. funicular or hilar outgrowths (true arils),
2. outgrowths or swellings of the exostome (arillodes),
3. small swellings of the raphe (strophioles),

the latter two categories ranking as 'false arils'. Later, Planchon admitted that these structures do intergrade. Baillon (1874), rejecting Planchon's categories, used the term aril in a wider sense, using it to label all fleshy appendages and distinguishing them only by use of an adjective ascribing their origin, hence funicular arils, chalazal arils etc. Where the entire outer seed-coat was fleshy, he used the term 'generalized aril'. Pfeiffer (1891) had more sympathy for Planchon's (1845) approach than Baillon's. He was impressed by developmental studies and recognized three categories of fleshy appendage, dependent on the position of the 'growth centre' from which they originated:

1. 'funicular arils' from different parts of the funicle, hilum, raphe or chalaza.
2. 'exostomal arils' or proliferations from the micropylar region.
3. 'arils' which originate from an hour-glass-shaped primordium sited between hilum and exostome.

There is still a lack of a generally accepted terminology. Monographers of various plant groups e.g. Sapindaceae, Radlkofer (1933) in the 20th century have adopted their own interpretations, not always clearly defining them. In addition, a new term, 'elaiosome' was coined

by Sernander (1906) for all fleshy and edible parts of seeds and possibly seeds ( i.e. purely an ecological term) dispersed by ants.

At present, there is still a conflict between those who maintain the use of the word 'aril' in the general sense of Baillon (e.g. Corner, 1976) and those such as van der Pijl (1969) who recognize three distinct types of fleshy appendage in the sense of Planchon and Pfeiffer. Van der Pijl, through his publications on seed dispersal, has probably achieved the more widespread credence. In his view, the three categories are:

1. 'aril'-derived strictly from the funicle.
2. 'caruncle'-outgrowths of the raphe.
3. 'strophiole/arillode'-various outgrowths (not well delimited) of the exostome.

In addition, van der Pijl created a new 'catch-all' category, the 'arilloid', for structures of indeterminate (he is not an anatomist) but non-funicular origin.

The difficulty with the rigid three category approach is that so many intermediate types exist, especially in the Meliaceae. Not only do appendages arise jointly and indivisibly from, for example the raphe and aril together, but in other instances, according to Corner (1976,1:23) the aril can arise independently from two quite separated parts of the same seed, perhaps chalaza and exostome, and later merge.

Given this blurring of origin between supposedly distinct categories, it seems of little value to maintain them. Besides, the plethora of terms is confusing, one author's interpretation of 'arillode' for example is not another's. Whereas for Planchon (1845) it is an exostomal

(micropylar) outgrowth, for Pennington & Styles (1975) it is ' a fleshy outgrowth (which) forms a partially or completely free flap of tissue surrounding a part or a whole of the seed', that is, an aril in the sense of Corner and Baillon. In addition, it is dubious that, for example, the chalazal aril of one family is directly comparable ~~with~~ with the chalazal aril of another. 'The point is that among the genera of certain families, perhaps even among the species of a large genus..... the aril develops in different ways.

As an outgrowth, it is a phyletic character of the family, its precise manner of development seems to be generic or sub-generic.' (Corner, 1976,1:23)

The approach taken in this work has been to refer to the distribution of fleshy tissue without using any terms apart from 'aril' or 'sarcotesta'(see below), and often simply to refer to, e.g. ' a fleshy layer ... extending from raphe on each side' ( Heynea trijuga Roxb. ex Sims) where possible.

In the discussion at the tribal level, the questions of terminology are considered in the context of evolution & classification. Here, only aril (& sarcotesta) are used, each usually with a qualifying prefix such as raphe-aril, chalazal-funicular-aril etc.

Sarcotestal seeds.

As Corner (1976) points out, sarcotestas, although fleshy, do not have the status of appendages. They are less specific in their site of origin, often covering the entire seed-coat and are equivalent to Baillon's 'generalized aril'. The term 'sarcotestal' has had less controversial use than that of 'aril'. However, its application can be just as vexing. There are two fundamental and very different sarcotestal

states: bitegmic and pachychalazal seed-coats can both be sarcotestal but are not homologous as assumed by most authors. One such is van der Pijl (1955, 1956, 1957, 1969) whose lack of perception in the matter is a major flaw in his theory of seed evolution, as pointed out by Corner (1976,1:24). This is not suprising since van der Pijl was not an anatomist. Too often, phylogenetic conclusions are drawn from seed structures on the basis of only superficial observation. To be sure of homologies, anatomical investigation is vital, as in this case. In the Meliaceae, both sarcotestal types, one primitive, the other derived commonly occur, very often in the same genus, most demonstrably in Chisocheton.

Sarcotesta and Aril.

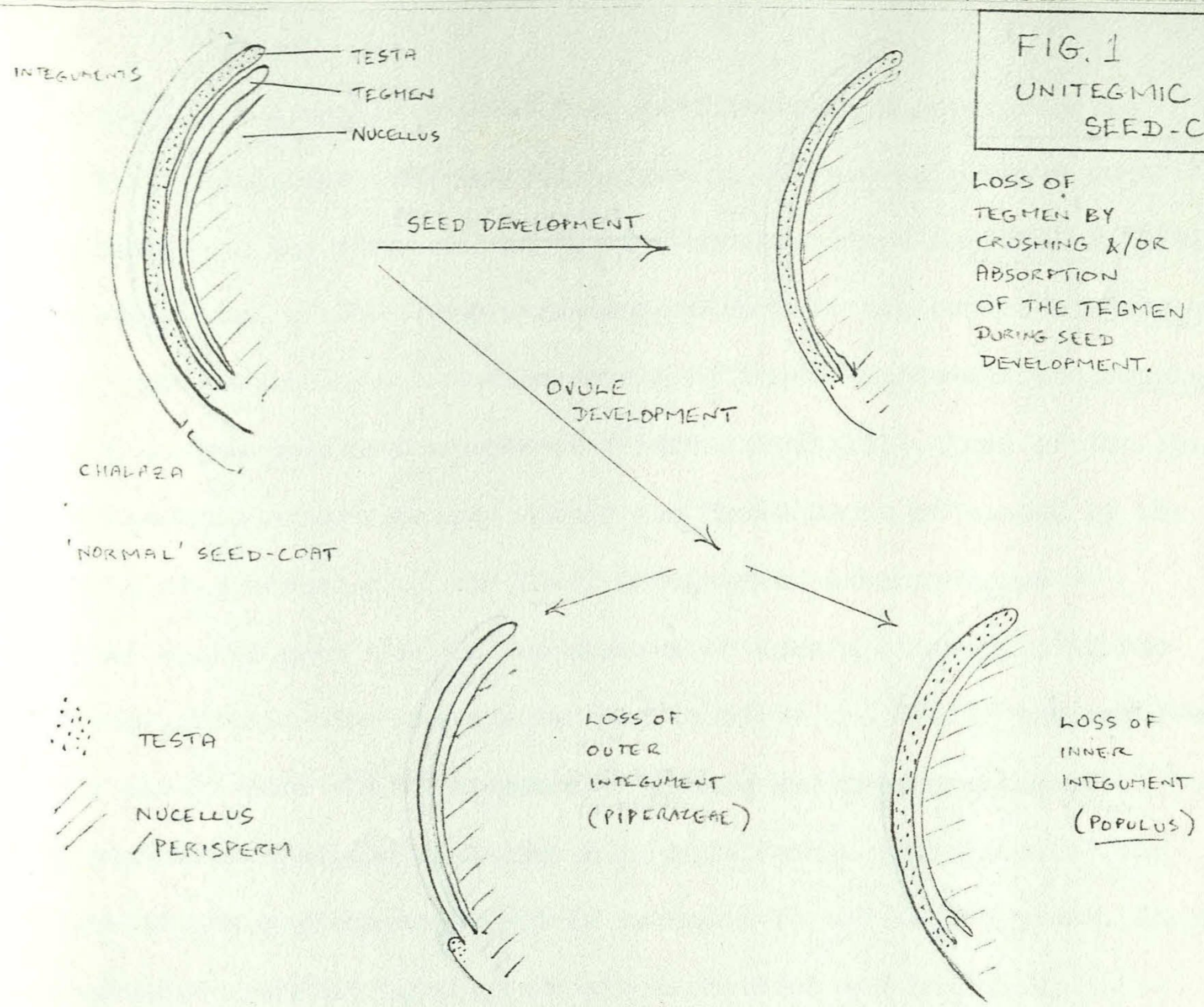
The distinction between the two is not so clear-cut as it seems. Thus, as suspected by Pennington & Styles (1975), " Studies.... may indicate that there is no fundamental morphological difference between them". The truth is that not only can a funicular aril-merge into a raphe-aril, but a chalazal-aril can merge into a pachychalazal sarcotesta. This can be particularly confusing when the seed is not completely pachychalazal as in Chisocheton. The relationship between these structures is examined within each tribe, particularly in Turraeeae, Trichilieae and Guareeae.

Unitegmic seed-coats

'Without doubt, the possession of two integuments is the primitive condition in dicotyledons' (Sporne, 1974:154). The weight of evidence cited there, undoubtedly favours that view and that unitegmy, that is the possession of a single integument, is derived. There are two well known types of unitegmy. The first is by loss of either of the two

# FIG. 1
## UNITEGMIC SEED-COATS

LOSS OF TEGMEN BY CRUSHING &/OR ABSORPTION OF THE TEGMEN DURING SEED DEVELOPMENT.




UNITEGMY BY LOSS OF AN INTEGUMENT




UNITEGMY BY CHALAZAL OUTGROWTH

integuments. A probable loss of the outer integument occurs in the ovules of Piperaceae: the single integument of Peperomia shows much resemblance to the inner one of Piper (Warming, cited in Bouman, 1984). A probable loss of the inner integument occurs in the ovules of Populus where some species have a weakly developed inner integument and Populus tremula L. has only one integument (Sporne, 1974:154). Loss of the inner integument can occur commonly during the development of a seed by the crushing or absorption of the inner integument. A second type of unitegmy occurs when the chalaza appears to form a large part of the seed-coat. Usually the chalaza is restricted to the end of the raphe and is the point where the integuments originate and the nucellus is confluent with the seed-coat (see e.g. Netolitzky, 1926). But, ' The chalaza of the perichalazal seed is extended in the median plane. In the pachychalazal seed it develops in all directions and builds by intercalary growth a new container for the endosperm and embryo. The wall of the container is single and is constructed by the multiplication of cells where the two integuments adjoin the nucellus and chalaza; generally it becomes highly vascular from extensions of the chalazal vascular supply. The two integuments persist at the micropylar end of the seed in a more or less vestigial state' (Corner, 1976,1:5).

A third 'path to unitegmy' has been described by Bouman and Chalis (1977) in Ranunculaceae, in which the tegmic and testal primordia 'fuse' in a complicated way to form a common structure which covers the seed. The significance of this discovery is not clear. I have not come across any other work which repeats or confirms their results.

The terminology of seeds with 'expanded' chalazas (see fig. 1) seems to have started in 1949 with Corner's (1949) 'perichalaza' reported from the Annonaceae (see quote above) this occurs when the chalaza is

expanded towards the micropyle in the median plane only, usually associated with a pre-raphe and/or antiraphe. No perichalaza was encountered in the materials examined here. He was followed by Periasamy (1962: 68) who coined the word 'pachychalazal' for those seeds where ' the chalaza may show an overall increase in size so that a wider part of the seed becomes occupied by the chalaza than was the condition before fertilization.' Periasamy seems to exclude from his definition of pachychalazal those unitegmic parts of the seed-coat which are 'sharply demarcated' from (i.e. not confluent with) the nucellus. Corner (1976,1:22-23) however, seems to include them. This part of the seed-coat, neither chalazal, pachychalazal ( in the sense of Periasamy, not of Corner), testa nor tegmen seems to have remained without a distinct name until recently, when von Teichmann et al. (1988) suggested the term 'peritesta' for it. Usual practice (e.g. Schmid, 1986) has been to refer to it (and the pachychalaza from which it is rarely distinguished by authors, or apparently by anatomical characters, e.g. Chisocheton in the Meliaceae) simply as 'testa'. The latter solution is not at all satisfactory since there can be a great deal of difference in anatomical characters (cf. Chisocheton) between the outer integument of a bitegmic seed-coat and that of a unitegmic one. Corner's usage is adopted here, for practical reasons.

# CHAPTER 4

## THE MELIACEOUS SEED

### 1. Conventions in Terminology.

The terms used here in describing the seed surface follow those of Barthlott and Ehler (1977), those for the anatomy follow Corner (1976). The latter is the standard work on dicotyledonous seed anatomy and consequently every effort has been made to make the descriptions given here compatible with it. However, some of the terms used there, although they must now be considered standard in seed anatomy, rest uneasily with conventional anatomical usage, so are explained here.

After the name and authority of the taxon, the provenance and any collector's notes of importance concerning maturity or ecology of the fruits and seeds is given. The most frequent collectors are abbreviated thus: Dr.D.J.Mabberley as 'D.J.M.' and Dr.T.D.Pennington as 'T.D.P.' Reference is made to descriptions of previous authors where appropiate. A description of the gross morphology (working from the outside inwards) is given, first of the fruit, then of the seed, in 'telegraphic' style, omitting articles in order to save space. Anatomical descriptions are then given of the bitegmic portion of the seed-coat working from the outside in. Measurements in micrometres are abbreviated to 'um'.

First the outer integument (the testa) is described, then the inner integument (tegmen). Longitudinal section is abbreviated to 'L.S.', transverse to 'T.S.'. Corner abbreviates the outer epidermis to o.e.,

the inner to i.e.. In order to avoid confusion with the commonly used abbreviation of id est, I was advised by David Cutler to use instead O.E. and I.E. respectively and these are adopted in the text as well as the plates and descriptions. The outer periclinal and inner periclinal walls of these epidermal walls are referred to as 'o.p.w.' and 'i.p.w.' respectively, again, in accordance with Corner. The intervening tissue is referred to as 'testal mesophyll' or just 'mesophyll' and abbreviated in the plates to 'Meso-'. The tegmen usually consists of an upper fibrous lignified portion, the exotegmen (abbreviated to Exo- in the plates) and a lower parenchymatous portion, the endotegmen ( abbreviated to Endo- in the plates). The component cells of the former are referred to as 'exotegmic fibres'. Seed-coats with a hard exotegmen ('exotegmic seeds') usually have either columnar cells- 'palisade exotegmen' or prostrate, fibrous cells- 'fibrous exotegmen'. However, in the Meliaceae, although the cells are basically of the fibrous category, they vary in length to breadth ratio (L.S.) from >20:1 to about 1:1 (verging on the 'palisade' state) even in a single genus. There is no doubt that these cells are homologous despite the range in shape, so they are all referred to as exotegmic fibres, in keeping with Corner. However, in vegetative anatomical parlance, the shorter cells would be termed 'sclereids' and only the longer ones 'fibres'. The phrase that embraces both being 'sclerotic cells'. Occasionally an inner epidermis (I.E.) is distinct in the mature seed. Elliptic cells filled with a hard, luminous dark-brown substance that fills the lumen and seems to permeate the cell-wall are referred to as 'tanninized cells', 'tanniniferous cells' or 'tannin-cells'.

The testa and tegmen are usually clearly distinguishable by anatomical 'markers' (see e.g., introduction to discussion) and by an intervening

layer of cuticle or occasional air-spaces. If not, sections taken near the chalaza or micropyle (where least crushing and absorption seem to occur) may reveal whether the seed-coat is bitegmic or unitegmic, and if the latter, whether by crushing and absorption of one of two integuments (usually the inner integument, the tegmen) during the development of the seed or simply by the seed-coat being formed from one integument rather than two. In the latter instance, vestiges of the testa and tegmen often occur near the micropyle as in e.g. Chisocheton sarawakanus (C.DC.) Harms or Malleastrum gracile Leroy. If the chalaza can be viewed as 'the whole region where the integuments originate' (Corner, 1976), then this type of seed-coat can be viewed as an extended chalaza or, to quote Corner: 'Pachychalazal seeds in which the chalaza may form the greater part of the seed-coat.' Corner's usage is followed here and consequently, such examples are called 'pachychalazal' or 'chalazal'. This interpretation is slightly contentious, in that some (e.g. Periasamy, 1962) would define the chalaza as the place where the integuments both originate and are confluent with the nucellus. The two do not necessarily coincide (see fig. 1 and literature review: unitegmic seed-coats). In a mature seed, where the nucellus may be completely absorbed, it is difficult, as he points out, to distinguish whether a given part of the seed-coat is confluent with it or not. Thus, though Corner's usage may lump together two entities that are not strictly the same, it is practical in this case.

For the purpose of describing a pachychalazal or unitegmic seed-coat of uncertain derivation (the latter usually referred to in the description simply as 'seed-coat'), it is sometimes convenient to divide it into an 'upper' and 'lower' zone. Sometimes an attempt is made to

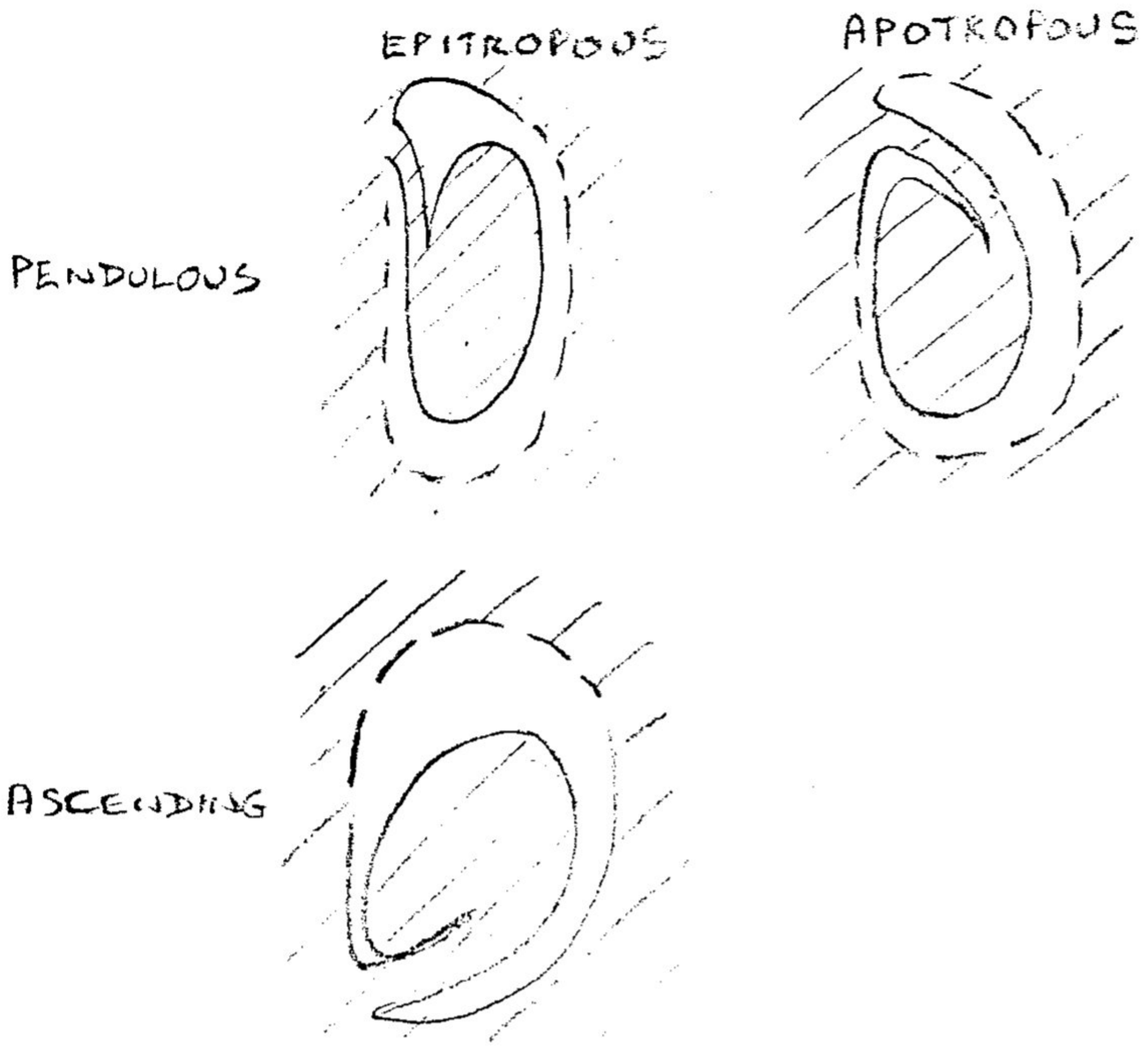
# FIGURE 2

## THE MELIACEOUS SEED - STRUCTURE & ORGANIZATION

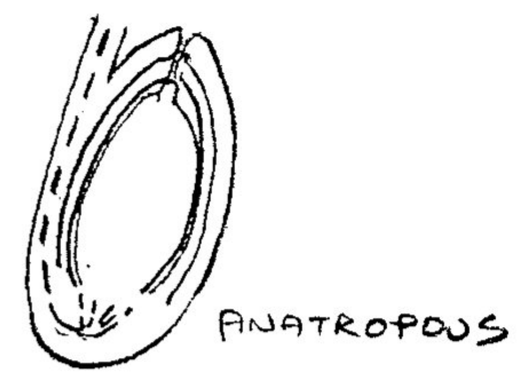
### SEED ORIENTATION

(AFTER GEESINK et al., 1981)

WITH RESPECT TO THE PLACENTA




### ORIENTATION WITHIN THE SEED





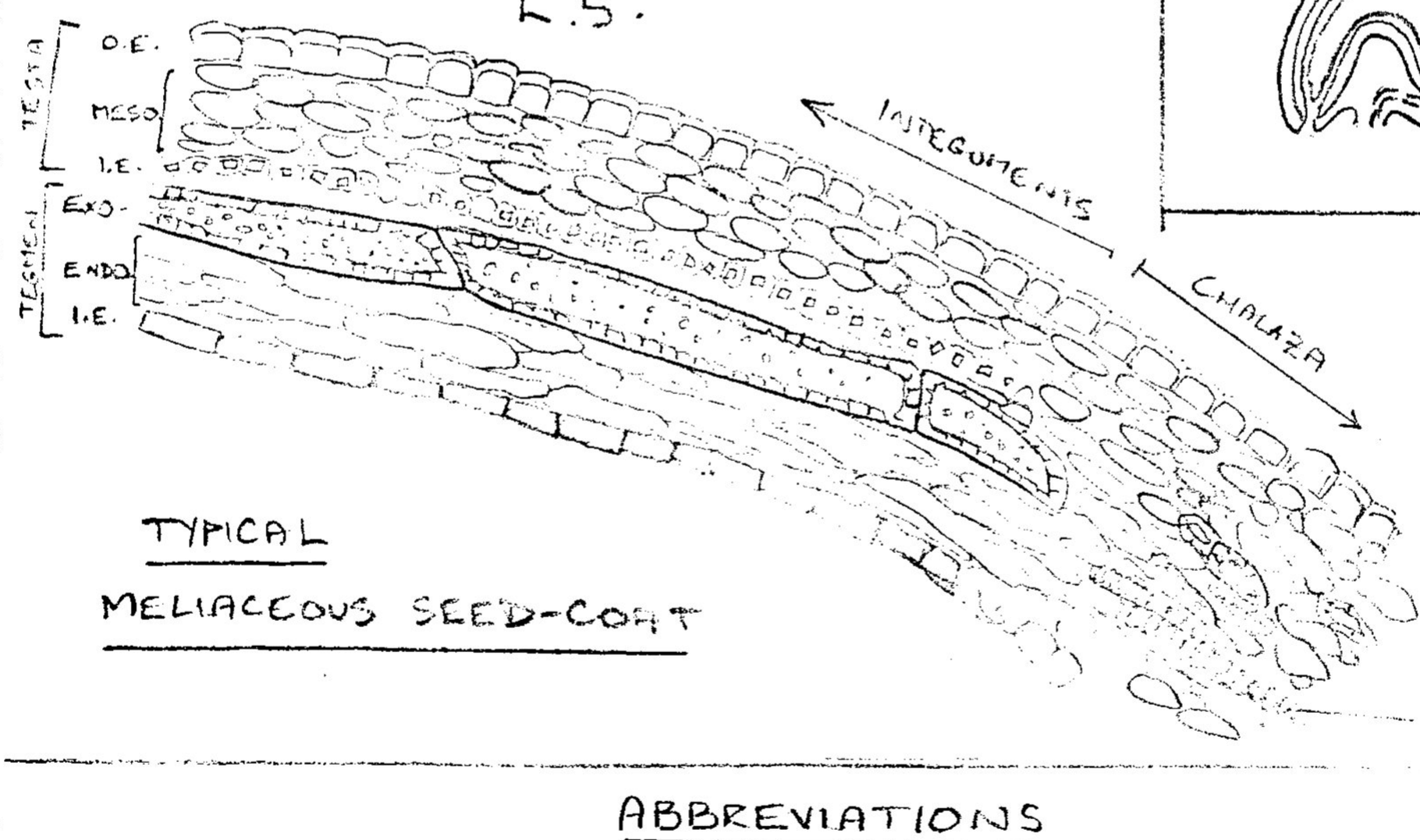


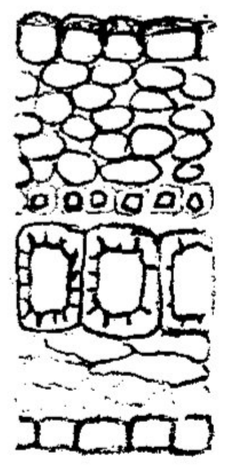






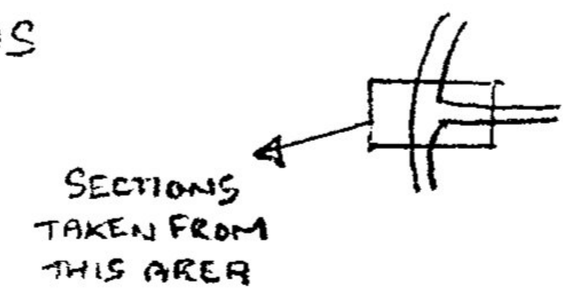
### TYPICAL MELIACEOUS SEED-COAT




### ABBREVIATIONS

O.E. OUTER EPIDERMIS
I.E. INNER EPIDERMIS
MESO. MESOPHYLL
EXO. EXOTEGMEN
ENDO. ENDOTEGMEN
V.B. VASCULAR BUNDLES
L.S. LONGITUDINAL SECTION
T.S. TRANSVERSE SECTION.




M. MICROPYLE
CH. CHALAZA
H. HILUM
R. RAPHE
COTS COTYLEDONS
RAD. RADICLE
F. FUNICLE
W.R.T. WITH RESPECT TO

contrast these zones in different species within a genus, but not usually between genera since their boundaries are artificially drawn.

In intensively investigated genera, where pachychalazal and bitegmic seeds occur in different species, e.g. Chisocheton, the chalaza of the latter type may be described in order to compare it with the pachychalaza of the first. In addition, perisperm (derived from the nucellus) endosperm and the embryo may be described since, in some genera (e.g. Chisocheton), it has taxonomically useful anatomical characters.

Further abbreviations used in the plates and descriptions are given in fig. 2. In the plate captions, botanical names are not underlined, and collection information not usually given (except when confusion might otherwise arise), since this appears in the descriptions to which the plates correspond, the appendix and is often given on the plate itself.

2. Pattern of construction.

Meliaceae seeds are usually pendulous and epitropous (but apotropous sensu Geesink et al. (1981: 212) in Synoum) in relation to the placenta. They are usually anatropous (but hemi-anatropous in most Turraeeae and Cipadessa, occasionally orthotropous, e.g. Astrotrichilia, some Guarea spp. and all Chisocheton spp. and campylotropous in Calodecaryia and Nymania), usually with a distinct funicle and raphe (except the orthotropous species), terminating in a small (10% or less of seed area) chalaza excepting in pachychalazal species. In some genera, particularly in the Trichilieae, a distinct raphe-like vascular bundle, the pre-raphe, proceeds from the chalaza towards the micropyle within the testa. No instance of a perichalaza has been discovered in species of the tribes covered here, though Corner mentions such a construction in

Lansium, Aglaia and Swietenia. Integument vascularization occurs in a few bitegmic genera, e.g. Chisocheton and Heynea (vascularized tegmen), Dysoxylum and Trichilia (vascularized testa) and is usual in the pachychalazal seed-coats.

The O.E. consists of isodiametric or longitudinally extended cells, often with a thick o.p.w. and cuticle, but very little surface sculpturing. Rarely the cells are columnar (in Heynea with a linea lucida).

The mesophyll consists of parenchyma, but is sometimes aerenchymatous, rarely the walls are thick and pitted. At the raphe (when arillate) and when the testa is fleshy, it is this layer that proliferates, the cells becoming thin-walled and lacunae (cf. Chisocheton) often develop between them. The latter appear to be derived from extremely large, thin-walled cells with fine, very pale, granular contents that appear to undergo lysis in the mature seed, leaving lacunae.

The I.E. also consists of isodiametric cells, as the O.E., but usually they are smaller, with thinner walls. Usually, each lumen contains and is nearly occluded by a single prismatic crystal of calcium oxalate.

The exotegmen usually consists of a single layer of longitudinal fibres of variable length. In T.S. they are isodiametric or columnar. Sometimes two or more layers of fibres are developed. In some species the lowest layers are of a length and shape different from the upper layers, and sometimes they are transverse in orientation. The exotegmic fibres are usually lignified and thick-walled, with various types of end-walls and pitting. The endotegmen is usually parenchymatous and crushed at maturity. Where an I.E. is distinguished, it is cuboidal or rectangular in T.S. and often with a dark lumen, but usually it is crushed and absorbed.

In the following chapters are presented the descriptions and plates of those genera investigated here. They are grouped into the Pennington and Styles (1975) tribes and presented in their order.

Each tribal account is prefaced with an introduction explaining the taxonomy (based on morphological, wood anatomical and seed anatomical characters) and geographical distribution of the tribe as currently understood, together with a critical examination of previous seed anatomical work. In this setting, the descriptions and plates are presented and discussed, first assessing the taxonomic utility of individual seed structural characters, and then investigating the use of these characters in defining the component genera, in indicating their generic affinities and infra-generic variation. This may be of assistance in arriving at an improved classification. This is followed by an examination of the use of these characters in tribal delimitation. Penultimately, seed characters are discussed (often at length) as a basis for 'phylogenetic speculation' . Finally, under 'ecological aspects', the functional aspects of seed-coat structure are considered, particularly in relation to dispersal agents.

Where it has not been possible to present data on a tribe due to lack of material, or time, a brief account of existing work is given at the end of the preceding tribe in the Pennington and Styles (1975) sequence.

# CHAPTER FIVE

## TURRAEEAE

### INTRODUCTION

The tribe Turraeeae differ from other Meliaceae in their simple leaves (except most Munronia, Naregamia and Turraea streyi White and Styles), hermaphrodite flowers, usually with a cylindrical staminal tube, style-head modified to form a receptaculum pollinis, seed endospermous and with radicle exserted.

The tribe consists of six genera: Turraea the 'core' genus, with 24 species in Africa, perhaps 35 in Madagascar and the Mascarenes and about six species (one sp. fide Mabberley, pers. comm.) in tropical Asia and Australia. It is surrounded by five small 'satellite genera': Munronia with about ten species from India Eastwards to Malesia; Calodecaryia with two species in S.W.Madagascar, Nymania monotypic in S. Africa; Naregamia one species in Angola, one species in India; Humbertioturraea about three to four species in Madagascar (Pennington & Styles 1975). The distribution is summarized in table 1.

Seeds of at least one representative of each genus were surveyed anatomically and micromorphologically in order to assess the value of seed micro-characters in this tribe. Previous investigations of Naregamia have been made by Nair (1960), though his study was largely embryological and he did not record the structure of the mature seed-coat. This is unfortunate, since many important and characteristic

| AREA \ GENUS | NYMANIA | CALODECARYIA | TURRAEA | NAREGAMIA | HUMBERTIO-TURRAEA | MUNRONIA |
|---|---|---|---|---|---|---|
| AFRICA | 1 | | 24 | 1 | | |
| MADAGASCAR & MASCARENES | | 2 | } c.35 | | 3-4 | |
| INDIA | | | } 1 | 1 | | } c.10 |
| MALESIA & AUSTRALASIA | | | | | | |

TABLE 1. GEOGRAPHICAL DISTRIBUTION OF TURRAEEAE SPECIES.
(DATA FROM PENNINGTON & STYLES, 1975)

| GENERIC DIAGNOSTIC CHARACTERS (CHARACTER STATES DEFINED IN TEXT) \ SPECIES EXAMINED / TOTAL IN GENUS (fide PENNINGTON & STYLES, 1975) | NYMANIA 1/1 | CALODECARYIA 1/2 | TURRAEA 8/60 | NAREGAMIA 1/2 | HUMBERTIO-TURRAEA 2/4 | MUNRONIA 4/10 |
|---|---|---|---|---|---|---|
| 'MACRO' CHARACTERS: RAPHE-ARIL (VERSUS SARCOTESTA) | — | — | + | + | — | — |
| LARGE HILUM (15-25% SEED SURFACE) | — | — | — | — | + | — |
| TEGMIC 'SKIRT' | — | — | — | — | — | + |
| EMBRYO STRAIGHT (VERSUS EMBRYO CURVED) | — | — | — | — | + | — |
| CAMPYLOTROPOUS (VERSUS HEMIANATROPOUS) | + | + | — | — | — | — |
| MICROMORPHOLOGICAL CHARACTERS: MACRO-VERRUCAE | + | — | + | + | — | — |
| TESTA CELLS SLIGHTLY CONVEX TO CONCAVE | — | + | + | — | + | + |
| TESTA CELLS PAPILLATE-HAIRY | + | — | + | + | — | — |
| TESTA CELLS LONGITUD. EXTENDED | — | — | — | — | + | — |
| ANATOMICAL CHARACTERS: TESTA SIMPLE HYPODERMIS | — | + | — | — | — | — |
| MULTIPLE HYPODERMIS | — | — | — | — | + | — |
| MESOPHYLL LACUNAR | + | — | — | — | — | — |
| I.E. WITH CRYSTALS | + | — | +(−?) | + | + | + |
| TEGMEN EXOTEGMEN MULTIPLE | — | + | — | — | + | — |
| EXOTEGMIC FIBRES LONGITUDINAL & TRANSVERSE | — | — | — | — | — | + |
| EXOTEGMIC 'FIBRES' LENGTH:BREADTH < 2:1 | — | — | +− | + | — | — |
| EXOTEGMEN O.P.W SINUATE | — | — | +− | + | — | — |

TABLE 2 GENERIC DISTRIBUTION IN TURRAEEAE OF SELECTED SEED CHARACTERS.

features do not appear in the seed-coat until the very last developmental stages (Corner, 1976,1:2). Corner also investigated the seed structure of Turraea pubescens Hell. ( i.e. T. virens L.-S.E. Asia). Both these studies tend to confirm that the usual Meliaceae pattern of seed-coat homologies (Corner, 1976,1:185) prevails in the Turraeeae. In brief, the inner epidermis (I.E.) of the outer integument (testa), consists of small, rounded, longitudinally rectangular cells (in L.S.) each often containing and largely occluded by a single prismatic crystal of calcium oxalate, whereas the outer epidermis (O.E.) of the inner integument (tegmen) consists of very large, longitudinally directed, lignified, pitted, often fibrous cells (exotegmic fibres). These anatomical 'markers' largely obviate the need for the developmental studies normally necessary to establish homologies.

Fleshy seeds are usual in the Melioideae, of which the Turraeeae form part. All the genera studied here have fleshy tissue on their ventral seed surfaces, variously known as arils or sarcotestas, of importance in animal dispersal. Part of this study is directed at an investigation of their anatomical bases. In some genera, these structures are very small (possibly reduced), e.g. Nymania.

Hemi-anatropous seeds, with slightly curved embryos are usual in the tribe, particularly Turraea, whereas in most Meliaceae, anatropous seeds and straight embryos are the norm. Leroy (1960), in describing Calodecaryia, convincingly showed, adducing correlated floral characters in support, how this genus might represent an intermediate state between the Turraea condition and that of the otherwise somewhat isolated Nymania where the embryo is very strongly curved and the seeds markedly campylotropous.

# PLATE 1

A-NAREGAMIA ALATA, SEED SURFACE, HIGH MAGNIFICATION.

TESTA CELLS PAPILLATE TO HAIRY.

B-NAREGAMIA ALATA, SEED SURFACE, LOW MAGNIFICATION.

NOTE 'MACRO-VERRUCAE'.

C-NYMANIA CAPENSIS, SEED SURFACE, HIGH MAGNIFICATION.

NOTE TESTA CELLS PAPILLATE TO HAIRY & WITH

CUTICULAR SCULPTURING.

D-NYMANIA CAPENSIS, SEED SURFACE, LOW MAGNIFICATION.

NOTE MACRO-VERRUCAE.

E-TURRAEA LEROYANA, SEED SURFACE, HIGH MAGNIFICATION.

NOTE TESTA CELLS PAPILLATE.

F-TURRAEA LEROYANA, SEED SURFACE, LOW MAGNIFICATION.

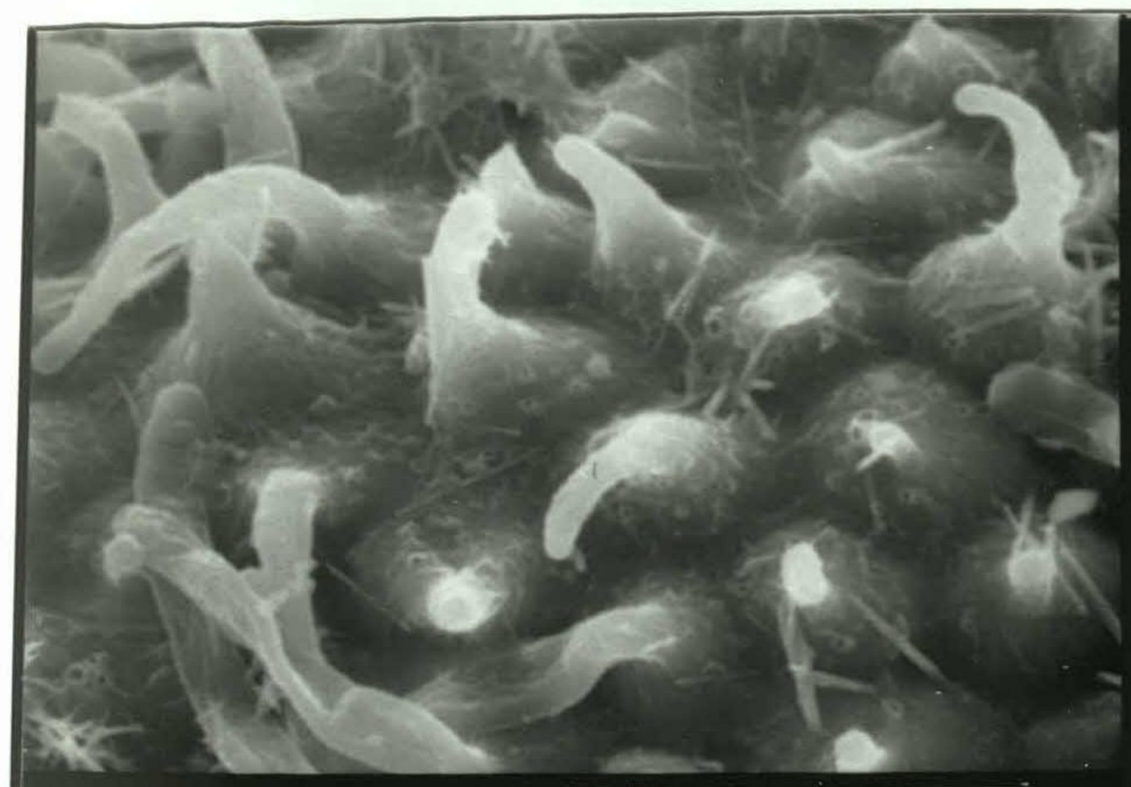
NOTE MACRO-VERRRUCAE.

G-TURRAEA HETEROPHYLLA, SEED SURFACE, HIGH MAGNIFICATION.

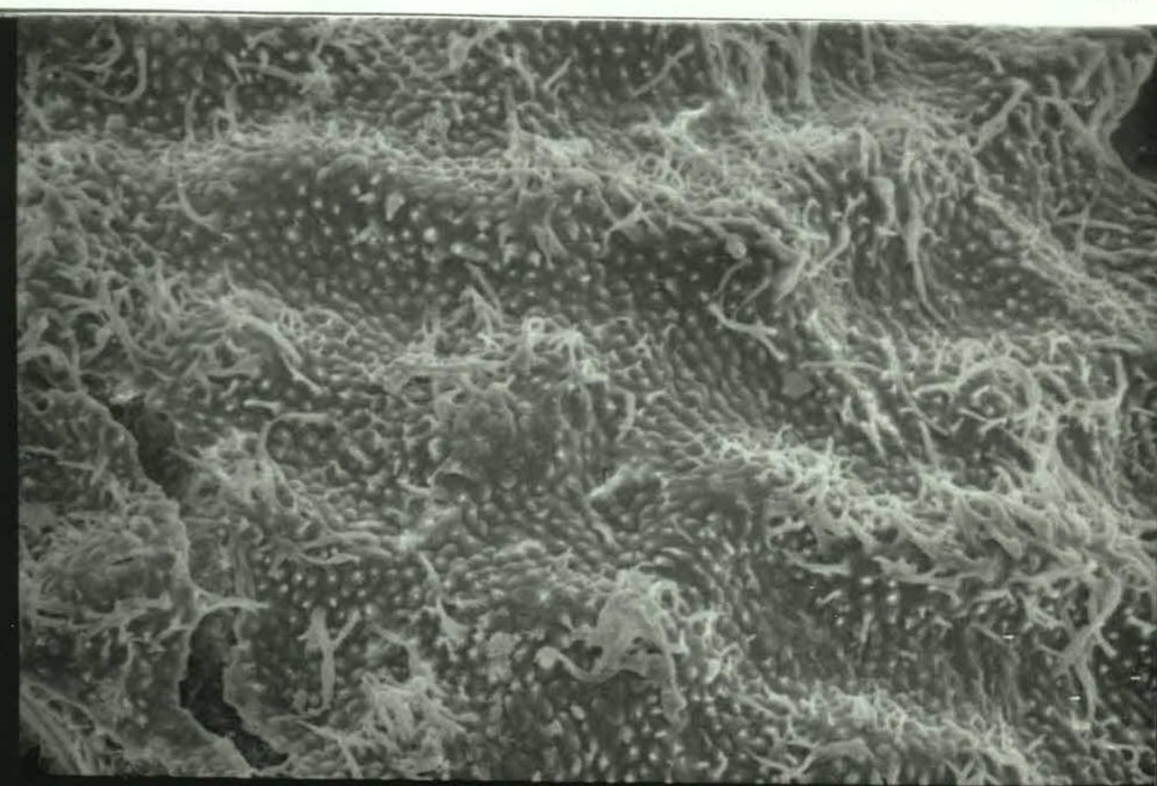
NOTE TESTA CELLS CONCAVE

H-TURRAEA HETEROPHYLLA, SEED SURFACE, LOW MAGNIFICATION

NOTE LACK OF MACRO-VERRUCAE, SURFACE SMOOTH.



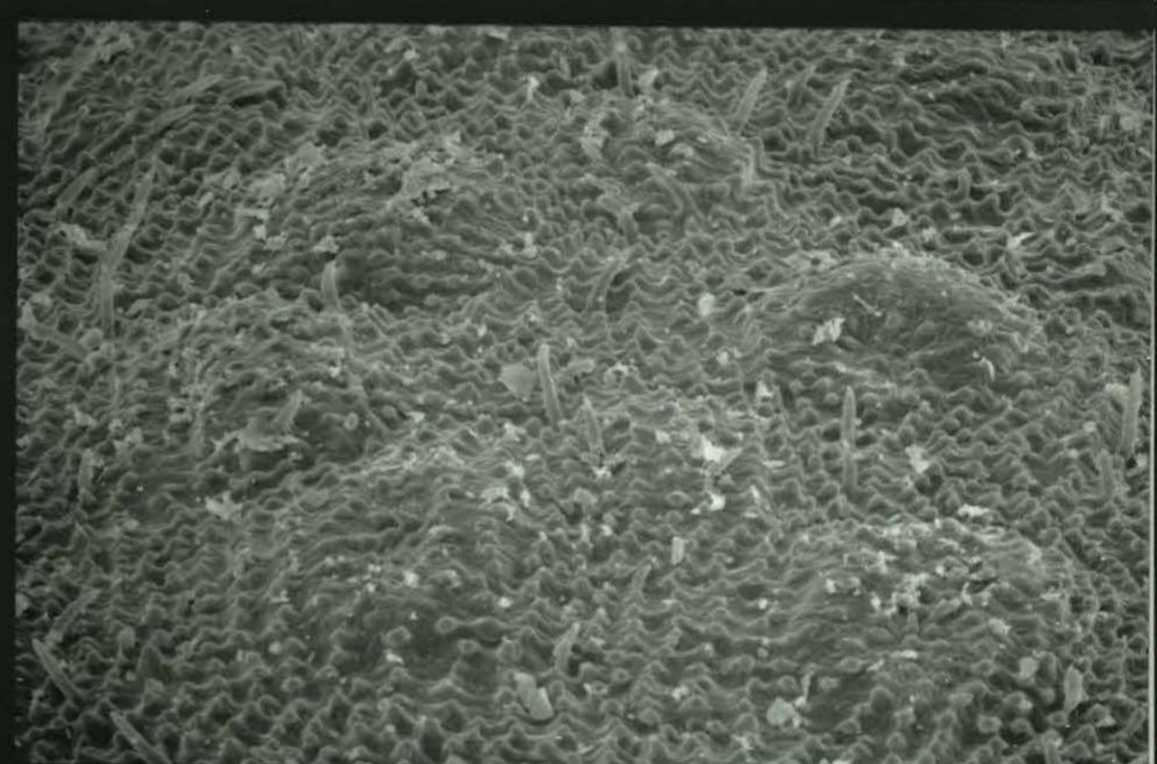
A 0001 25K 50um



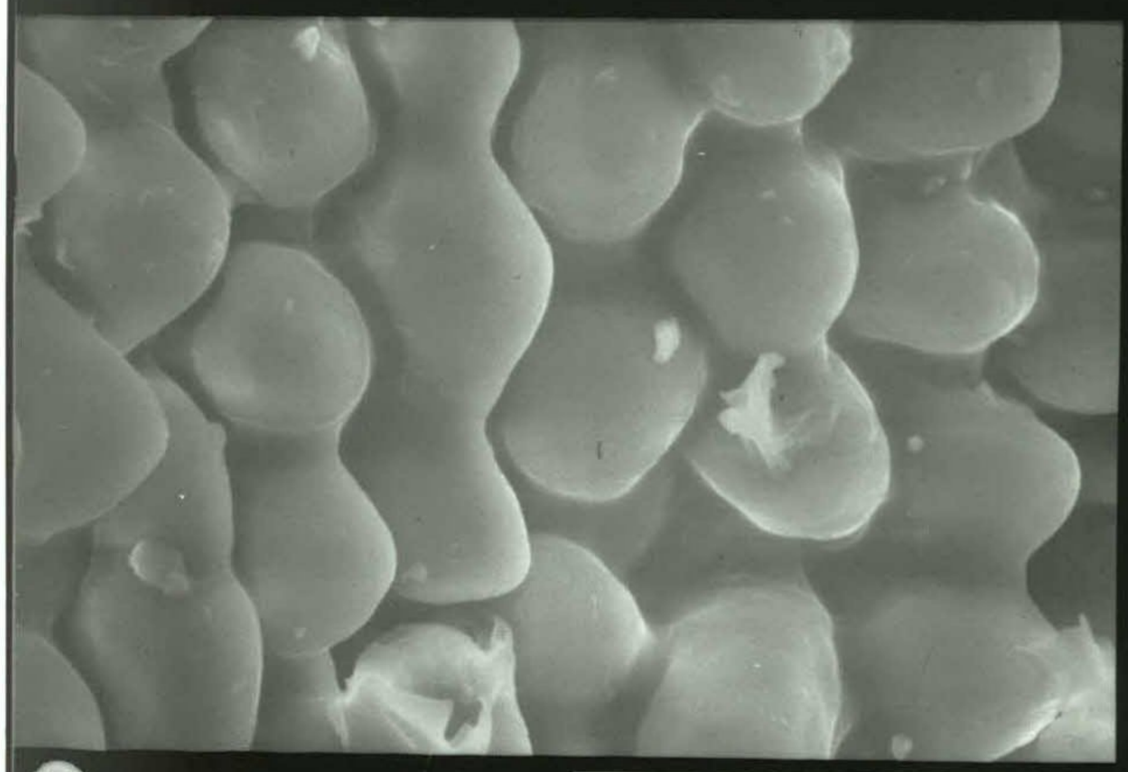
B 0002 25K 500um



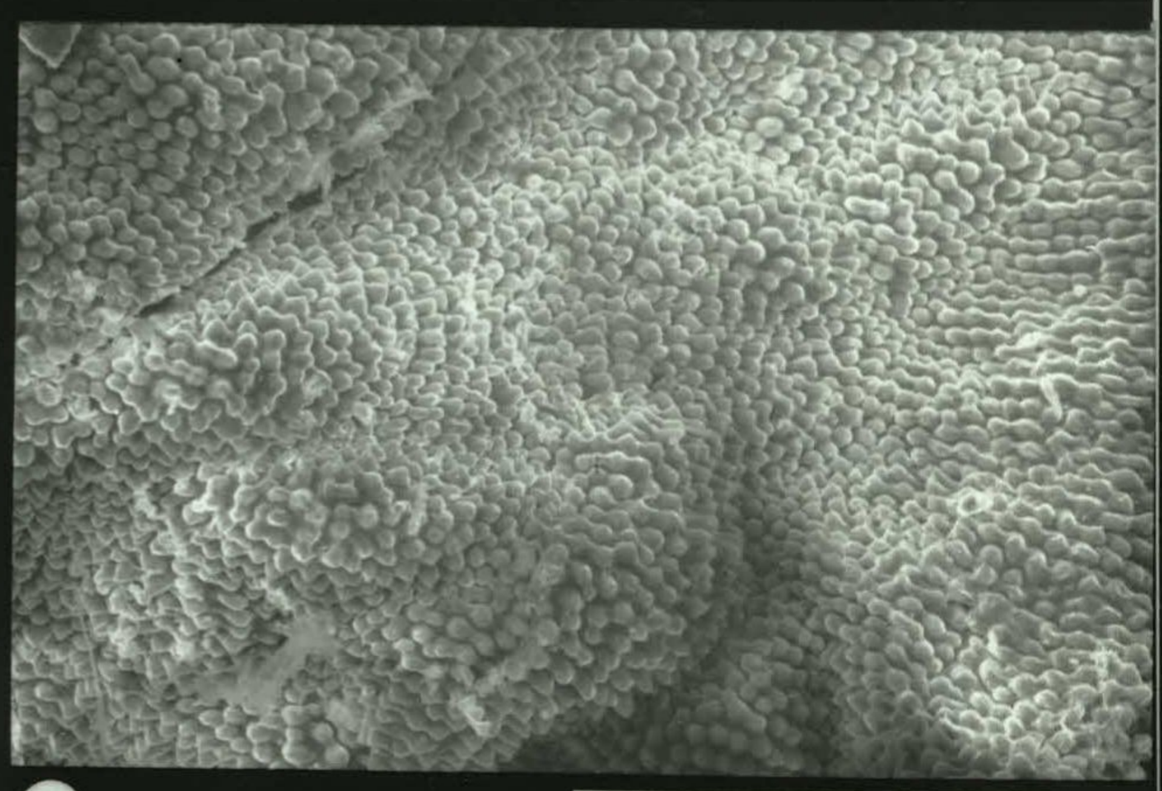
C 0013 25K 50um



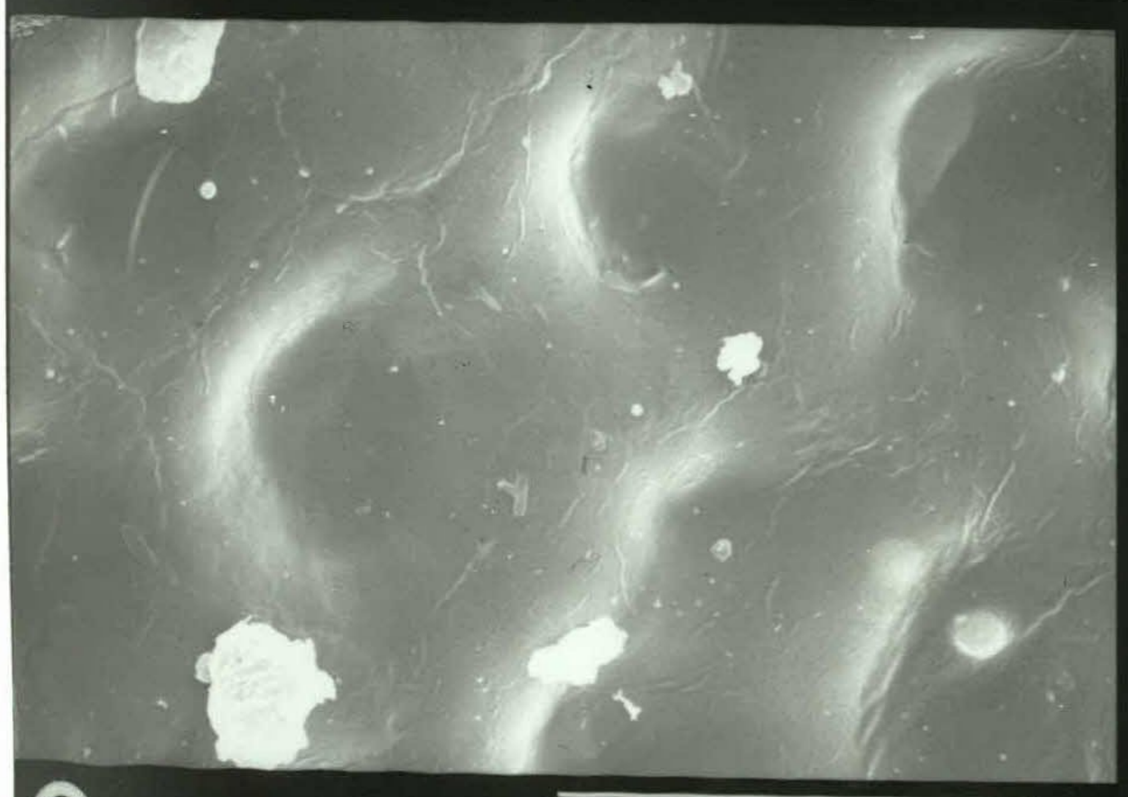
D 0002 25K 500um



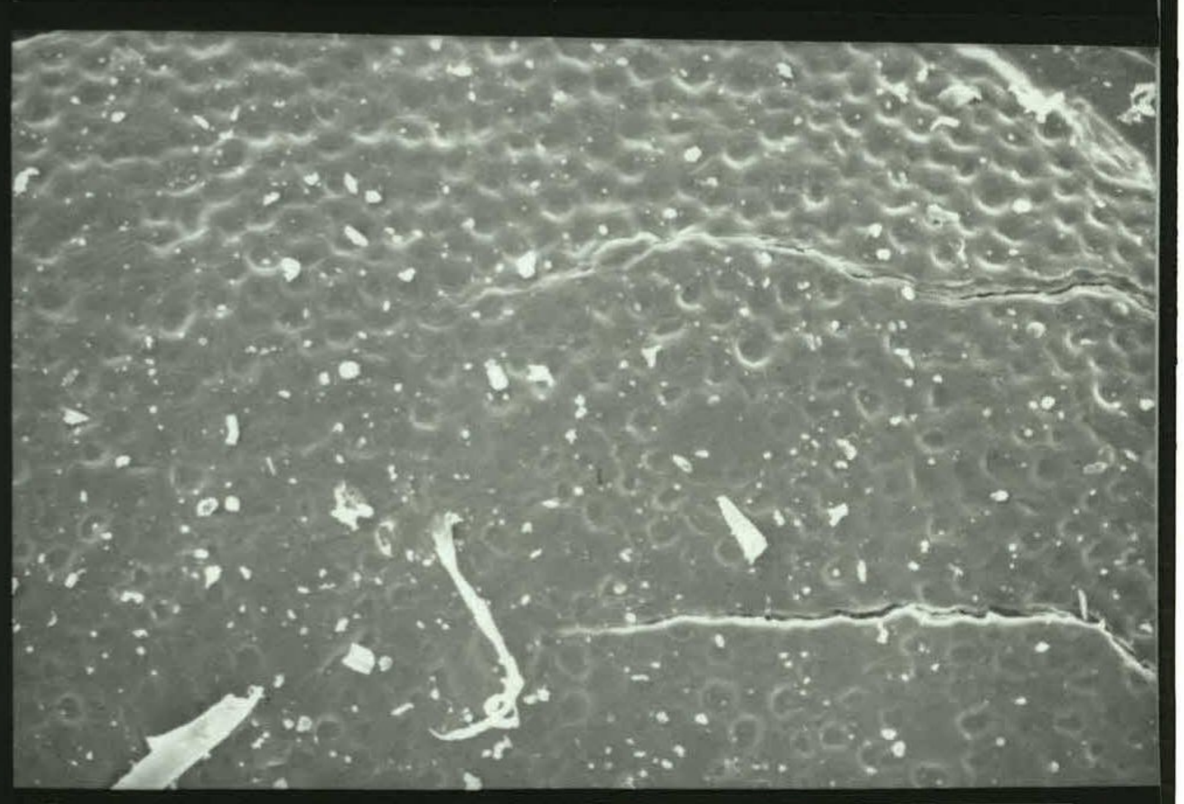
E 0004 25K 50um



F 0006 25K 500um



G 0015 25K 50um



H 0019 25K 500um

## MICROMORPHOLOGICAL RESULTS

The outer epidermal cells of the testa are generally isodiametric polygonal (rarely, e.g. in Humbertioturraea malifolia (Baker) Cheek ined., elongated polygonal, length: breadth ratio 2:1) with thick, straight anticlinal walls. Anticlinal boundaries are either raised (e.g Turraea nilotica Kotschy & Peyr.) or sunken (Turraea floribunda Hochst.). Outer periclinal walls can be tabular to convex (e.g. Munronia pinnata (Wall.) Theob.), but are more usually tabular to concave (e.g. Calodecaryia crassifolia J.F.Leroy, Humbertioturraea & most Turraea). Within Turraea, concave-tabular outer periclinal walls occur in Turraea nilotica, tabular in T.mombassana Hiern ex C.DC. and concave in T. heterophylla Sm. (see Plate 1).

Papillate or hair-like testa cells (highly convex outer periclinal walls) occur in Turraea, Naregamia & Nymania (see Plate 1). In Turraea leroyana Cheek ined., they are domed to papillate, whereas in Naregamia alata and Nymania, they are papillate to hairy.

Fine (cuticular?) sculpturing was not detected in any species except Naregamia alata which has micro-verrucae up to 2.5um diam. with up to 3 verrucae per 20um and Nymania with 15 finely folded ridges per 20um.

'Macro-verrucae', occurring as scattered or chains (usually transverse) of raised bumps, each consisting of 20-40 testa cells, were found in Turraea leroyana, Naregamia alata & Nymania. In the first, the bumps are 150-250um across, in the second about 150um across and in Nymania, 300-350um across.

## ANATOMICAL RESULTS

Turraea heterophylla Sm.

This description based on live material from Oxford Botanic Garden (Voucher FHO).

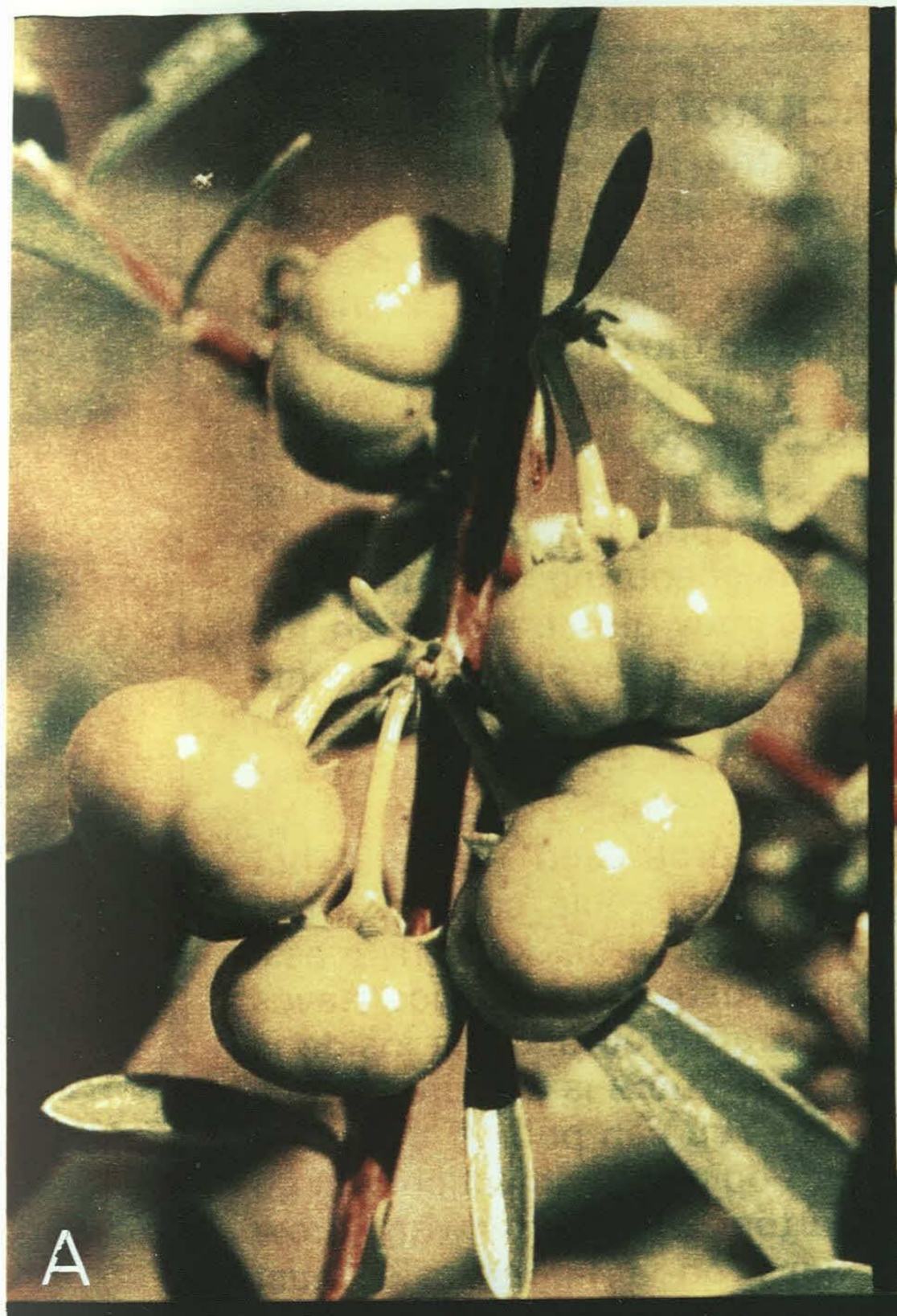
PLATE 2

A-TURRAEA OBTUSIFOLIA, FRUITS BEFORE DEHISCENCE

B-TURRAEA OBTUSIFOLIA, FRUITS AFTER DEHISCENCE. NOTE RED TESTA, ABSENCE OF VISIBLE FLESHY TISSUE. X 2.

C-TURRAEA HETEROPHYLLA, FRUITS BEFORE DEHISCENCE. NOTE ELONGATED SHAPE AND SINUOUS WALLS.

D-TURRAEA HETEROPHYLLA, FRUITS AFTER DEHISCENCE. NOTE ORANGE FLESHY RAPHE-ARIL AND ARIL-LIKE FRUIT SEPTA. X 0.5.


A


2

B


C

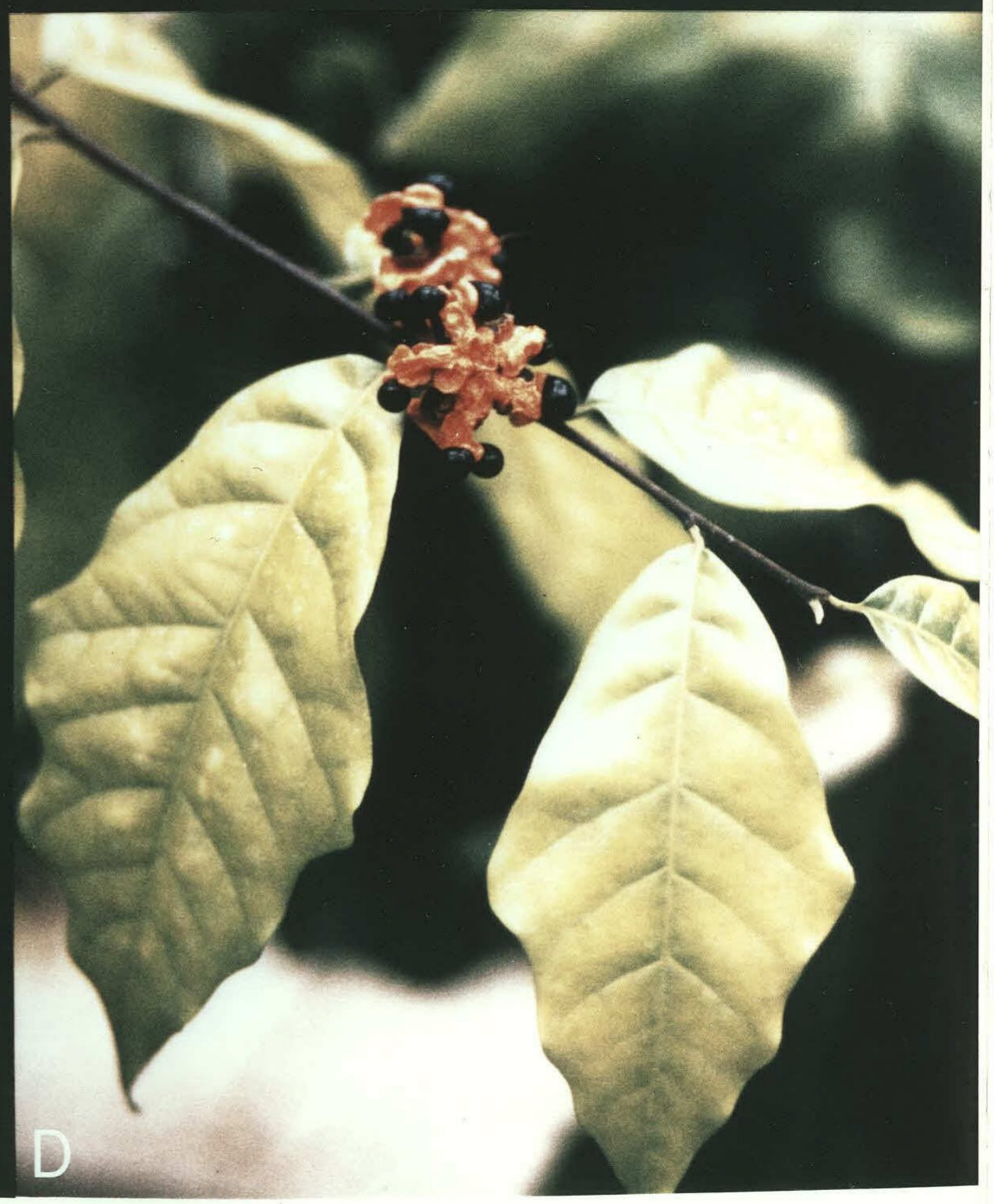

D

PLATE 3

A- TURRAEA ROBUSTA, FRUITS DEHISCING.

NOTE LARGE RED-ORANGE FLESHY RAPHE-ARIL WHICH ALMOST ENVELOPS TESTA. X 1

B- TURRAEA CORNUCOPIA, FRUITS.

NOTE SMALL, RELATIVELY INCONSPICUOUS PALE ORANGE RAPHE-ARIL. X 1.5


3
A
B

PLATE 4

A-D TURRAEA HETEROPHYLLA, VIEWS OF SEED

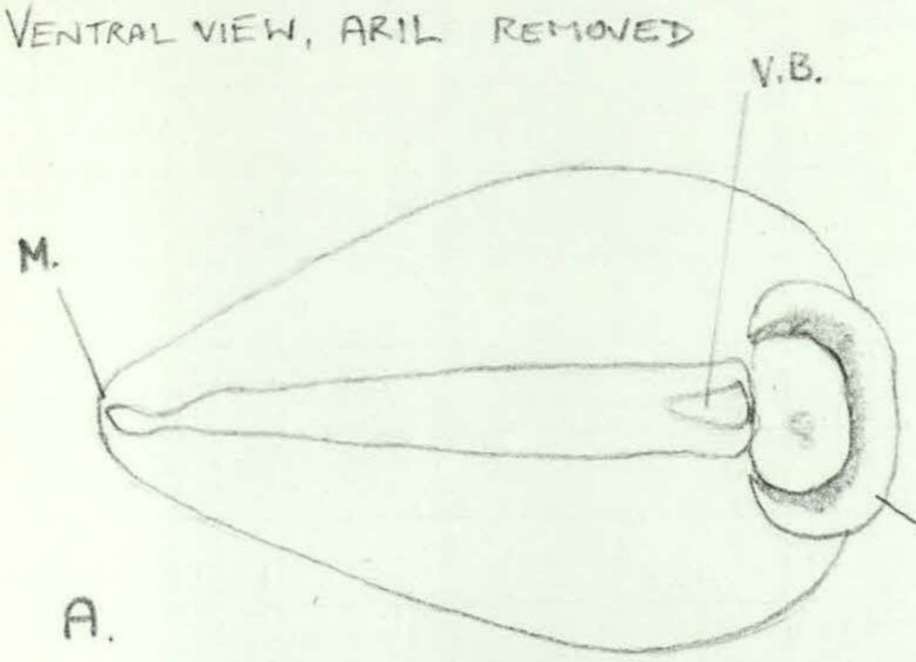
E-F TURRAEA HETEROPHYLLA,

SEED-COAT IN SECTION. NOTE VARIATION IN TESTAL MESOPHYLL,

CHARACTERISTIC TESTAL O.E. & EXOTEGMEN.

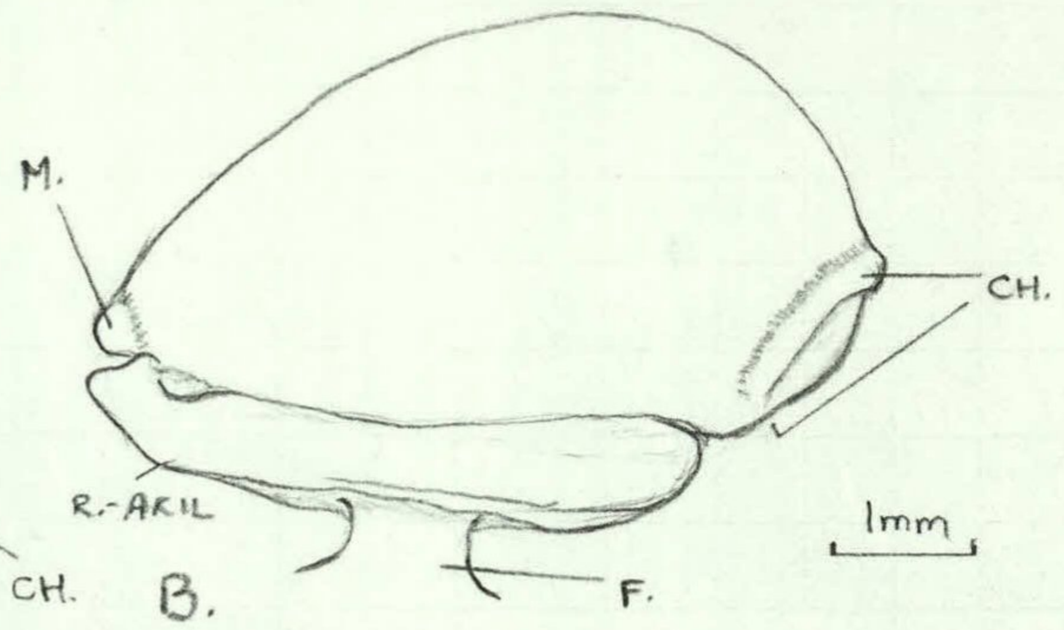
# TURRAEA HETEROPHYLLA Sm.

VENTRAL VIEW, ARIL REMOVED



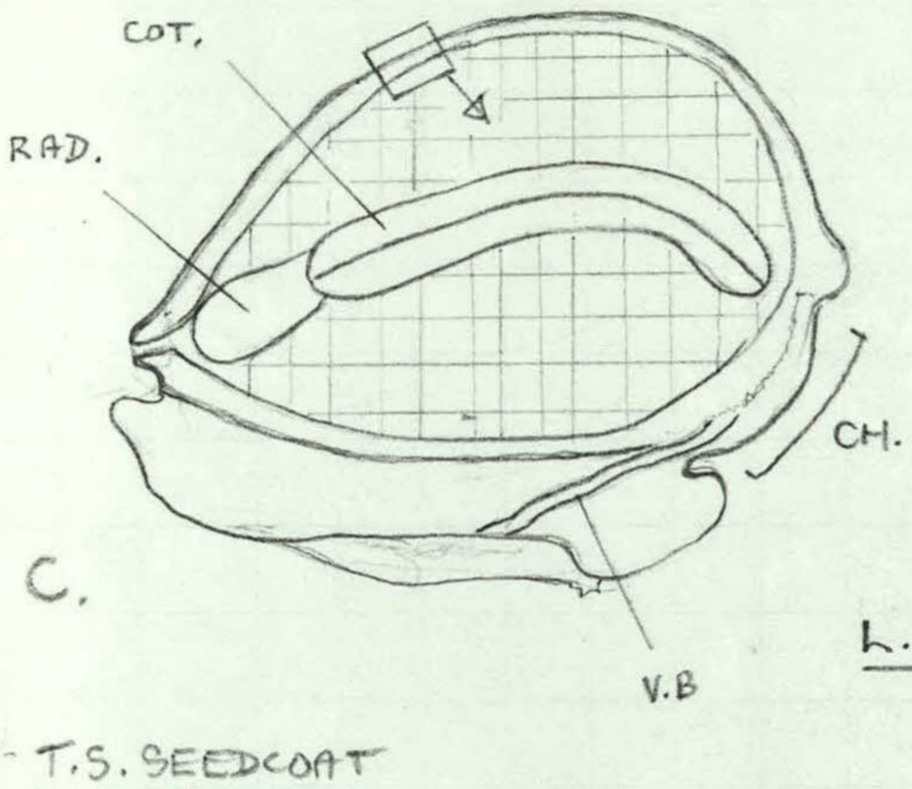

A.

LATERAL VIEW
ARIL ATTATCHED



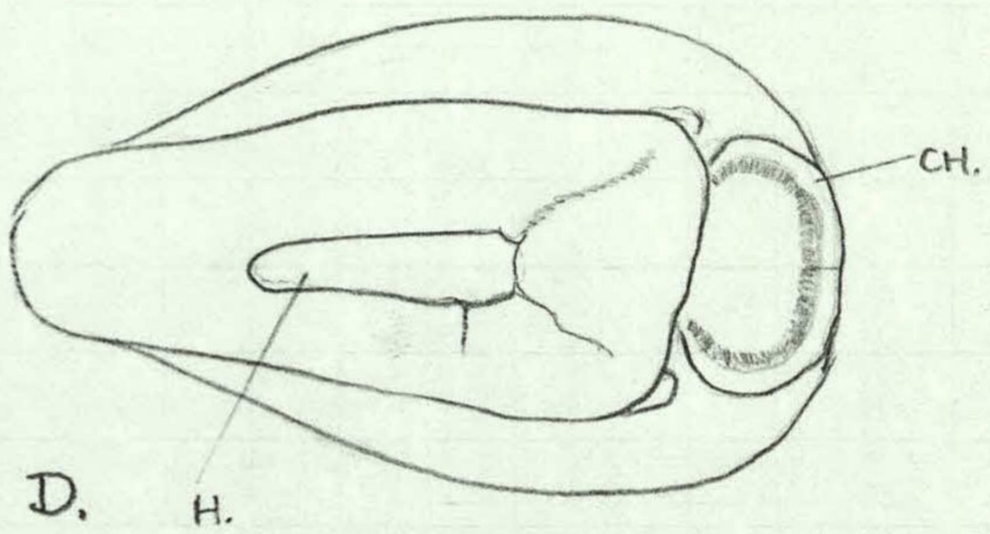

B.

LONGITUDINAL SECTION, SUB-MEDIAN.
(SEED 1)




C.

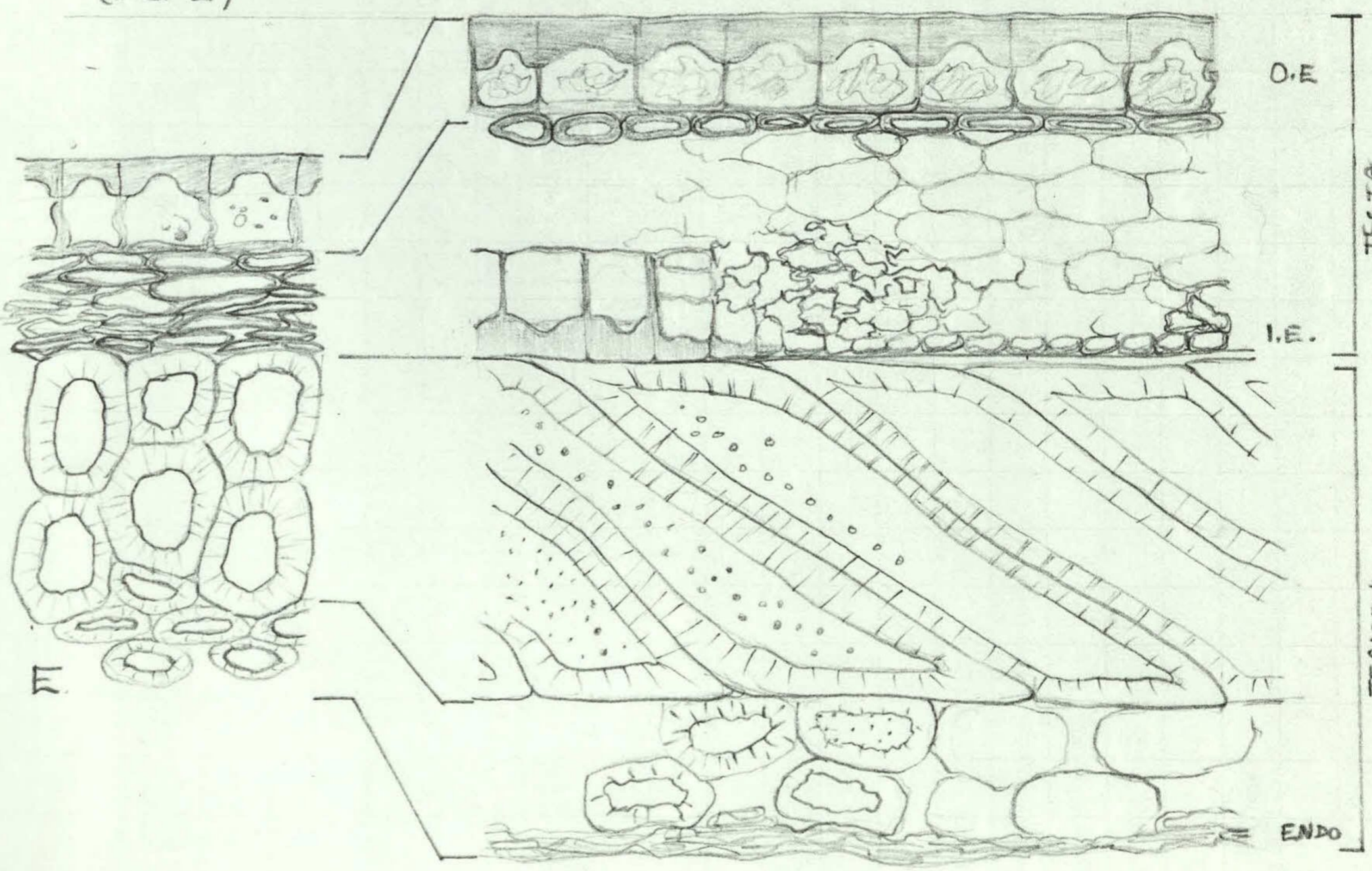
VENTRAL VIEW, ARIL
ATTATCHED




D.

L.S. SEEDCOAT (SEED 1)

T.S. SEEDCOAT
(SEED 2)




E.

F.

50um

PLATE 5

A-B TURRAEA LEROYANA, SEED-COAT IN SECTION,

NOTE SINUATE O.P.W. OF EXOTEGMEN, COLUMNAR TESTAL O.E.

WITH CONVEX O.P.W., UNDIFFERENTIATED TESTAL I.E.

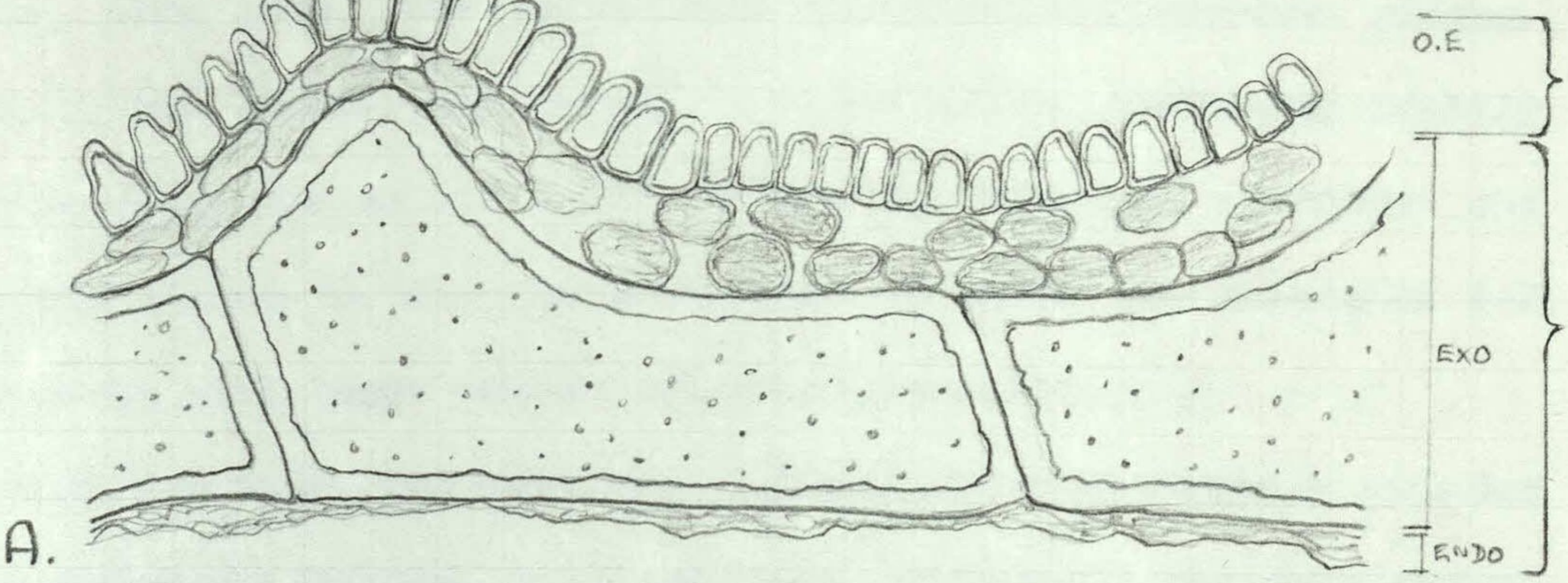
C-D TURRAEA SERICEA, SEED-COAT IN SECTION,

NOTE DISTINCTIVE THICKENING OF TESTAL O.E. O.P.W.,

PERSISTENT ENDOTEGMEN AND TEGMIC I.E.

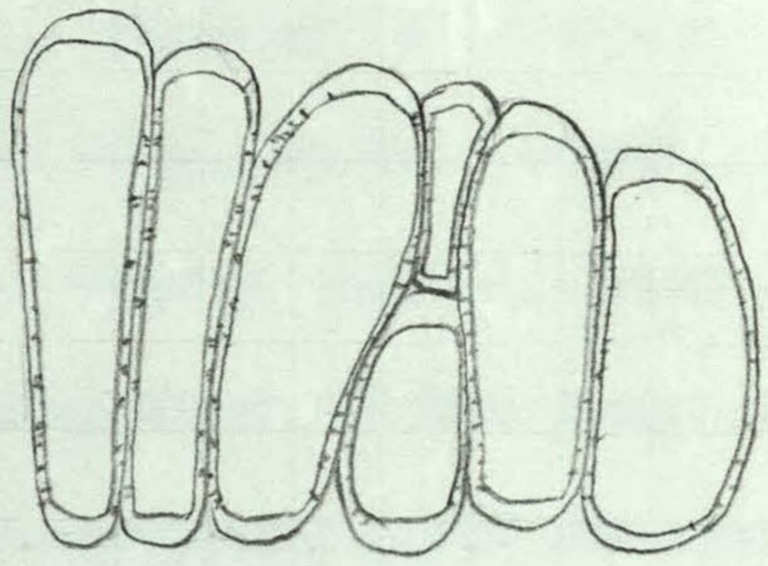
TURRAEA LEROYANA Cheek ined.

L.S. SEEDCOAT




A.

T.S. TEGMEN

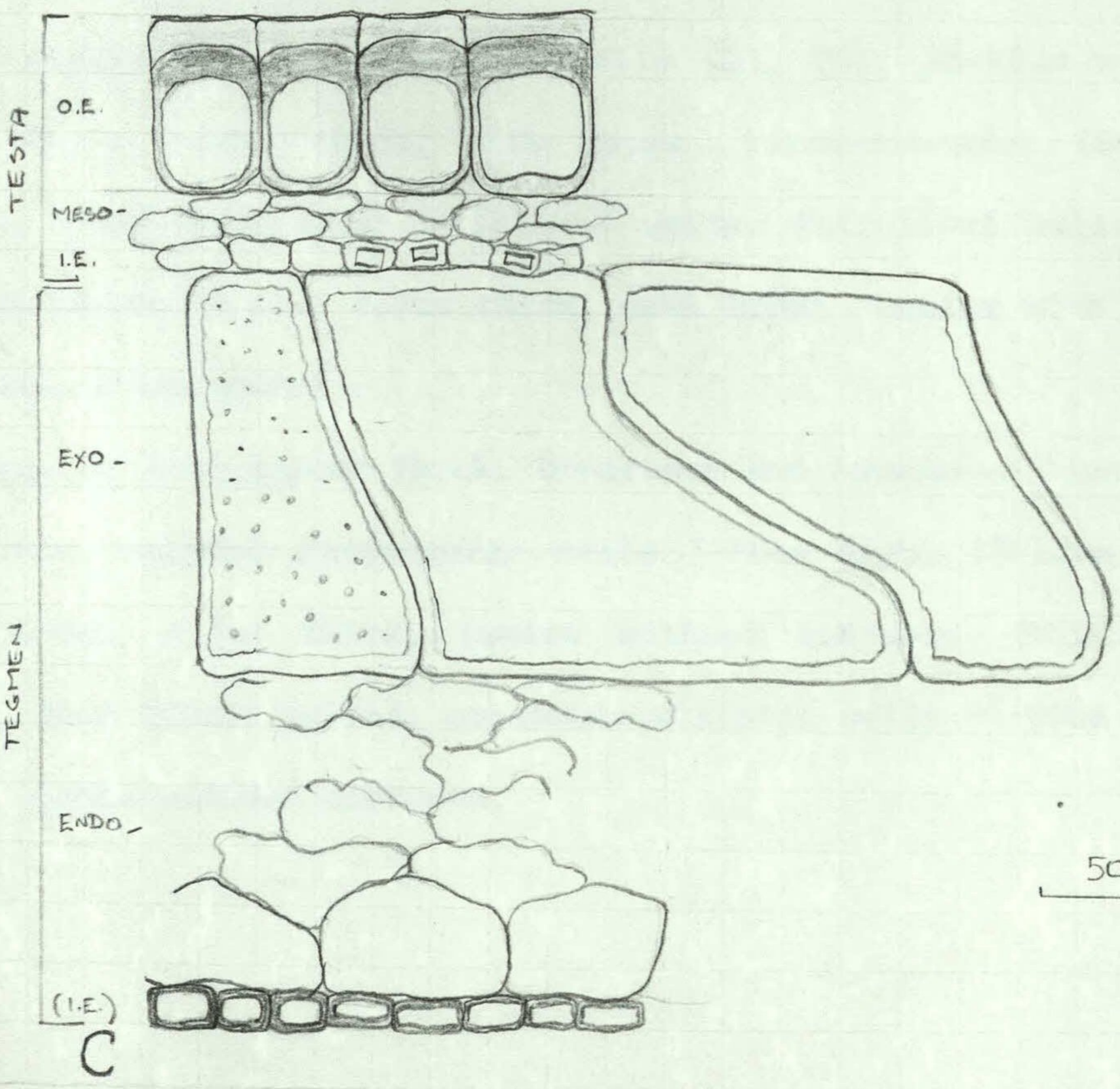


B.

50um

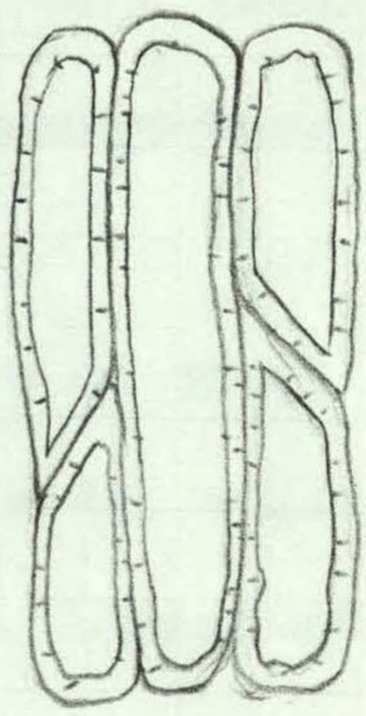
TURRAEA SERICEA Sm.

L.S. SEEDCOAT




C

T.S. EXOTEGMEN



D.

50um

GROSS MORPHOLOGY

Undehisced fruits green, ovoid, slightly distended, narrowly ovoid, 25mm long, 12mm wide, the walls with longitudinal sinuate ridges. Dehiscing by 5-6 valves, each woody, c.1.5mm thick, reflexing tightly and bearing along the entire inner surface an enlarged, succulent and bright orange septum to the placental edge of which are connected 1-2 jet black seeds with large ventral orange raphe-arils.

Seeds ovoid, 6mm long, 3mm wide, the chalazal end sub-truncate, c.1.5mm diam.,the micropyle pointed, c. 0.3mm diam. Raphe-aril narrowly ovate, c.5.5mm broad, 2.5mm wide, forming a cushion 1mm thick. Hilum longitudinal, narrow, 1.7mm long, 0.5mm broad, central. seed-coat c.0.1mm thick, longitudinal. Embryo curved, with foliar, transverse cotyledons c. 0.5mm thick (together), 3.5mm long, 2.5mm wide, radicle exserted, 1mm long. Endosperm occupying c.75% of seed.

ANATOMY

TESTA

Cuticle: even, 1-2mm thick, medium-brown.

O.E. single layer of cuboidal cells (LS, TS), 28-42um wide, 35-42um high. O.p.w. very thick, dark brown, plano-concave: 10um thick at centre, 14um thick near anticlinal walls. Anticlinal walls very thin, c.2-3um thick. I.p.w. c.7um thick, dark brown. Lumina with orange-brown cytoplasmic contents.

Mesophyll: 7-10 layers thick. Uppermost and lowermost layers of small, prostrate, rounded rectangular cells 7-10um high, 15-22um wide, walls dark brown, c.3um thick, lumina without contents. Middle layers of large, thin (<1um) walled, prostrate elliptic cells 26-60um wide, c.15um high. Lumina without contents.

I.E. single layer of small prostrate rectangular cells, c.7um high and 10um wide, walls 2-3um thick, lumina colourless. Occasionally expressed as the O.E., then as large cuboidal-columnar cells 22-29um wide, 28-45um high, o.p.w. 10um thick, plano-convex, mid-brown, anticlinal walls c.5um thick, cytoplasmic contents orange.

TEGMEN

Exotegmen 2-4 layers of sclerified, pitted and thick walled cells.

Upper layer 100-110um thick, but the cells longitudinally extended-rhombic in L.S., 140-315um in longest dimension (diagonally), 35-40um in narrowest dimension. Walls 7-10um thick, pale yellow, densely pitted, pits to 3um diam. In T.S., appears 2 cells thick, cells rounded, 35-42um wide, 28-50um high.

Lower 1-3 layers much smaller, prostrate elliptic cells, 22-56 um wide, 15-40um high, walls 7-10um thick, lowermost cells smallest, with thinnest walls.

Endotegmen completely crushed.

Naregamia alata Wight and Arn.

This description based on Sethi, Negi et al. 25904. Limited to 1 capsule.

Collector's notes: not available.

Nair(1959):'Testa. Soon after fertilization the integuments undergo conspicuous changes. In the micropylar region the cells of the outer epidermis of the inner integument elongate radially, while in the lower portion they undergo tangential elongation and become very conspicuous in the seed. The hypodermal cells divide so that the inner seed-coat consists of 5 to 6 layers.

PLATE 6

NAREGAMIA ALATA

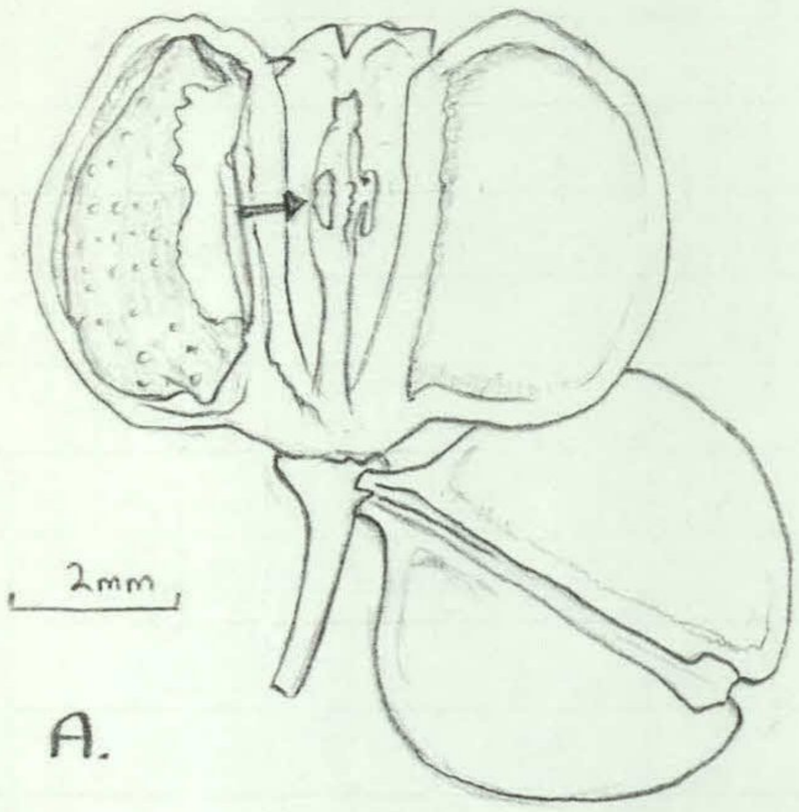
A THREE-LOCULAR FRUIT WITH SEED.

B-F SEED DISSECTED.

# NAREGAMIA ALATA W x A.

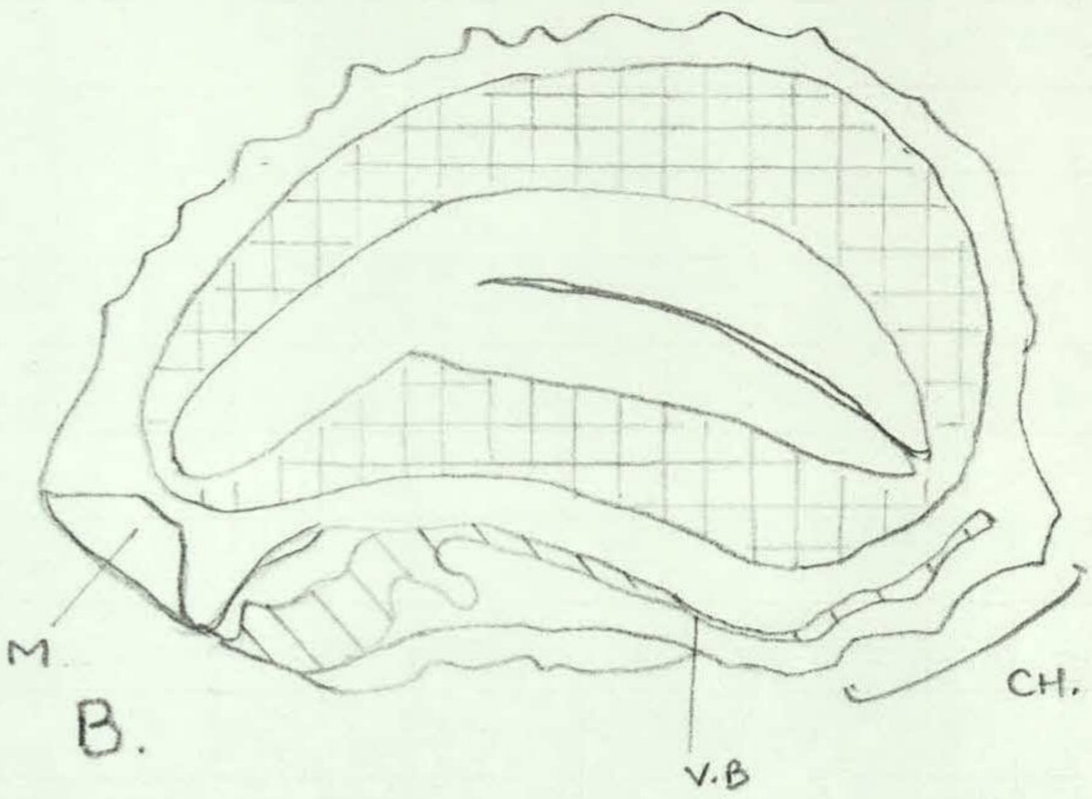


FRUIT: LATERAL VIEW (ONE VALVE DISPLACED)




A.

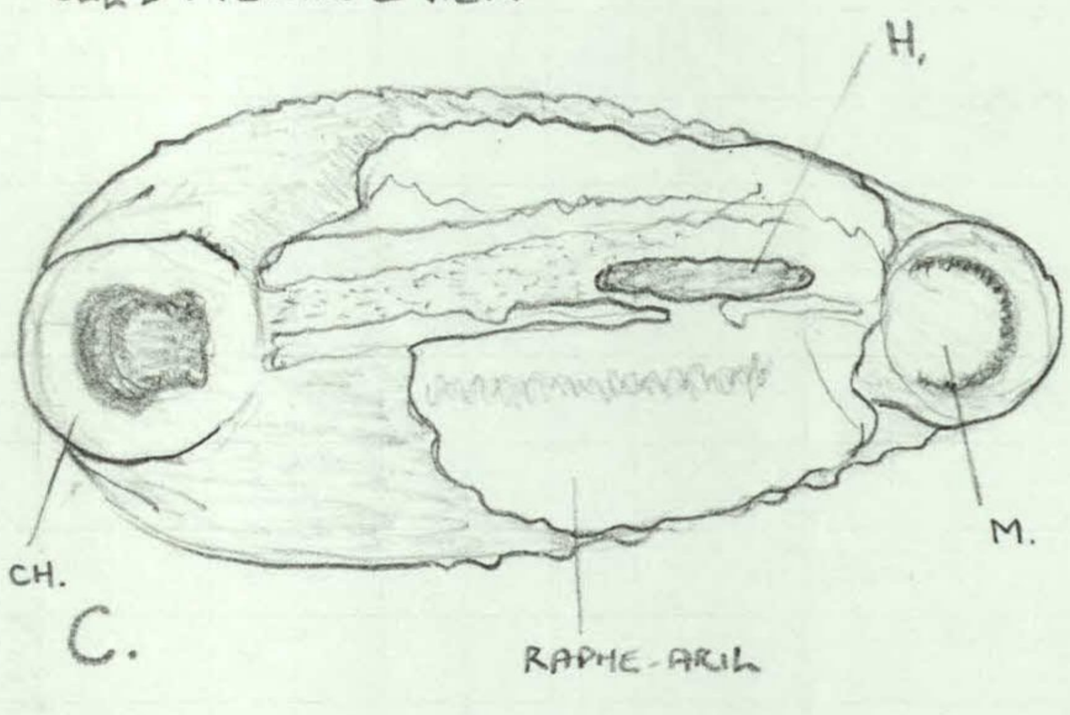
SEED: LONGITUDINAL SECTION



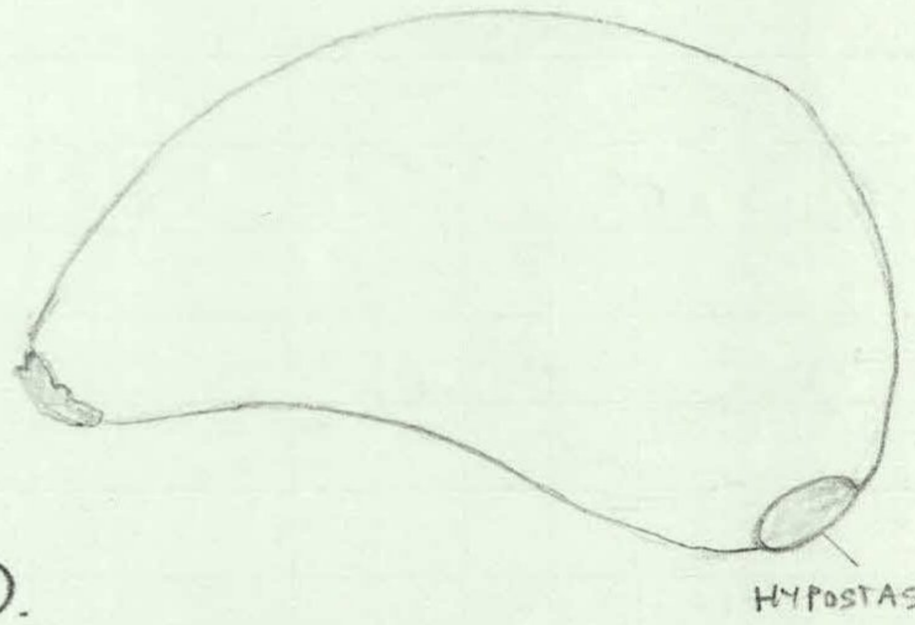

B.

ENDOSPERM: LATERAL VIEW

SEED: VENTRAL VIEW

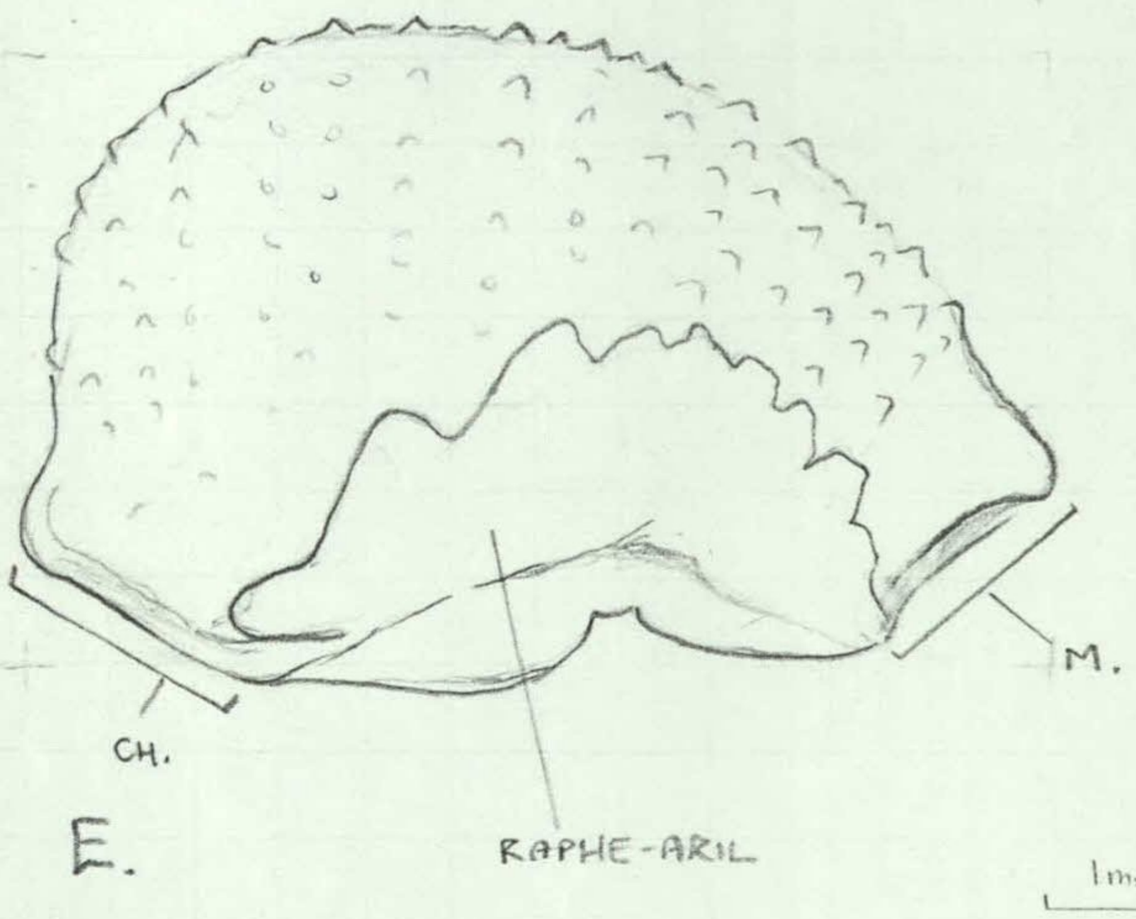



C.



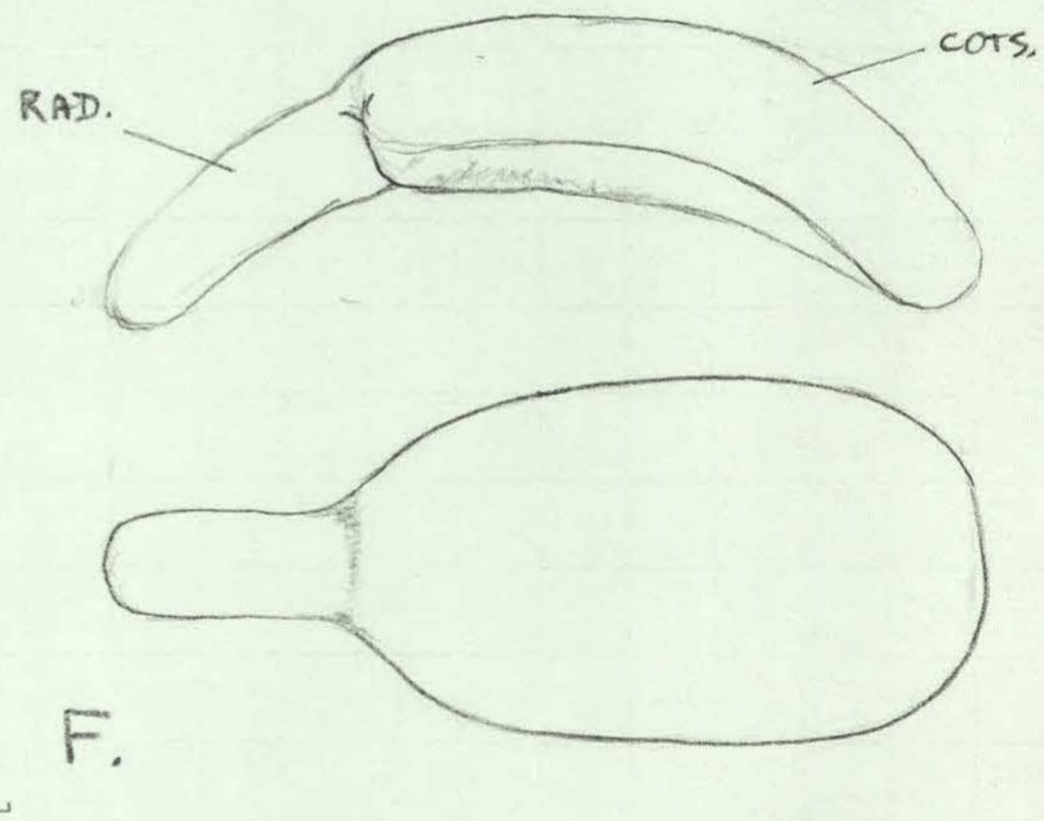

D.

SEED: LATERAL VIEW




E.

EMBRYO: LATERAL (ABOVE) & PLAN VIEWS




F.

1mm

PLATE 7

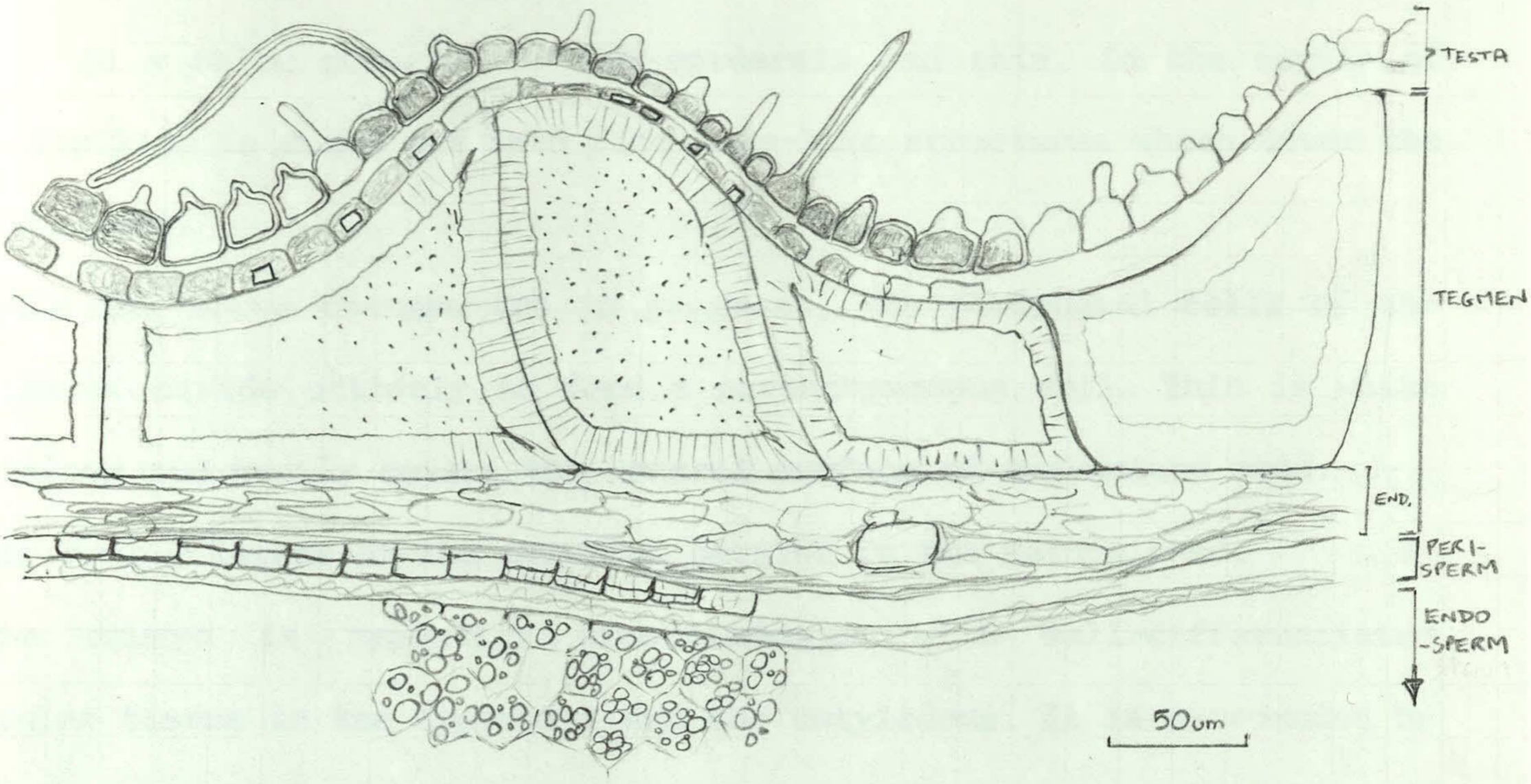
NAREGAMIA ALATA

A-C SEED-COAT IN SECTION. NOTE TESTAL O.E. PAPILLATE TO HAIRY

TESTAL I.E. WITH ENDOCRYSTALS, EXTEGMEN WITH SINUATE O.P.W.

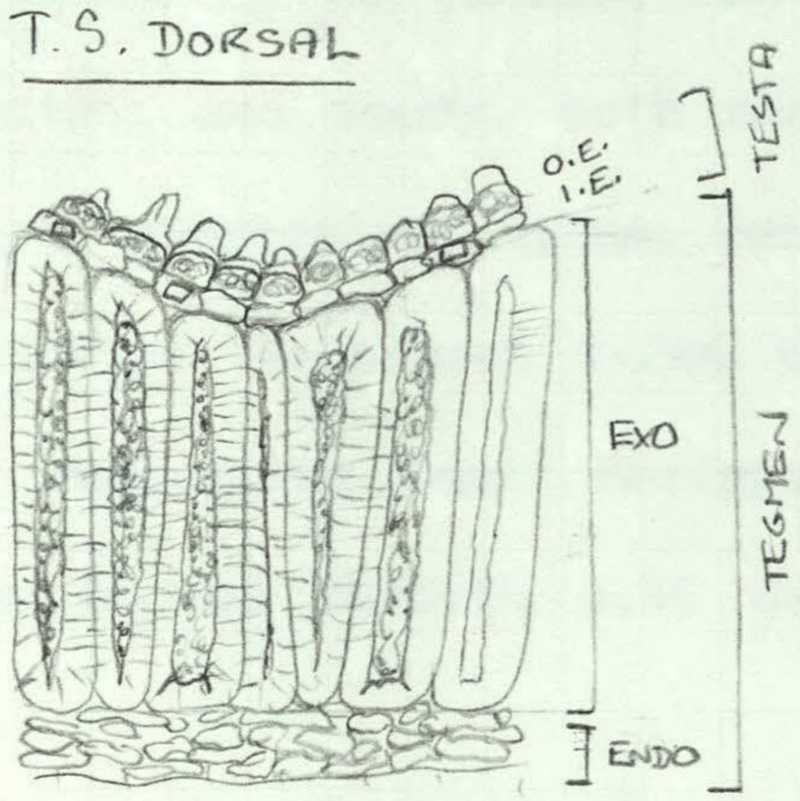
NAREGAMIA ALATA W&A.

LONGITUDINAL SECTION (DORSAL)




A.

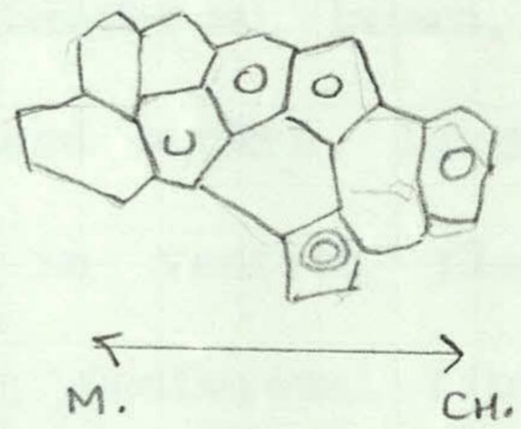
T.S. DORSAL




B.

PARADERMAL O.E. TESTA

(DORSAL)




C.

The outer integument remains 2 layered except in the micropylar region where it is three to four layers thick. The cells of the outer epidermis elongate rapidly, become papillate, and the walls become thickened. There is a thick cuticle for the epidermis and this, in the region of the papillae is drawn out into fine hair-like structures which cover the mature seed.

While the above changes are in progress, the peripheral cells of the funiculus divide actively to form a parenchymatous aril. This is white in colour and partly covers the ventral surface of the mature seed.

Only 2 or 3 layers of the nucellus persist in the mature seed.

The embryo is typically dicotyledonous with well-differentiated vascular tissue in the hypocotyl and the cotyledons. It is surrounded by 5 to 7 layers of endosperm tissue. The seed is dark brown, slightly curved and its surface is ridged'.

GROSS MORPHOLOGY

Fruit a small (7mm long, 4.5mm wide) sub-spherical, dry, loculicidal capsule, thin papery pericarp with 3 locules, one seed to each.

Seeds 4.5mm long, 2.5mm wide, slightly curved ovoid-ellipsoid in shape with a thin fleshy flap with sinuose margin issuing from the ventral raphe and pre-raphe and covering c.1/5th the lateral sides, extending longitudinally to chalaza and micropyle. Seed-coat brown, verrucose, puberulent and woody, both ends truncate and sunken, larger chalaza, smaller micropyle. Hilum central, sunk in ventral fleshy layer, 0.75x0.25mm. Seed-coat 1-2mm thick, tegmic, individual fibres visible under dissecting lens. Perisperm <1mm. Endosperm to c. 0.75um thick. Embryo curved through c.45 degrees, 4mm long. Cotyledons ellipsoid,

c.2.5mm long, c.1.75mm wide and 0.5mm thick. Radicle exserted, 1.5mm long.

ANATOMY

TESTA

Cuticle <0.25mm, even, thin, colourless.

O.E. single layer of shortly tangentially extended quadrangular cells (± isodiametric in paradermal view), o.p.w. convex, sometimes extruded to form a papilla or hair (complete range of intermediates). O.p.w. 2um thick, colourless. I.p.w. and anticlinals 0.5-1um thick, colourless. Lumina dense medium dark brown.

Hairs sinuous, often prostrate, to 140um long, 7um wide, walls 2um thick, colourless, without cuticular sculpturing. Arising from otherwise normal epidermal cells.

Mesophyll: not detected in most of seed-coat except ventrally, where proliferates and extrudes at raphe to form fleshy flaps.

I.E. single layer (rarely 2) of smaller shortly tangentially extended polygonal cells, isodiametric in paradermal view, 10-12um high, to 15um wide; walls and lumina dense medium brown. Cells with a single large yellowish prismatic crystal to 5um long and 3.5um high. Contrasts poorly with the lumina and thus difficult to discern. This layer often partly detached from layer above.

TEGMEN

Exotegmen a single layer of very shortly fibroid cells with thick (8-16um) yellowish walls, very highly pitted with small simple pits and dark yellow contents. Cells usually longitudinal, often with square end walls and almost isodiametric in L.S.; in T.S., appear narrowly columnar. In L.S., their upper wall curves sharply, giving rise to the

warty appearance of the seed-coat on exterior. Typical cell 180um long in L.S., 22um wide in T.S. and 130um high. At chalaza, fibres become much stouter, to 280um long.

Endotegmen usually crushed to 2 or 3 layers (Nair records 5-6 layers in immature seeds). Cells tangentially extended quadrangular, 15um high, 35um wide. Walls 1um thick, medium brown. Lumina without contents.

PERISPERM

2(-4) layers thick, cells quadrangular, tangentially extended 7um high, 24um wide, walls 1.5um thick.

ENDOSPERM

Without outer epidermis. Upper layers apparently partly absorbed and compressed (crushed layer of cells 8um thick between endosperm and perisperm). Cells isodiametric, 6-or 7-angled, 30-40um diam. Loosely filled with large ± spherical, pale yellowish lipid bodies, c.4um diam. Cell walls very thin and difficult to discern.

Humbertioturraea malifolia (Baker)Cheek

This description based on Cheek 2-20-1

Collector's notes:'Fruits exceptionally large...confused with those of Strychnos. Glossy green, ...., no ridges...Always borne singly and pendulous, when cut open seeds fill 2/3 of the capsule and are much larger than those of any other Turraea seen. With an 'aril' attached to the lower and proximal part of the seed, covering it - adnate and sarcotestal rather than placental derived fleshy structure? Fruits still unripe, 3 pickled, the rest bagged to mature a little before pickling.

PLATE 8

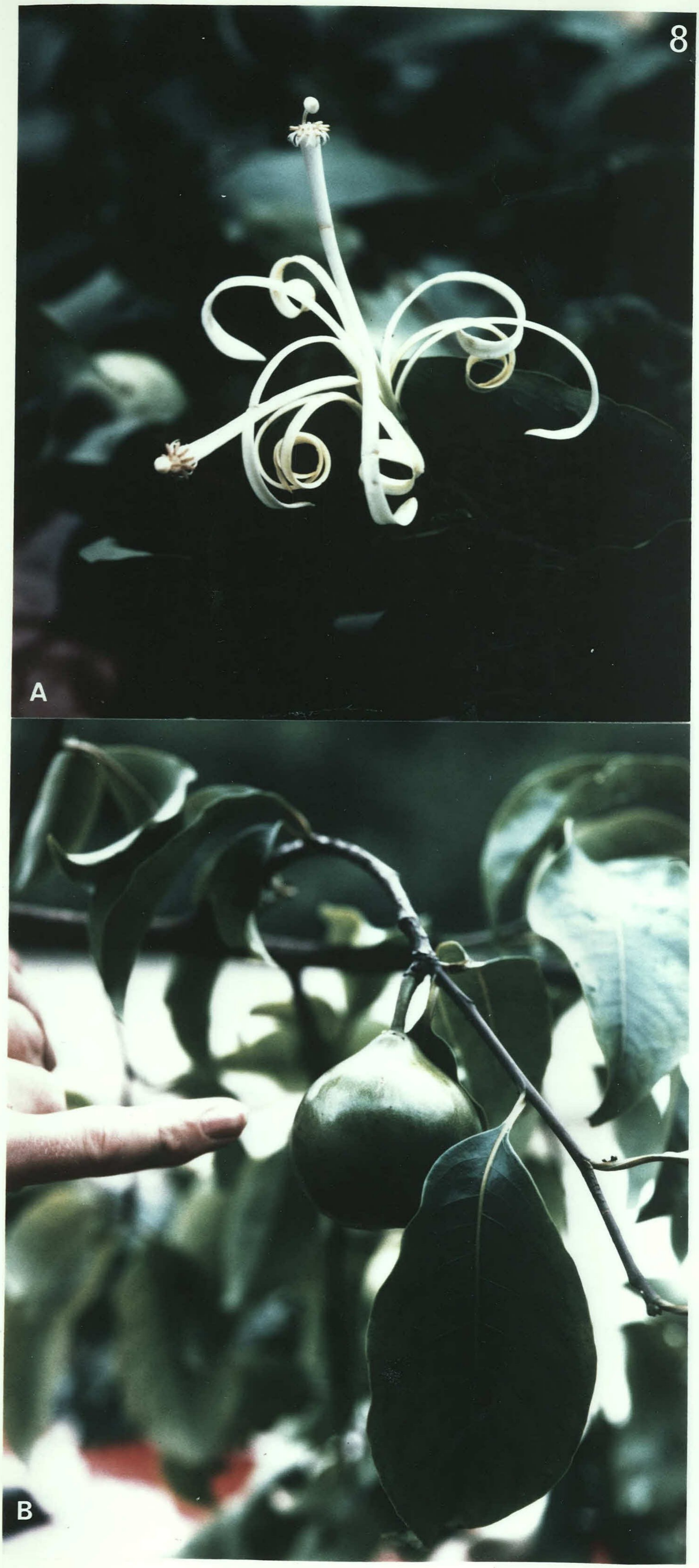
HUMBERTIOTURRAEA MALIFOLIA

A FLOWERS - INDISTINGUISHABLE FROM THOSE OF

TURRAEA SECTION RUTAEA X 1.

B FRUIT - INDEHISCENT & LARGER THAN MOST TURRAEA X 0.5

8



A

B

PLATE 9

HUMBERTIOTURRAEA MALIFOLIA

A-C FRUITS NOTE LARGE SIZE OF SEED IN RELATION TO FRUIT

(cf. TURRAEA) AND THICK PERICARP.

D SEED WITH REMAINS OF FRUIT PULP- APPEARS ARILLATE.

E-L SEEDS IN VARIOUS VIEWS AND SECTIONS,

NOTE VERY LARGE, FLESHY HILUM & SARCOTESTA.

NOTE ALMOST STRAIGHT EMBRYO.

HUMBERTIODENDRON MALIFOLIA (Baker) Cheek

FRUIT: L.S.
1cm

FRUIT: (MIN. SIZE.) PLAN VIEW
1cm

FRUIT: LATERAL VIEW (LARGEST)
1cm

A.

B.

C.

SEPTUM/ENDOCARP
CHALAZAL FLESHY Z.
SEED AS EXTRACTED FROM PULP.
PSEUDO-ARIL (FLESHY TISSUE)
SEPTUM/ENDOCARP

D.

LATERAL VIEW SEED 1
CHALAZAL FLESHY ZONE.

E

M.

REVERSE LATERAL SEED 1

F

H.

ENDVIEW SD 1

G

H.
M.

LATERAL VIEW. SEED 2

H

M.

REVERSE LATERAL VIEW/SD 2

I

ENDVIEW SD 2.

J

M
fleshy testa
H.

KEY

SURFACE: HILUM
SECTION: FLESHY TISSUE

SECTION: ENDOSPERM

1cm

CHAL. L.S.
T.S. L.S
MACERATION
V.B
M.
H.

K

T.S.

L

PLATE 10

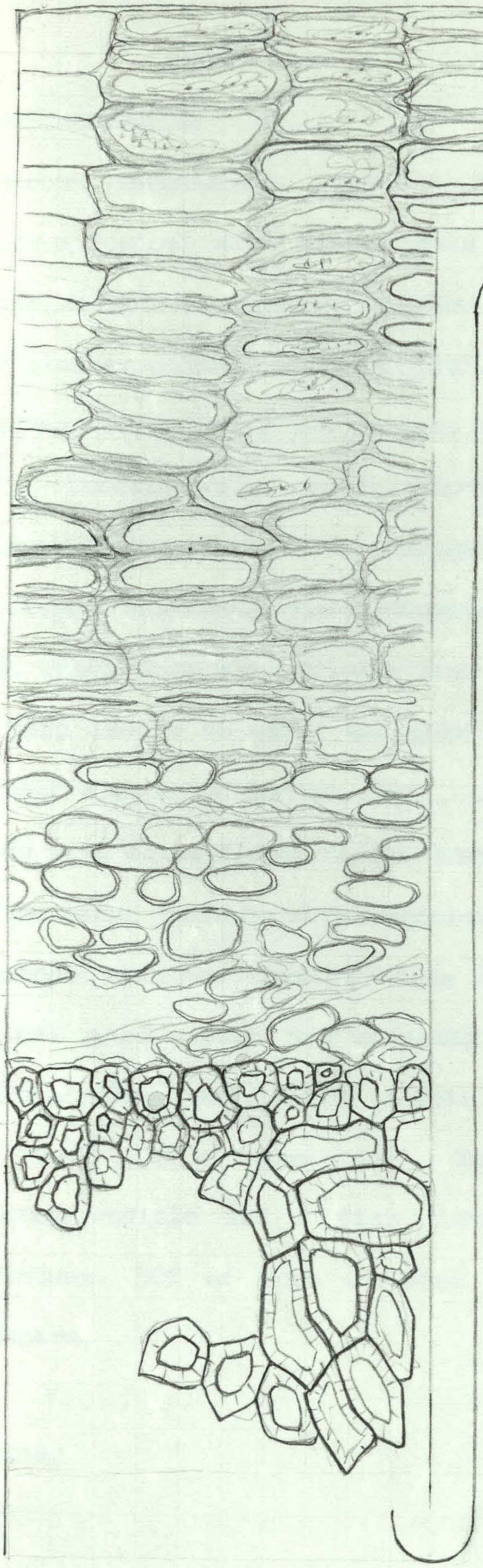
HUMBERTIOTURRAEA MALIFOLIA

A SEED-COAT IN SECTION. NOTE MULTIPLE HYPODERMIS, SPARSNESS OF TESTAL I.E. CRYSTALS (NONE VISIBLE HERE) AND MULTIPLE EXOTEGMIC FIBRES.

HUMBERTIOTURRAEA MALIFOLIA (Baker) Cheek

10.

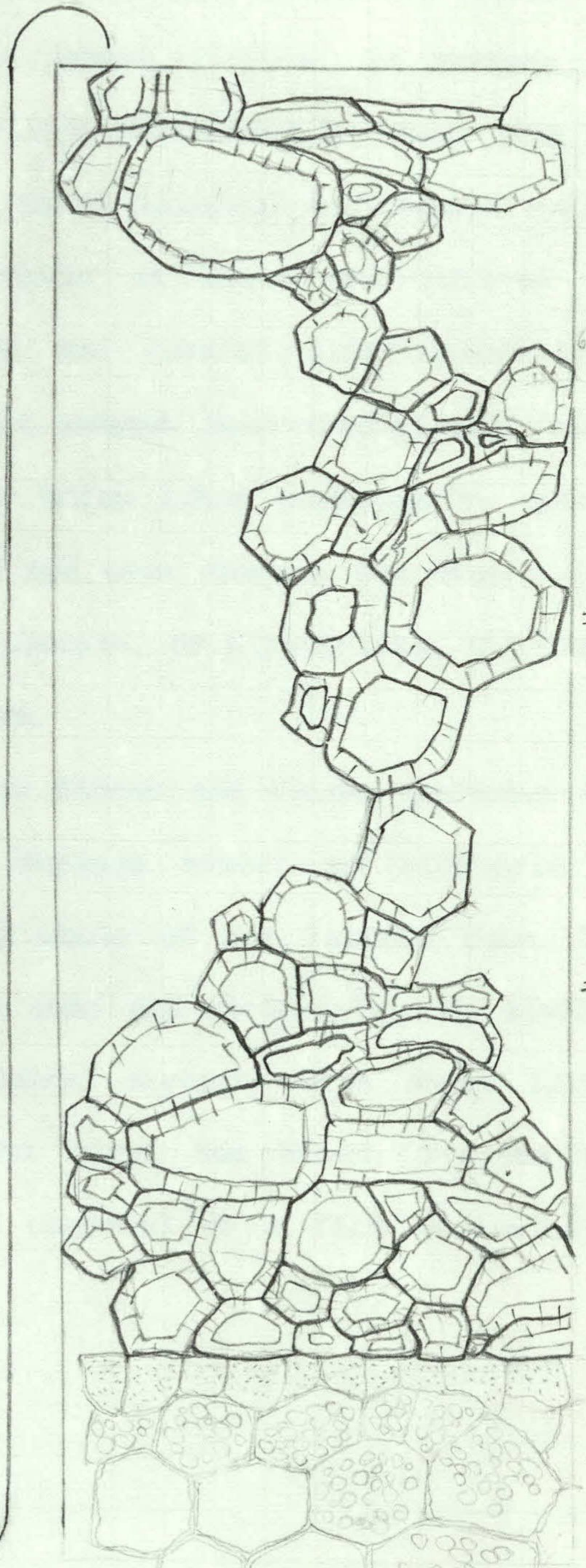
T.S. SEEDCOAT



A.

LEFT OF PLATE

RIGHT OF PLATE




50um

Subsequently, bagged fruits became soft and pulpy through to the seeds (no hard endocarp), no suggestion of regular fruit dehiscence.'

GROSS MORPHOLOGY

Fruits indehiscent, shortly obovoid with a distal boss, to oblate-spherical with distal boss and short, proximal, broad stipe; glossy, glabrous. Breadth 40-60mm, length 35-58mm. In average fruit, seed cluster c.35mm broad, 25-30mm long surrounded by about 10mm fleshy pericarp. Seeds 0-1-2 per locule, to 10 locules, 6-7 mature seeds per fruit. Fundamentally ovoid, micropyle at acute end (distal side), chalaza (c.10mm broad) at obtuse end (distal side).Laterally seed compressed: obscurely orange-segment shaped. Seed-coat glossy, mid-dark brown apart from where fleshy near hilum (this irregularly, usually a rim only 1mm or so wide) and near and over chalaza (an area c.8x10mm) and near micropyle. Latter small, obscure, or nipple-like, 0.5-1mm from border with hilum-fleshy testal area.

Hilum large usually with vascular fibres and fleshy pericarp tissue attached, oblique, running from chalaza almost to micropyle along proximal seed vertex and covering whole of one lateral face. Tegmic seed-coat very hard, thick (almost 1mm) and straw-coloured, similar to the 'shell' of a hazel-'nut'. Embryo straight with short (1.5-2mm) exserted radicle and 2 flat (12mm long, 8mm broad, 1-1.5mm thick) cotyledons. 50% or more of seed composed of a firm yellowish-white endosperm.

ANATOMY

TESTA

Cuticle: even, 0.5um thick, unsculptured.

O.E. Highly multiplicative, 16-20 cells (c.350um) thick. Cells storied in columns of up to 14. Cells prostrate highly extended ellipsoid (L.S. and T.S.), isodiametric to slightly extended quadrangular, 4- to 8-angled in paradermal section. Walls with amber, non-pitted thickenings, 4um thick (anticlinal and periclinal walls). Lumina with remains of protoplasmic contents, 15-20um high, 42-75-100um wide.

Mesophyll 8-12 layers (but evidence of crushing suggests loss of layers), 140um thick; nondescript prostrate-elliptic (T.S.,L.S.) cells, ± randomly orientated in tangential plane. 18-22um high and 25-40um wide. Walls 2um thick, pale brown. Lumina without contents.

I.E. Not distinct, probably owing to absence of crystals, irregular upper exotegmic boundary and crushing. Crystals do occur in short chains of up to 6 cells in lower layers but only sporadically.

TEGMEN

Exotegmen also multiplicative, very thick: about 35 layers (c.900um) of tangentially orientated (predominantly longitudinal) short fibres. In T.S., circular, 17-35um in diam. or slightly prostrate elliptic (e.g. 60um wide, 35um high), in L.S. 120-155-190um. Walls straw-coloured, 7um thick, plentifully pitted. Pits sometimes branched. Lumina without contents.

Endotegmen completely crushed.

ENDOSPERM

Very variable in thickness: 100um (when pelliculate) to 2000um. Cells isodiametric, 5-7-sided in section, 35-55(70)um square. Walls rather thin, 0.5-1um, lumina filled with spherical lipid plastids 3-5um diam.

PLATE 11

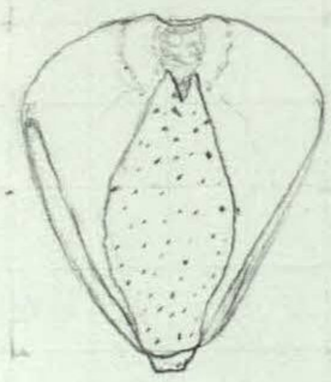
A-G HUMBERTIOTURRAEA SP. (FROM DRIED MATERIAL)

NOTE DIFFERENCE IN SIZE & POSITION OF HILUM COMPARED WITH H. MALIFOLIA (CF. PLATE 9), BUT MULTIPLE TESTAL HYPODERMIS, MULTIPLICATIVE EXOTEGMEN & STRAIGHT EMBRYO AS IN THAT SPECIES. TISSUES DISRUPTED BY DESICCATION SO DISTRIBUTION OF SARCOTESTA UNCLEAR.

H-I HUMBERTOTURRAEA MALIFOLIA, NOTE LONGITUDINALLY ELONGATED O.E. TESTA CELLS & SHORT FIBRES.

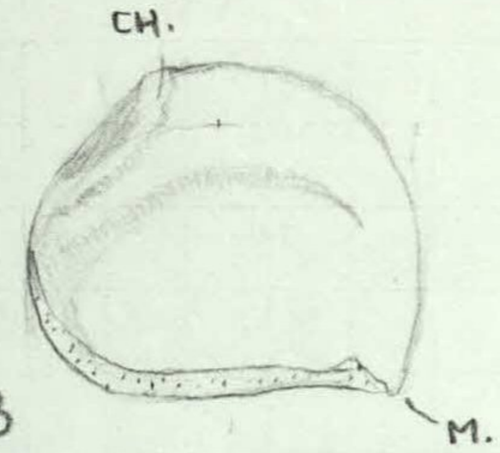
HUMBERTIOTURRAEA SP. LEANDRI 2945

CHAL. END VIEW



A

LATERAL VIEW




B

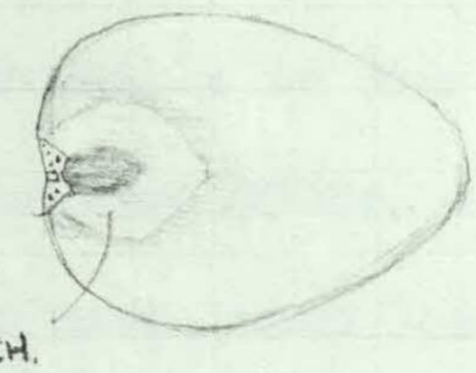
MIC. END VIEW




C

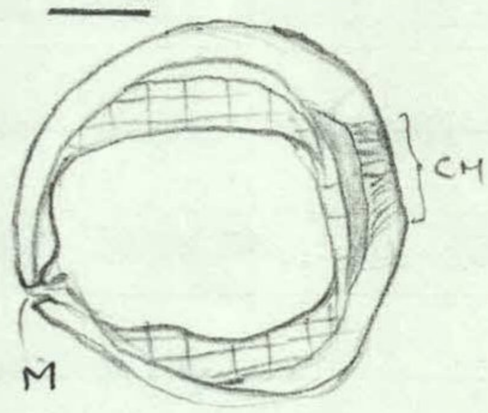
1cm

DORSAL (ABAX.) VIEW




D

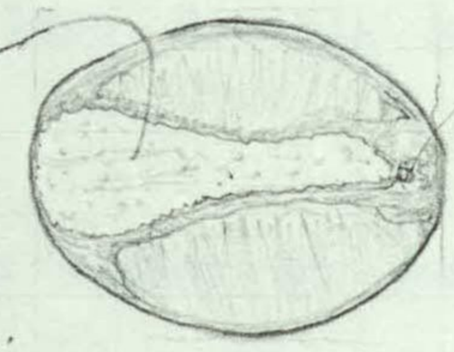
L.S.




E

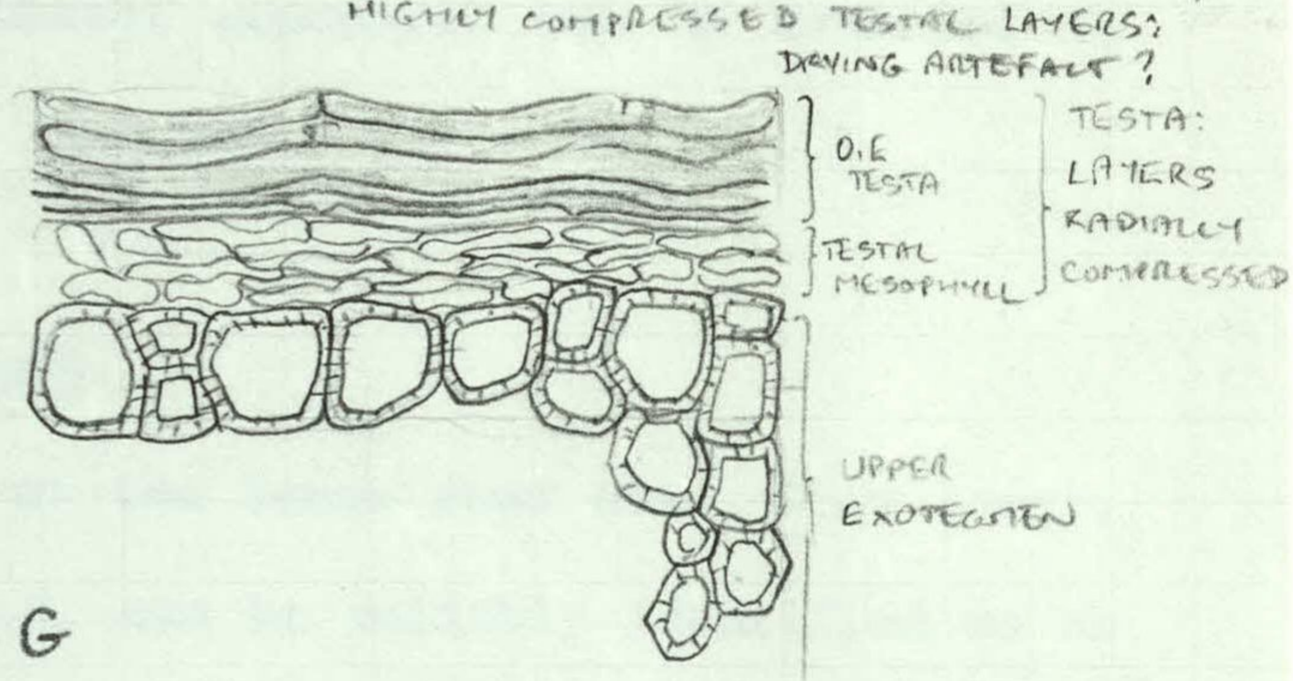
VENTRAL (ADAX.) VIEW

H. OR SCAR LEFT BY REMOVAL OF FLESHY TISSUE




F.

T.S. UPPER SEEDCOAT. LEANDRI 2945
(ONLY UPPER LAYER OF EXOTESTA INC.)
HIGHLY COMPRESSED TESTAL LAYERS: DRYING ARTEFACT?

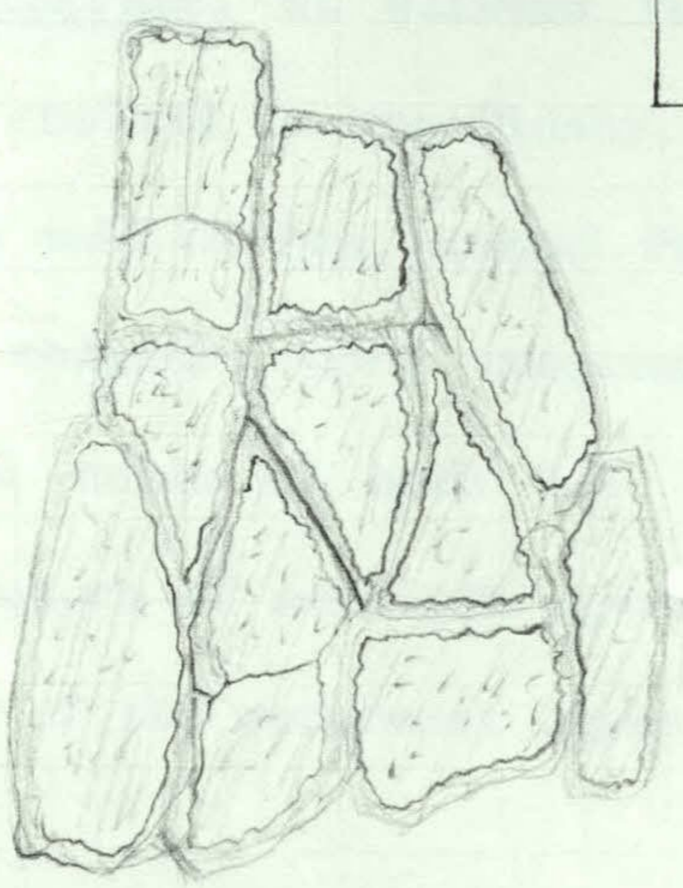



G

50um

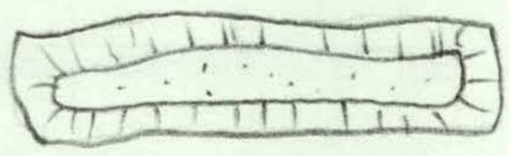
HUMBERTIOTURRAEA MALIFOLIA

TESTAL O.E.
PARADERMAL VIEW OF UPPER LAYER.



H.

EXOTESTAL FIBRE - OPTICAL L.S:
: MACERATION.



I

50um

Upper layer epidermal, cells sub-cuboidal, c.14-20um square, without plastids, but with dense protoplasmic contents.

FLESHY ZONE

Towards hilum, upper part of seed-coat becomes swollen, soft and yellowish in colour. The transition from the normal, hard state to the fleshy takes place very gradually in the testa: outer epidermal layers gradually decrease slightly from 350um, c.16-20 layers, to 200um, c.10 layers, cells increasing in size, with less thickening.

Mesophyll increases dramatically from 8-12 to c. 40 cell layers or c.500um, cells appearing less densely packed and coloured, but the dimensions ± unchanged.

These data from section taken at junction of fleshy and normal seed-coat. Further toward hilum, testal mesophyll can be expected to proliferate: thickest part of flesh is c.2mm.

VARIATION:'Turraea sp.', LEANDRI 2945.

This dried collection on account of the large seed size (15mm long), multiplicative tegmen and testal O.E. can be reliably identified as an Humbertioturraea. It differs from Cheek 2-20-1 in being smaller, in that the chalaza is non-fleshy, hilum more narrow, symmetrical and not taking up most of one lateral face of the seed. Anatomically, the testa is much thinner, more compressed. Probably an artefact of drying. Individual cells of both O.E. and mesophyll not distinguishable. The stacked nature of multiple epidermis results in amplification of o.p.w. concavity of the outermost layer.

PLATE 12

MUNRONIA PINNATA

A-NOTE TYPICAL TURRAEEAE FLOWERS: LONG STAMINAL TUBE & EXPANDED STYLE-HEAD. PINNATE LEAVES AND PETALS UNITED WITH STAMINAL TUBE ARE DIAGNOSTIC OF THE GENUS. X 1

B-FRUITS. NOTE SUPERFICIAL SIMILARITY OF SEEDS TO THOSE OF TURRAEA X 1

A

B

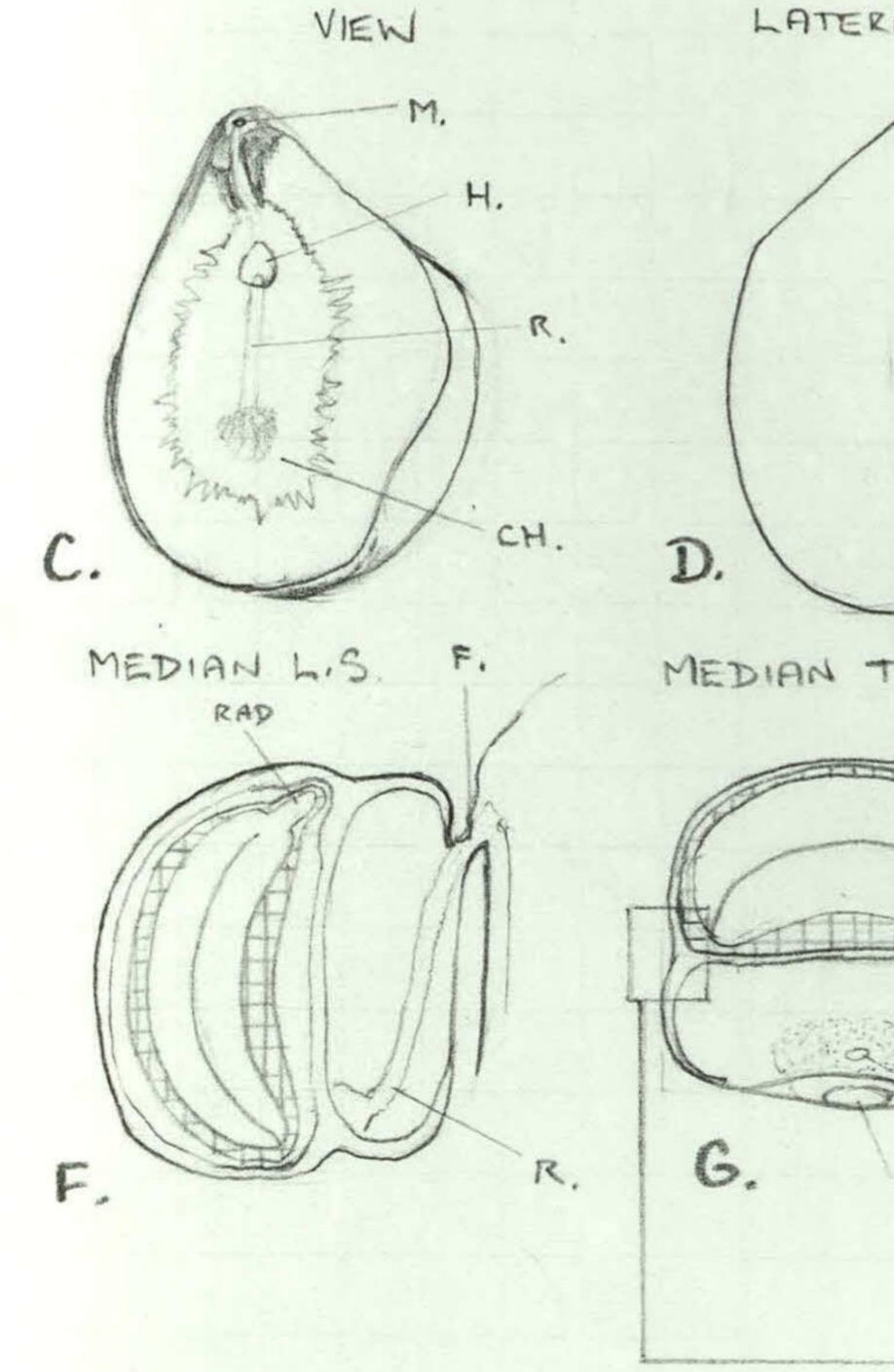
PLATE 13

MUNRONIA PINNATA

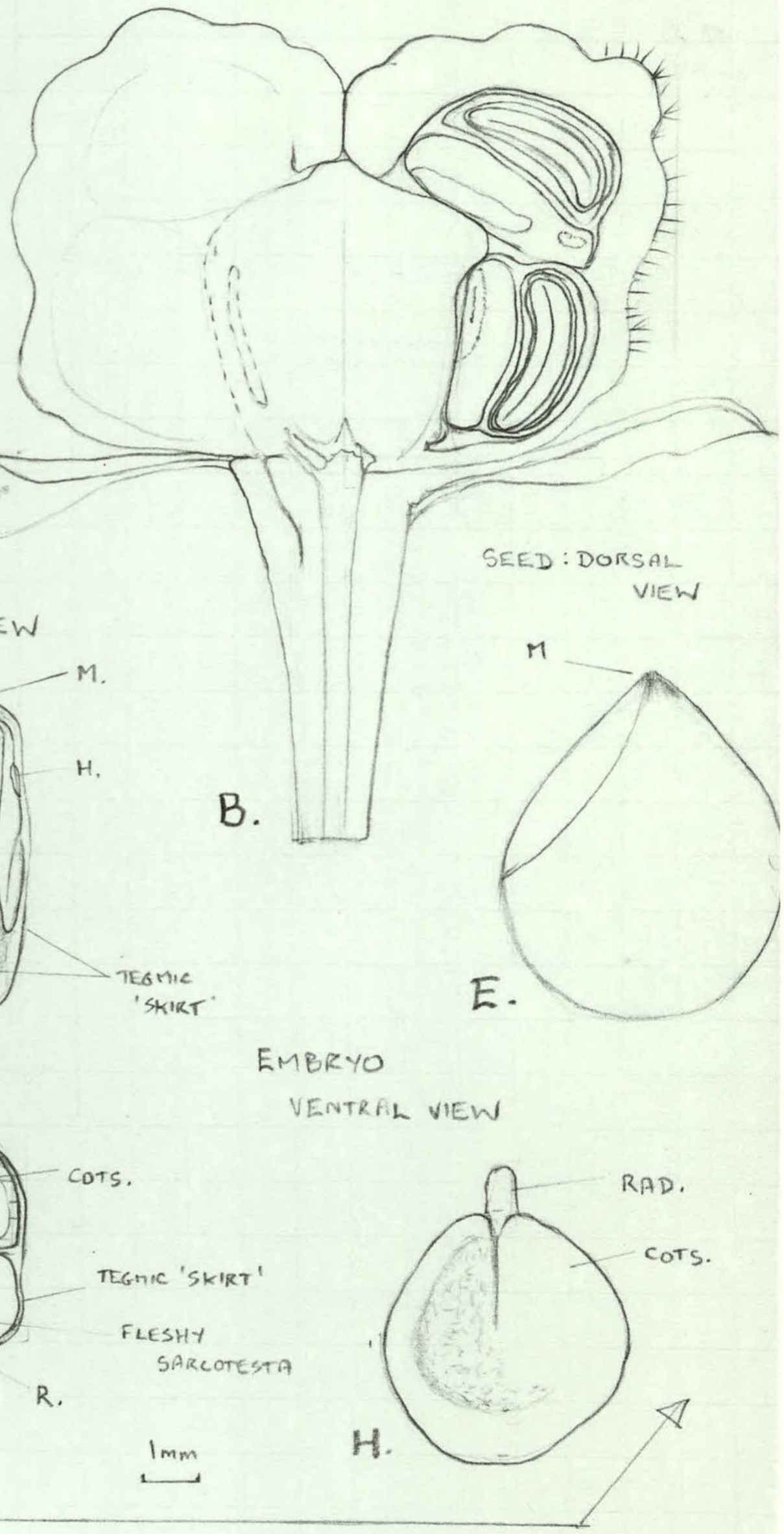
A-H FRUITS AND SEEDS, VARIOUS VIEWS. NOTE TEGMIC 'SKIRT' WHICH ENCAPSULATES VENTRAL FLESHY TISSUE. THE CURVED EMBRYO, COPIOUS ENDOSPERM AND EXSERTED RADICLE ARE TYPICAL OF THE TRIBE.

MUNRONIA PINNATA (Wall.) ~~Arn. Bxo.~~ Theob.

INFRUCTESCENCE



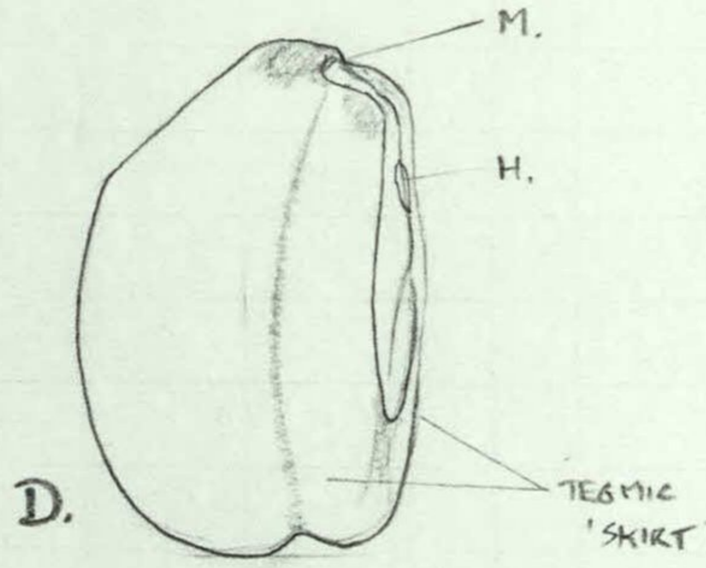

FRUIT. MEDIAN L.S.




SEED: VENTRAL VIEW




LATERAL VIEW




MEDIAN L.S.




MEDIAN T.S.




EMBRYO VENTRAL VIEW

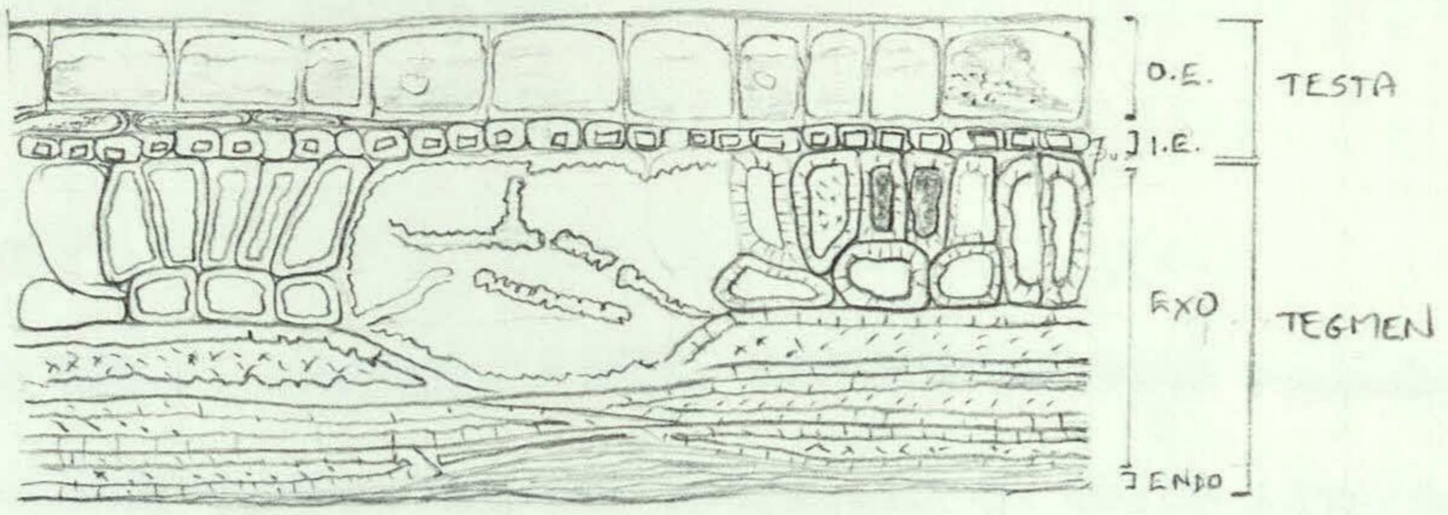
# PLATE 14

## MUNRONIA PINNATA

A-C SEED-COAT. NOTE VERY LONG & 'CROSS-PLY' EXOTEGMIC FIBRES WHICH CHARACTERIZE THE GENUS (A). THE INNER LINING LAYER OF ENDOCRYSTALLINE CELLS (C) HELPS TO ESTABLISH THE TOPOLOGY OF THE TEGMIC 'SKIRT'.

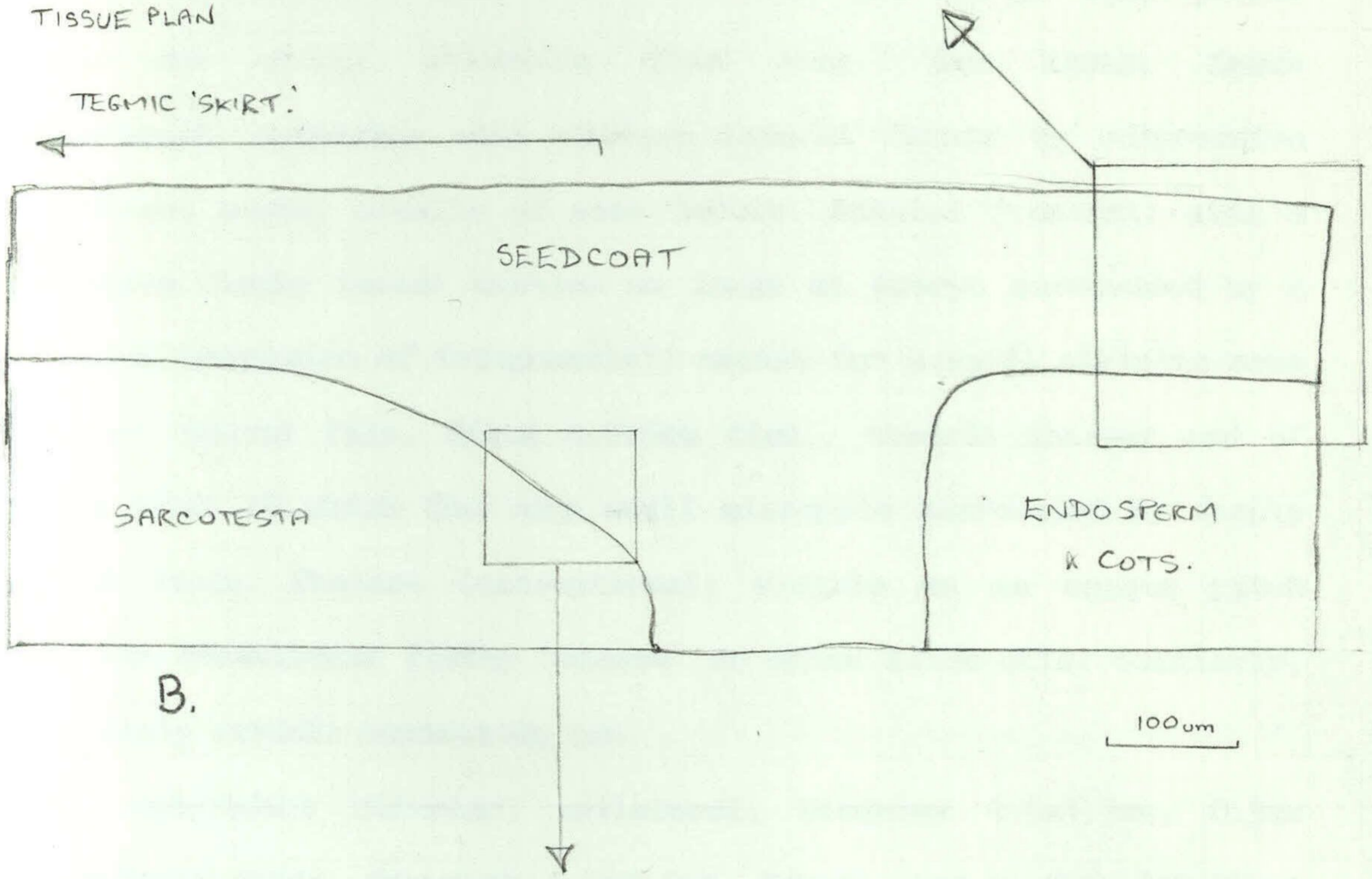
MUNRONIA PINNATA (Wall.) ~~A.DC.~~ Theob.

T.S. SEEDCOAT




A.

TISSUE PLAN




B.




C.

Munronia pinnata (Wall.) A.S.Theob.

This description based on Gee, s.n. (slightly immature)

Collector's notes: not available.

GROSS MORPHOLOGY

Fruit stellate-hairy, coarsely warty, dry loculicidal capsule dehiscing apically by 5 valves from a central columella on which inserted up to 10 seeds, two (superposed) per locule; fruits 15mm long, 13mm broad, pericarp 2mm thick; columella 11mm long, 9mm broad. Seeds ovoid-spheroid, sometimes with oblique lateral facets by compression with adjacent seeds, usually of same locule. Adaxial (ventral) side a large, thick fleshy testal cushion as large as embryo surrounded by a bony tegmen (inversion of integuments!) except for a small elliptic area (4x2mm) on ventral face. Hilum c.0.5mm diam., towards sharper end of seed, at point of which the very small micropyle surrounded by deeply pigmented testa. Chalaza (conventional) visible as an opaque patch through the translucent fleshy 'window' on which hilum sits. Similarly, raphe plainly visible connecting two.

Embryo cotyledons circular, collateral, biconvex 4.5x4.5mm, 0.5mm thick. Radicle short, exserted, 1.5x0.5mm. Embryo clad in thin (<0.25mm) layer of endosperm which in turn wrapped in the seed-coat. Exceptionally, tegmen extended adaxially to form a 'skirt' around the testal fleshy layer.

ANATOMY

TESTA

Cuticle: even, colourless, <1um thick.

O.E. single layer of shortly columnar to shortly tangentially extended quadrangular cells (T.S. and L.S.), 21-24um high, 14-35um wide. Walls colourless, o.p.w. to 3.5um thick inner surface concave, i.p.w. to 2um thick, anticlinal walls 1.5um thick. Lumina pale brown. In paradermal view, cells isodiametric, 6-7 sided with straight walls.

Mesophyll. Except for an occasional single layer of barely detectable highly tangentially extended ellipsoid cells, only 3-7um high and 14-23um wide with protoplasmic contents, mesophyll is absent except on adaxial surface of seed where it greatly proliferates to form the fleshy cushion largely encapsulated by the tegmic skirt. Cells ellipsoid, randomly orientated with air spaces, thin-walled, translucent, colourless contents, 45x30um.

I.E. single layer of small, shortly tangentially extended quadrangular cells (T.S. and L.S.), in paradermal section isodiametric, 6-7-angled. Cells 7(-10)um high and 9-12um wide. Clearly marked by presence in each of a large yellow prismatic crystal. Crystals uniform in shape: prostrate, 7um wide and 4um high. This distinctive layer occurs on the inside of the tegmic skirt, confirming the identification of the fleshy tissue as testal mesophyll.

TEGMEN

Exotegmen c.5 layers of long fibres in two parts, upper part (1-)2 layers thick, fibres orientated longitudinally, lower part 2-3 layers thick, lowest layer always much smaller in diam., fibres always orientated transversely, normal to upper fibres. Fibres are yellowish, with abundant, often interlocking slit-like pits , walls 3-5(-7)um thick. In transverse section, fibres of both parts usually columnar, up to 20um wide and 35um high. Fibre length 320(-560)um, end walls highly oblique.

Endotegmen often entirely crushed. Where spared, 1-2 layers of parenchyma, uppermost mingled with lowest (smaller) fibres, lowermost layer epidermal, prostrate quadrangular, cells without contents, walls c.1um thick, brown.

PERISPERM(L.S. only)

2-5 layers of highly tangentially extended (L.S.) quadrangular cells c.20um high and 40-120um wide. Walls thin, lumina with protoplasmic contents. Lowest part c.20um of crushed cell layers.

ENDOSPERM

Epidermis a single layer of small prostrate quadrangular cells with dense grey cytoplasm, 14um high, 20-28um wide. Subdermal cells larger, isodiametric or shortly extended polygonal 5-7-sided, to 35um diameter. Contents dense grey.

Calodecaryia crassifolia J.F.Leroy

This description based on Mc.Whirter 159

Collector's notes:'Fruits erect, brown.'

GROSS MORPHOLOGY

Fruits loculicidal capsules. 4 locular (1 to 4 fertile), 1 (to 2, collateral) seeds per locule. Overall breadth 5-11mm, height 5-6mm. Pericarp very thin (0.1mm), leathery, brown, smooth, sometimes with scattered necrotic areas.

Seeds sub-ovoid (if 2 seeds per locule, partly orange segment-shaped by mutual compression), placentation mid-axile. Hilum elliptic, 0.5-1mm long, placed slightly more than half way along dorsal

# PLATE 15

## CALODECARYIA CRASSIFOLIA

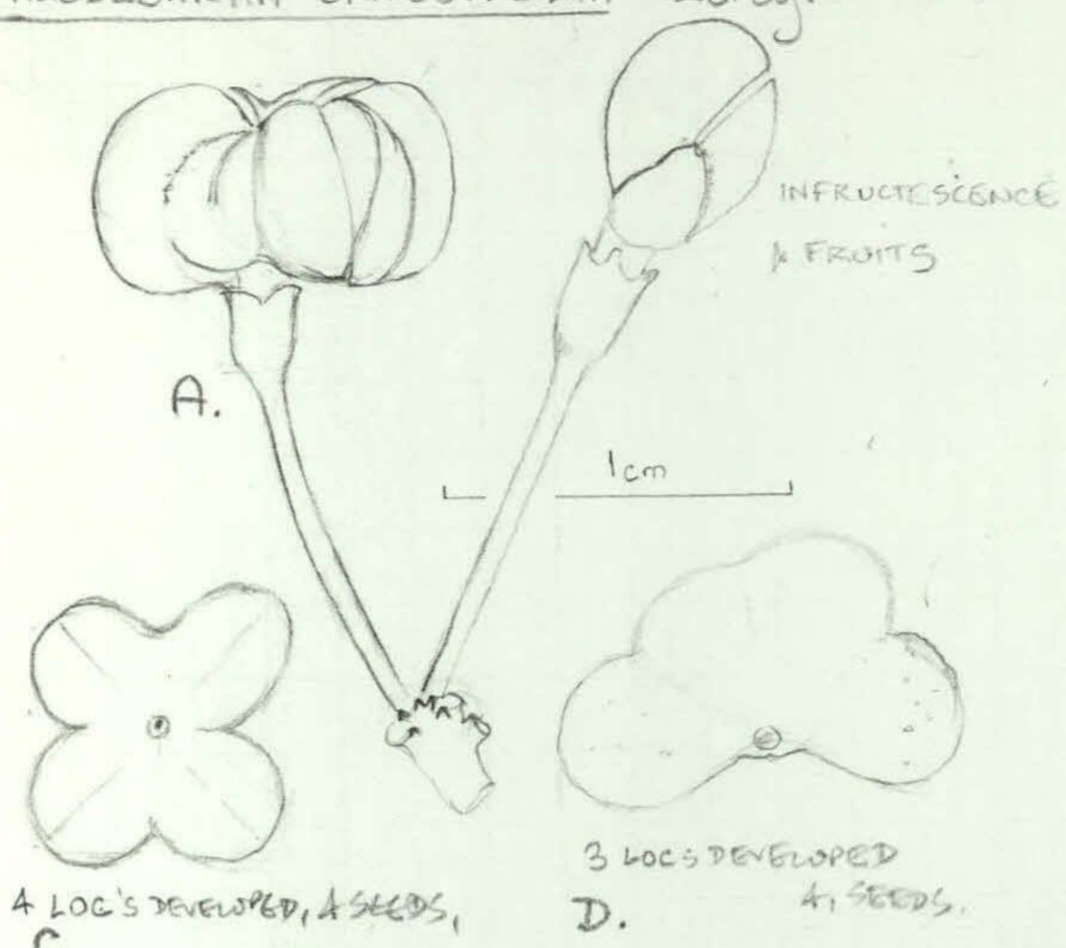
A,C & D- VARIATION IN FRUITS.

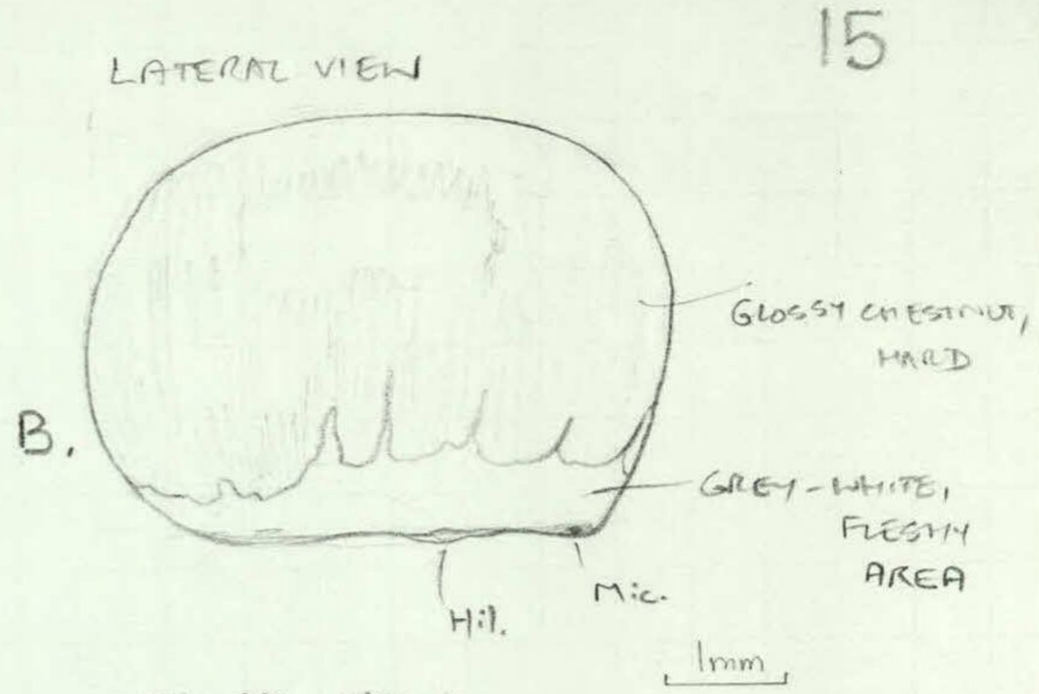
B & E- WHOLE SEEDS: NOTE VENTRAL DISPERSED SARCOTESTA.

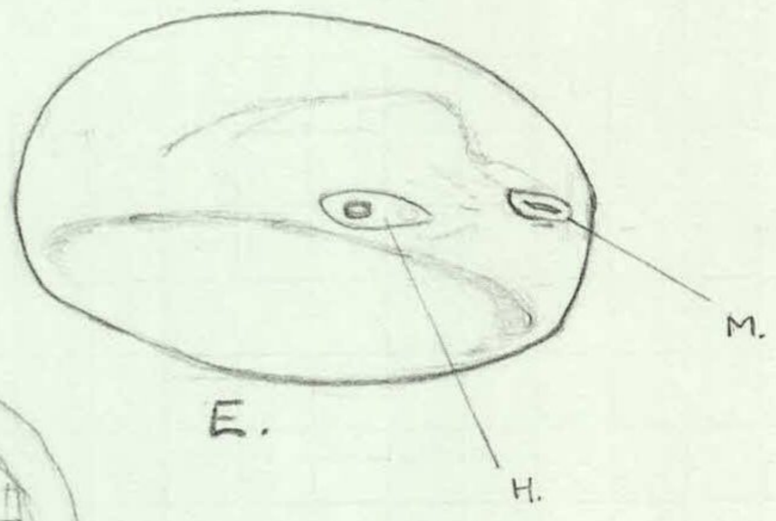
F & G- SEEDS IN SECTION: NOTE CAMPYLOTROPY AND HIGHLY CURVED NATURE OF EMBRYO.

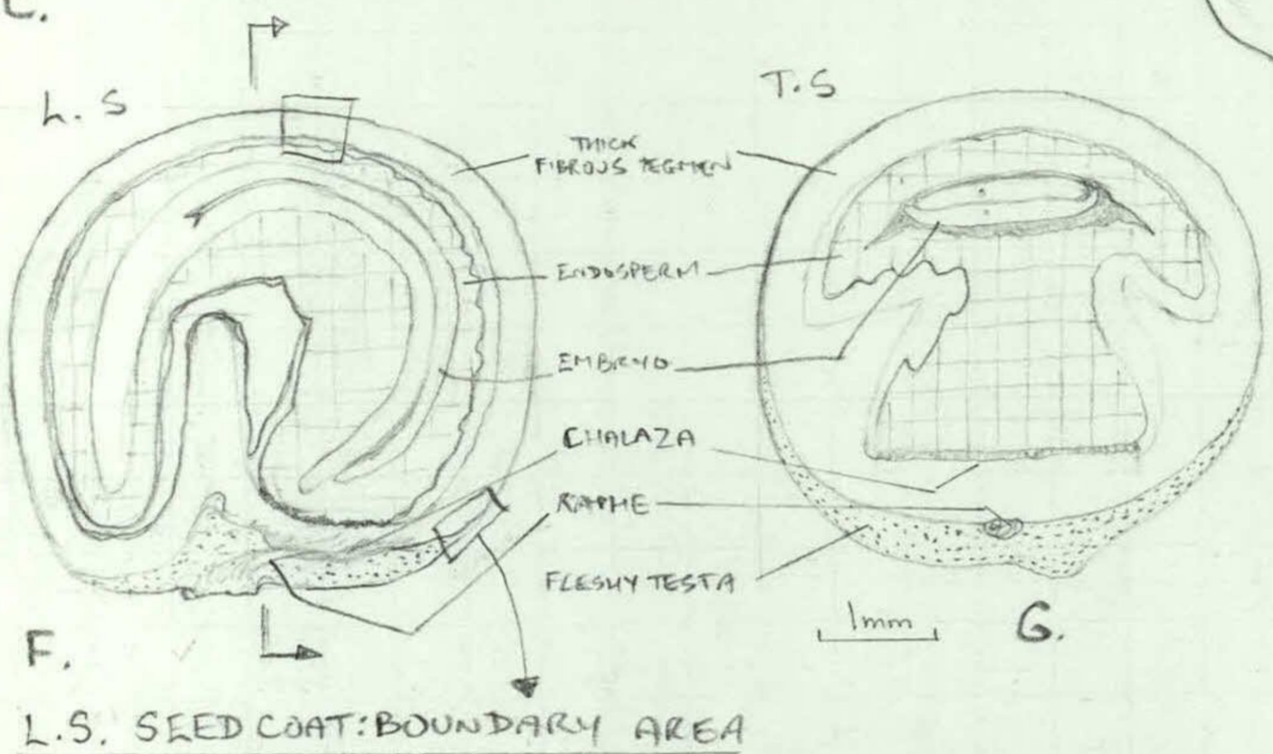
H- SEED-COAT IN SECTION: NOTE SIMPLE TESTAL HYPODERMIS, THICK THIN-WALLED TESTAL MESOPHYLL (CLOSE TO SARCOTESTA), ABSENCE OF TESTAL I.E. CRYSTALS AND MULTIPLE-LAYERED EXOTEMIC FIBRES.

# CALODECARYIA CRASSIFOLIA Leroy.

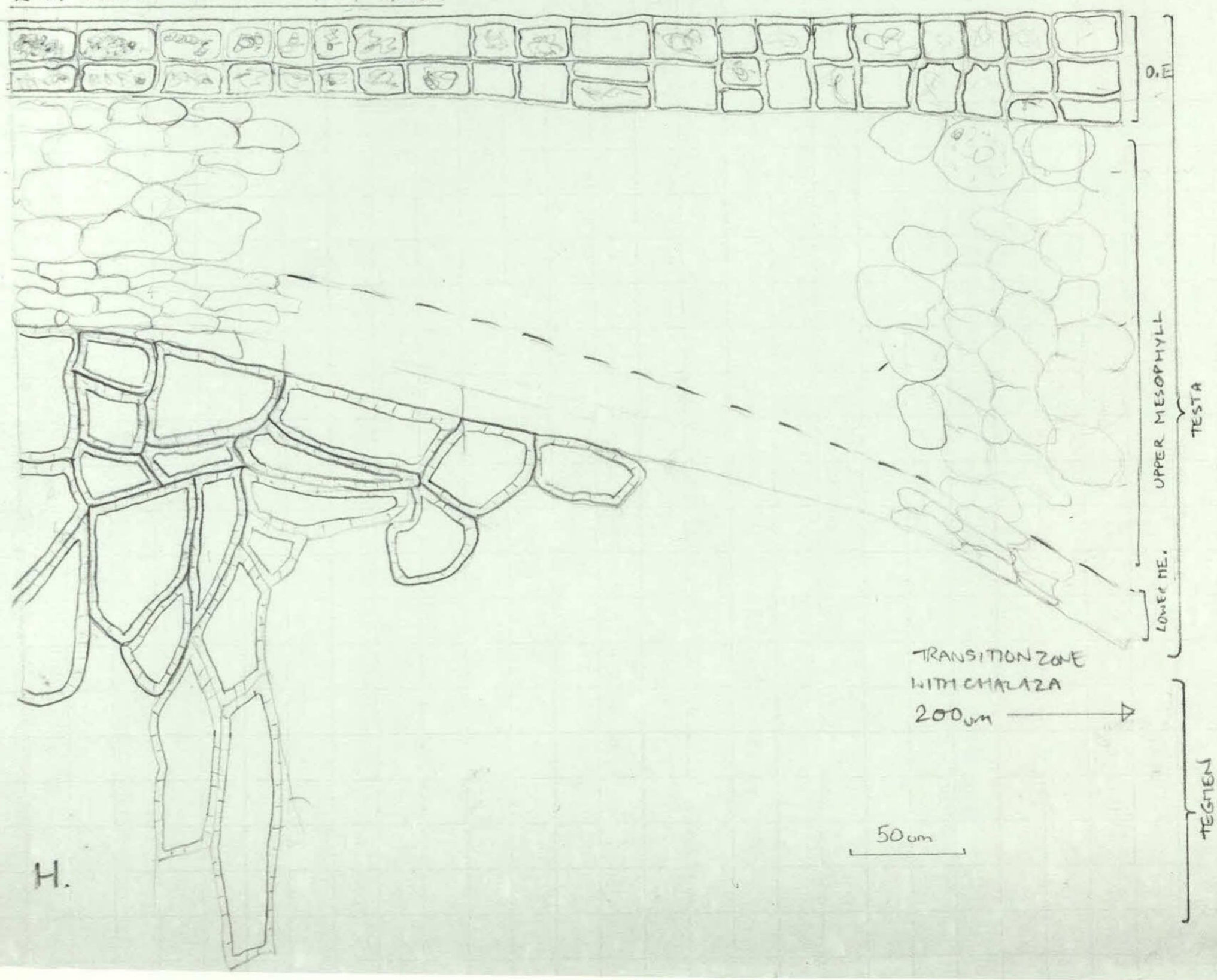



## L.S. SEED COAT: BOUNDARY AREA



# CALODECARYIA CRASSIFOLIA

## SEEDCOAT: L.S., DORSAL SURFACE (SEE TISSUE PLAN)

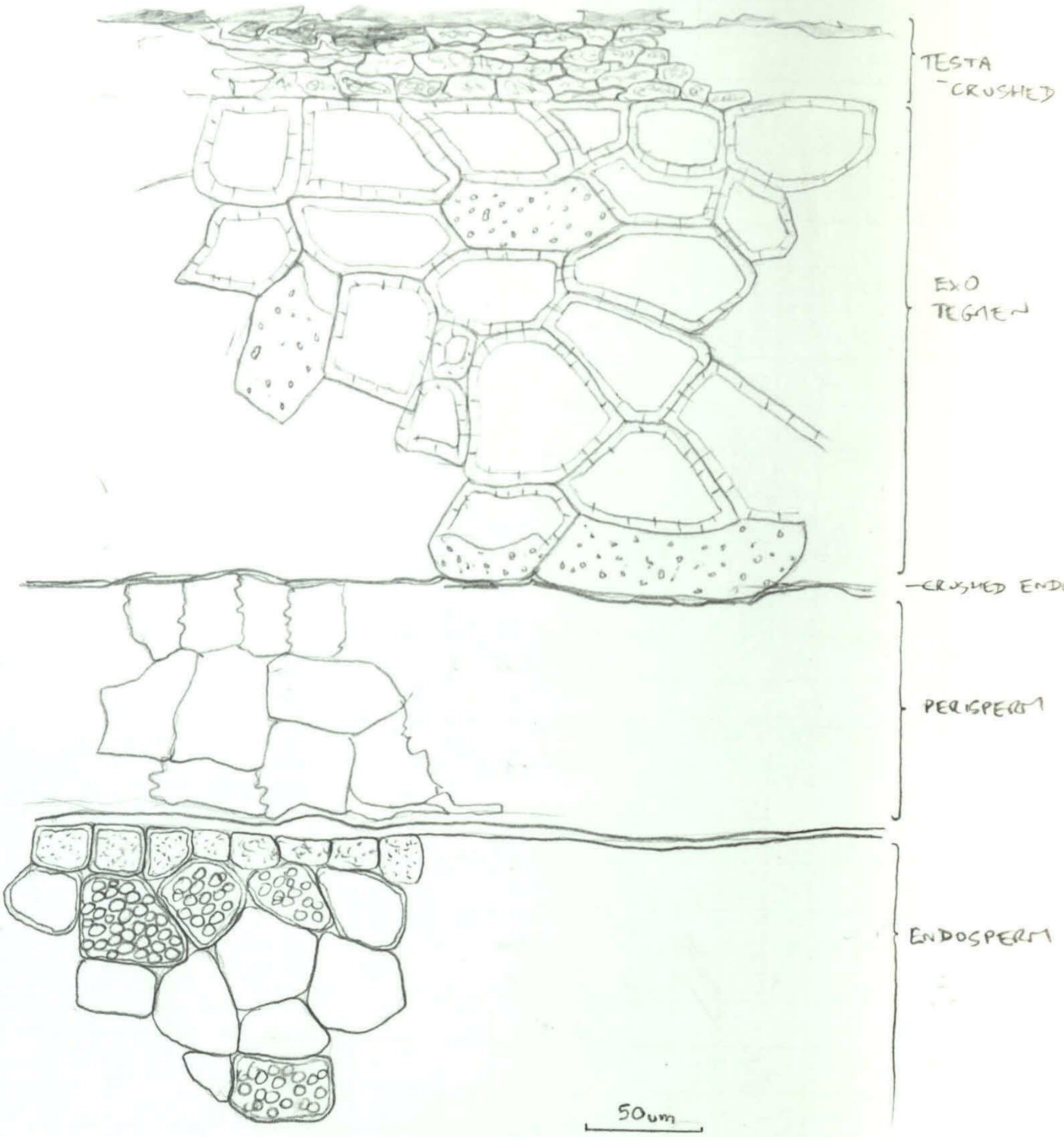


PLATE 16

CALODECARYIA CRASSIFOLIA

TYPICAL SEED-COAT: TESTA HIGHLY CRUSHED.

(proximal-placental) ridge toward micropyle (sulcus, 0.5mm at tip of seed, distal end of fruit). Seeds 3.5-5mm long, 3.2-4.5mm broad. Testa thin, glossy, chestnut-brown, smooth, hard except in radiating streaks from chalazal-micropylar area where pale grey thick and soft (succulent). Tegmen exceptionally thick (to 0.4mm) and bony. Chalaza not clearly distinct superficially. Roughly ellipsoid, about 2mm long. Between chalaza and micropylar areas, a bony intrusion almost divides the interior of seed. Some remnants of white spongy perisperm remains but mostly crushed by thick firm cream endosperm into which it invaginates shallowly. Embryo and embryonic pocket curved almost through 270 degrees, cotyledons, flat, collateral; radicle rather long 2.5-3mm, exserted.

ANATOMY

TESTA(From near chalaza, since in most of mature seed-coat testa crushed beyond description)

Cuticle: 1um, smooth.

O.E. 1-2-3 layers, cuboidal to radially extended quadrangular cells (T.S. and L.S.). In paradermal section, ± isodiametric, 5-6-sided. Periclinal walls pale-medium brown. Outer of upper layer to 5um, inner of lower 4um. Anticlinal walls comparatively thin. Protoplasmic contents coarsely granular, translucent towards chalaza but orange-yellow over most of seed-coat (partly accounts for colour dimorphism?).Cells 21-26um high, 17-42um wide.

Mesophyll, where spared, apparently 7 or 8 layers of prostrate ellipsoid cells, upper half with air-spaces and larger (14-25um high, 17-50um wide, walls 2um) than lower half which vertically compressed (c.30um wide, walls 1-2um). The mesophyll is the major constituent of

the fleshy layer. Immediately adjacent to the transition zone the maximum number of layers (10-14) occur.

I.E. not distinct. Cannot be distinguished from the lower mesophyll. No crystals.

TEGMEN

Exotegmen 5-6 layers, 200-225um thick (to 560um near chalaza). Short fibres, fairly randomly ordered 98-315um long, 28-42um broad. Walls relatively thin (3-4um) straw-coloured with many simple pits. No parenchymic mesophyll detected.

PERISPERM

2-3 layers (c.100um) thick, crushing evident. Undamaged cells large, thin-walled, without contents. Polygonal, isodiametric or shortly extended, 40-50um long, c.30um broad.

ENDOSPERM

Epidermis of small, ± cuboidal cells, 18-25um square, lumina almost colourless with finely granular contents. Single layer.

The bulk isodiametric, 5-angled, 30-50um square, filled with lipid bodies c.5um diam. spherical.

Nymania capensis(Thunb.)Lindb.

This description based on D.A.H.Taylor s.n. (Dried seeds)

Collector's notes:'Klappers (inflated capsules) red when young, going cardboard colour and dry when ripe .....Light red inflated calyx with 1-4 seeds. Stony, semi-desert wasteland.'

PLATE 17

NYMANIA CAPENSIS

A- FRUIT INFLATED; UNKNOWN ELSEWHERE IN THE FAMILY. X 1

B- FRUIT (SLIGHTLY IMMATURE, THOUGH FULL-SIZED) OPENED TO EXPOSE SEED: NOTE LARGE AIR-SPACE SURROUNDING SEED IN FRUIT LOCULE.

C- FLOWER: UNUSUAL IN FAMILY IN THE FREE FILAMENTS, VERSATILE ANTHERS AND OBLIQUE-LIMBED SYMMETRY. NOTE LINEAR LEAVES. X 1.



A



B



C

PLATE 18

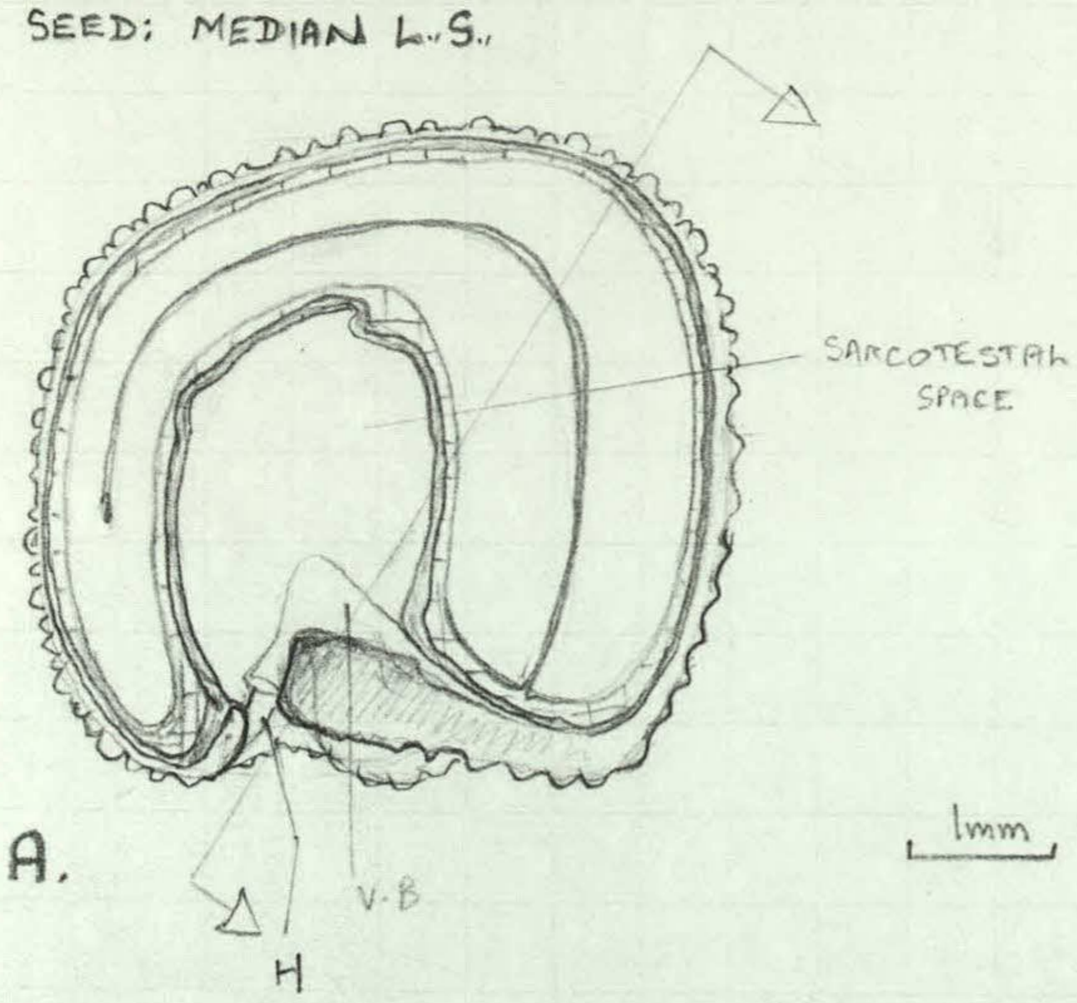
NYMANIA CAPENSIS

A-F FRUIT & SEEDS IN VARIOUS VIEWS. NOTE HIGHLY CURVED EMBRYO, CAMPYLOTROPY, RELATIVELY THIN ENDOSPERM, & LARGE CENTRAL LACUNAE LEFT BY BREAKDOWN OF SARCOTESTA (A & B).

# NYMANIA CAPENSIS (Thunb.) Lindb.

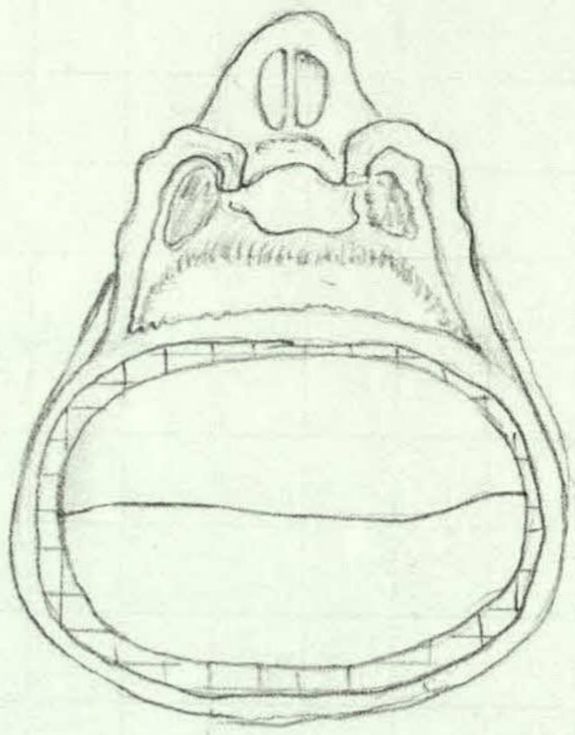


SEED: MEDIAN L.S.



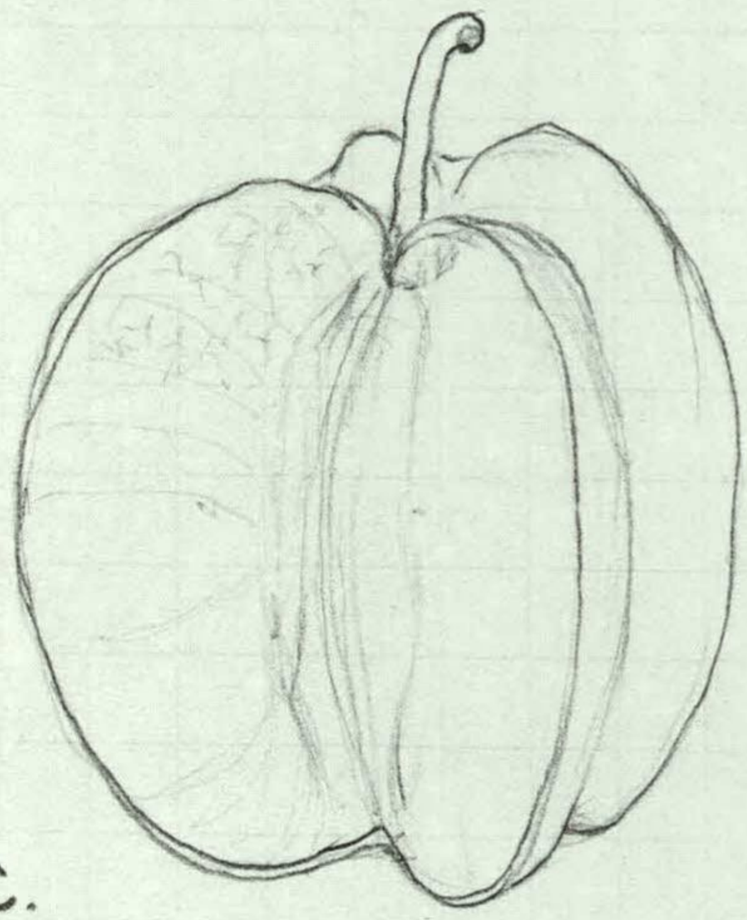

A.

SEED : T.S.



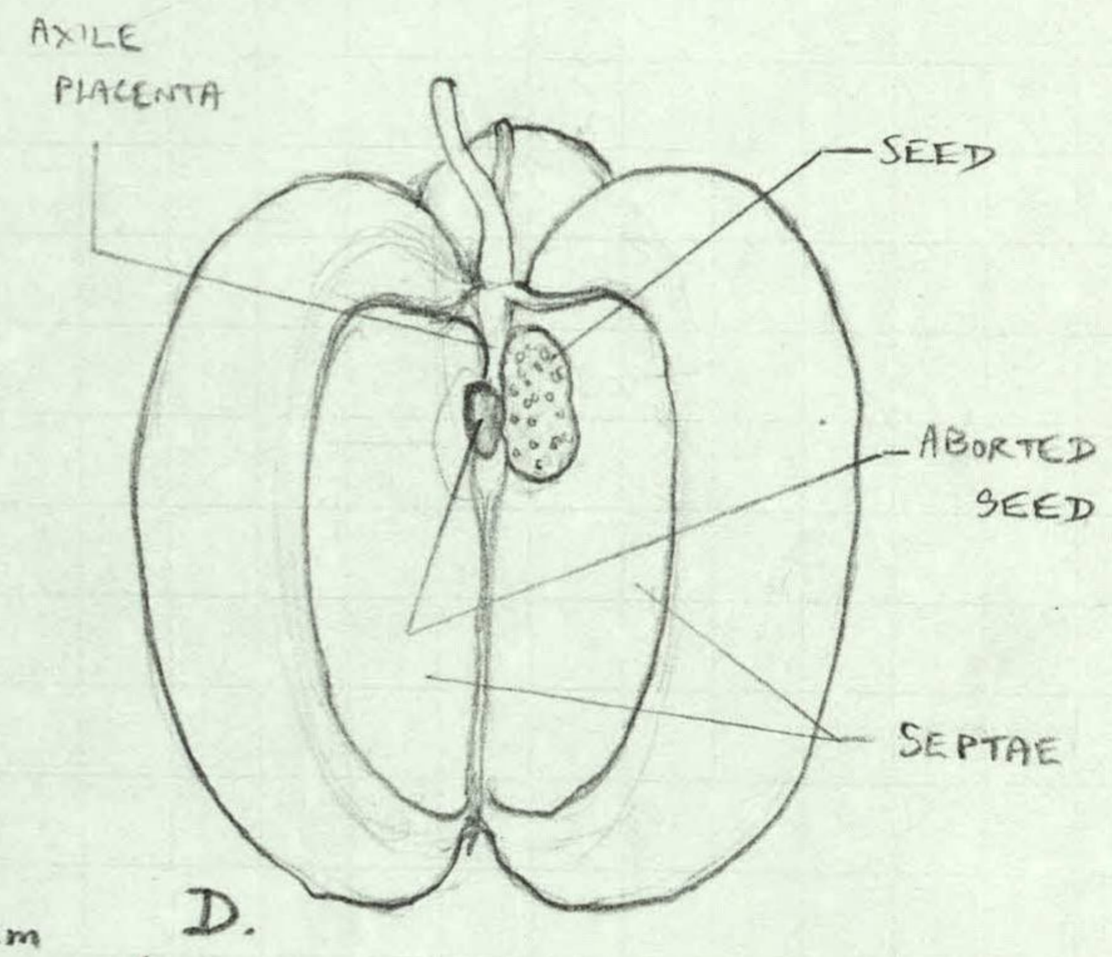
B.

FRUIT: LATERAL VIEW



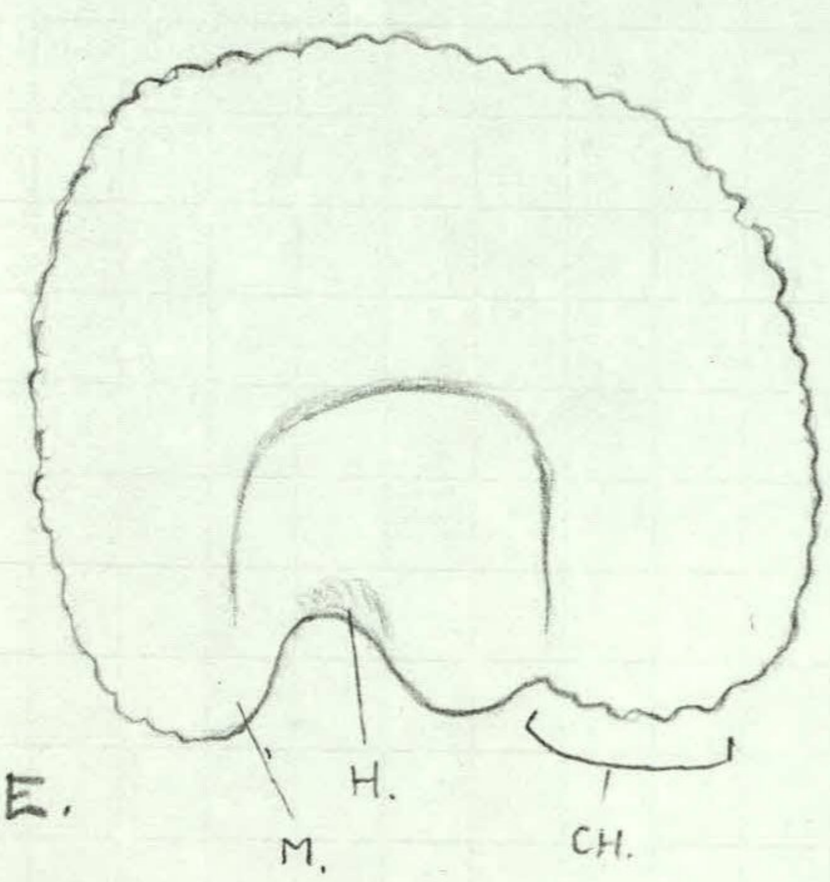
C.

FRUIT: LATERAL VIEW. ONE VALVE REMOVED



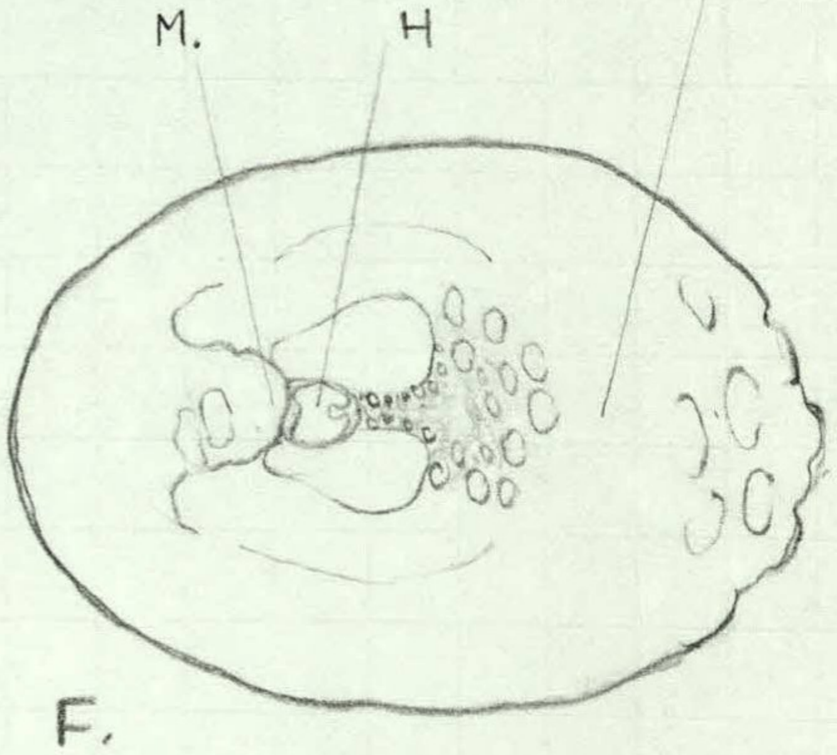

D.

SEED: LATERAL VIEW




E.

SEED: VENTRAL VIEW




F.

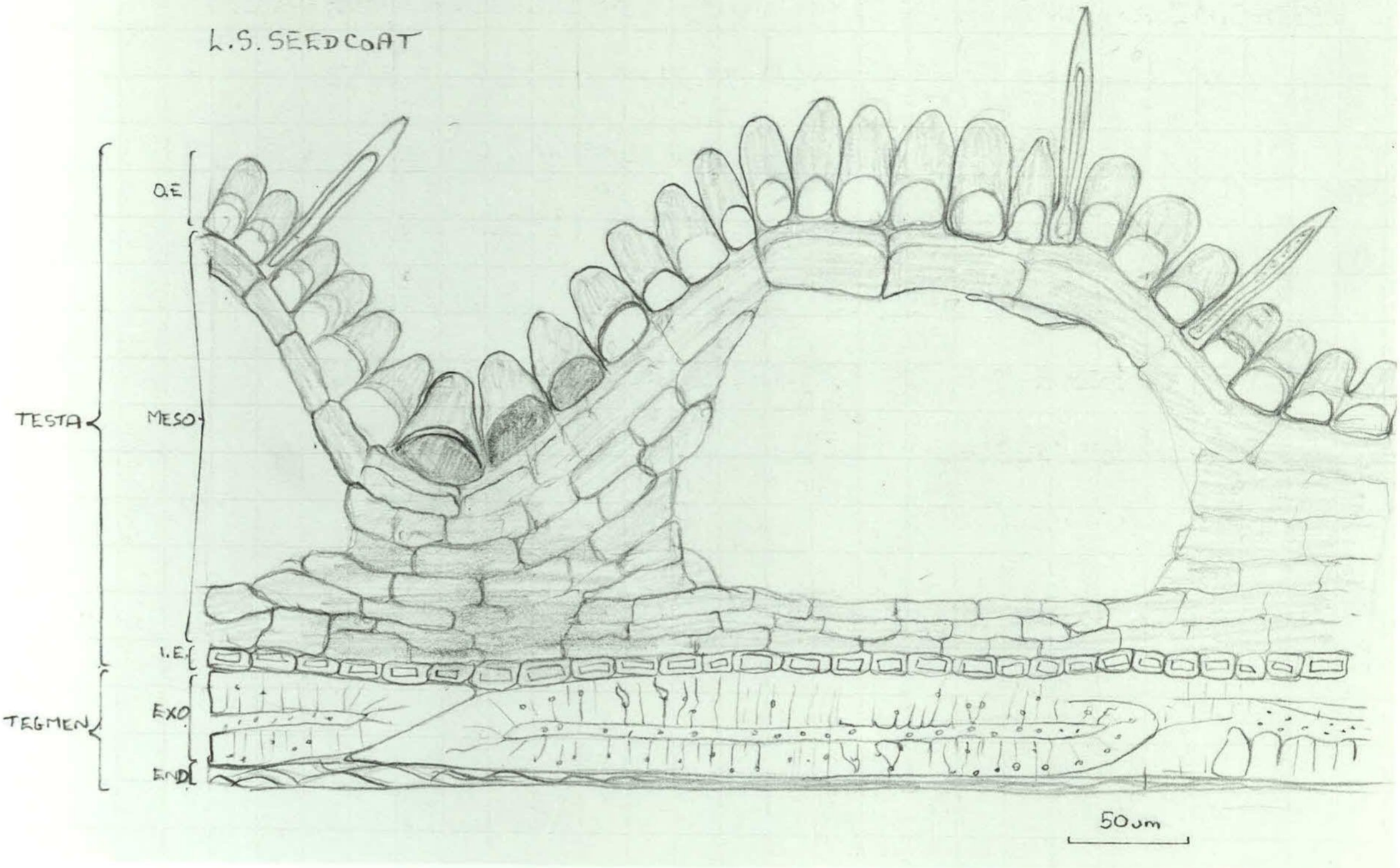
PLATE 19

NYMANIA CAPENSIS

SEED-COAT ANATOMY. NOTE TESTAL O.E.: PAPILLATE OR HAIR-LIKE CELLS. NOTE TESTAL MESOPHYLL: MULTI-LAYERED, WITH TANNIN (?) AND LARGE LACUNAE CAUSING 'MACRO-VERRUCAE' ON SURFACE. TESTAL I.E. (CRYSTALLIFEROUS) & EXOTEGMEN (LONG, FIBROUS, THICK-WALLED, LIGNIFIED, PITTED) TYPICAL OF MELIACEAE.

NYMANIA CAPENSIS (Thunb.) Lindb.

L.S. SEEDCOAT



# PLATE 20

## HELLEBORUS VESICARIUS

INFLATED, AIR-FILLED FRUITS, VERY SIMILAR TO THOSE OF NYMANIA CAPENSIS (CF. PLATES 17A & 18C). OTHER SPECIES OF HELLEBORUS HAVE NON-INFLATED, DEHISCENT FRUITS COMPARABLE TO THOSE TYPICAL OF THE TURRAEEAE. THIS SPECIES IS WIND-DISPERSED & GROWS IN STEPPE. NYMANIA ALSO GROWS IN AN OPEN, WINDY, HABITAT WHERE THE SAME TYPE OF FRUIT SEEMS TO HAVE BEEN SELECTED: CONVERGENT EVOLUTION OF FRUITS?




*Helleborus vesicarius.* Drawing by Joanna Langhorne

GROSS MORPHOLOGY(see also Pennington and Styles(1975), White(1986).)

Fruit red (immature) to pinkish yellow, dry, inflated, deeply 4(-5)-lobed apically loculicidal capsule, walls as greaseproof paper; loculi 1(2) seeded. Capsule to 3cm. Seed reniform, medium-brown, with a thick, rather woody, minutely verrucose, puberulent testa, adaxial depression filled with testal derived fleshy tissue which surrounds hilum; 4.5mm long, 3mm broad. Embryo strongly curved, embedded in thin (0.25mm) endosperm; cots. collateral, plano-convex in section, 1x3mm, radical exserted, rather short 1.5mm long.

ANATOMY

TESTA

Cuticle: even, thin, 0.5um.

O.E. single layer of columnar cells with very thick brown periclinal walls, 51-58um high, 20-28(-42)um wide (L.S. and T.S.). O.p.w. (to 35um) extremely thick, pale brown, strongly convex and protruded, forming a papilla which free or connate with neighbours; i.p.w. much thinner (18-22um) and dark brown, upper boundary convex. Lumina very small, crescent-shaped in radial section, without contents; periclinal walls usually meet, so lumina absent, marked only by contrast in pigmentation of upper and lower walls.

Hairs. Interspersed with papillae are short unicellular, non-glandular pointed hairs with ridged cuticle. Columnar in shape, apart from tapered tip; 70-90um long and 7-10um broad, walls pale straw, 2um thick. Lumina extends length of hair, contents medium brown, finely granular or absent, colourless.

Mesophyll: 100-200um thick of 5-7 layers of compacted shortly tangentially extended, rounded quadrangular cells, 22-35um wide, c.10um high. Upper layer exceptionally large: c.40um wide and 20um high. Walls and contents dense medium brown. Zone interupted by large tangentially ellipsoid lacunae, to 52um high and to 85um wide each of which results in a proportionately raised wart on outer seed surface.

I.E. single layer of small tangential shortly quadrangular cells, pale brown in colour, lumina occluded by a large prismatic crystal. Cells 11um wide, 8um high.

TEGMEN

Exotegmen 1(-2) layers thick. Fibres lengthy (to 265um) longitudinally orientated, deepish yellow, very thick (to 20um)-walled, pitted. In T.S. the fibres are columnar, to 45um high, 20um wide with (remarkably in this context) circular lumina, to 8um diam.

Endotegmen, a thin layer of crushed cells to 10um thick.

ENDOSPERM

Upper epidermis of sub-cuboidal cells, with pale, finely granular contents, 15-20um square.

Main tissue of isodiametric (5-7 sided in section) parenchyma, lumina filled with spherical lipid bodies. Cells 30-55um diam.

DISCUSSION

**Micromorphological characters: assessment of value.**

Generally, seed surface characters are comparatively uniform (cf. Orthocarpus in Scrophulariaceae, Chuang and Heckard, 1983), both within genera (e.g. Turraea) and between genera. It often seems true that tropical groups with thick-walled, complicated seed-coats and especially

those with fleshy fruits, have poorly developed surface sculpture compared with that of seeds of temperate, microspermous, thin-walled and dry fruited groups ( see e.g. Cheek, 1983). Some quantifiable variation does exist in anticlinal boundary elevation and in periclinal wall curvature within Turraea which may be useful in establishing infra-generic groups. Nymania and Naregamia with papillate/hairy, warty/ridged seeds are exceptional in that here the seed surfaces have cuticular microsculpturing and, more importantly, the seed surface characters form an important part in delimiting these genera from Turraea: indeed, for Naregamia, seed (surface) structure has been seen as the one suite of structures which 'immediately separates it (Naregamia) from Turraea'(Pennington and Styles, 1975).

The most interesting discovery of the survey was of a species of Turraea from Madagascar having papillate seeds with a verrucate/ridged ('macro-verrucate') surface. Material of this species was apparently unavailable to Pennington and Styles, for these characters seem to link Turraea much more closely than hitherto observed with both Naregamia and Nymania (see 'Generic Delimitation ' below). On the face of it, it seems unlikely that verrucate seeds, correlated with papillae/hairs as here, should arise de novo in unrelated groups.

**Anatomical characters: assessment of value.**

Testa. O.E. and cuticle: apart from the convexity and cuticular sculpture of the outer periclinal walls (o.p.w.) that form important characters in the delimitation of Nymania and Naregamia, the outer epidermis also provides important and apparently stable characters (within Turraea) in the nature, distribution, extent and colouring of

wall thickenings (cf. T.sericea Sm., T.heterophylla, and T. leroyana in Plate 4 & 5 ). The presence of a multiple hypodermis seems limited and characteristic of Humbertioturraea, but a single hypodermal layer also occurs in Calodecaryia.

Mesophyll varies from 0-10 layers thick. The cells are generally prostrate and longitudinally elliptic. In Nymania, they are up to nine layers thick and apparently deeply tanninized, whereas in Munronia, usually only one layer (with clear lumina) exists. Within Turraea there is great variation; T. leroyana with only one layer and T.heterophylla with seven to ten layers of three different cell types.

The testal mesophyll is usually the tissue that proliferates to form the bulk of the aril or sarcotesta (q.v.). As a source of taxonomic characters, the mesophyll is of comparatively little value since it is highly prone to artefact ( probably caused by desiccation). In one sample of Turraea heterophylla, some seeds had large complex, well-developed mesophyll, whereas other seeds had the mesophyll highly radially compressed and uninterpretable. The same occurs in other taxa to a less marked degree and renders the mesophyll characters of little use for comparative work. Nymania is exceptional in that the testal mesophyll is the thickest layer of the seed-coat, densely tanninized and apparently not so subject to artefacts. Moreover, it is alone in having very large ( to 85 X 52um) lacunae which are the sole source of the 'macro-verrucae' seen in the surface study.

I.E. Where radial compression occurs, this layer is often hard to detect. The cells are generally smaller and more rectangular than the mesophyll above, usually with the outer (lower) periclinal wall slightly thicker and sometimes with an intermittent airspace separating the layer

from the exotegmen below. In some Turraea species, e.g T.heterophylla, the characters of the O.E. are expressed intermittently in the I.E., but this was not detected in the satellite genera. A conspicuous prismatic crystal occurs in each cell in Nymania and Munronia. In Humbertioturraea and Naregamia they occur only intermittently. Similar obtains in Turraea where they are prominent in some species and not in others. Endocrystals were not detected in Calodecaryia. Their presence or absence does seem a useful character, but is reduced slightly by intermittent expression within a specimen. Dimensions and colour seem constant within species and are also potentially useful characters.

Tegmen. The exotegmen is probably the richest source of characters in the seed-coat. It usually consists of a single layer of lignified, pitted, longitudinally directed fibrous or rhombic cells (isodiametric or columnar in T.S.) which seem to form the strongest part of the seed-coat.

In Turraea, the fibres are often extremely short, almost isodiametric in L.S. (e.g. T.sericea), often with oblique end- walls and hence rhombic in shape (technically sclereids). The latter state is particularly marked in T.heterophylla, where the fibres are greatly extended diagonally, largely overlapping each other, so appearing to be two layers deep in T.S.. This species is also unusual in having two layers of prostrate elliptic sclereids below the fibroid layer. In T.S., Turraea fibres are highly columnar and are evenly thickened. The exotegmic fibres of Naregamia alata are very similar to those of Turraea, but differ from most in their highly concave o.p.w. (L.S.) which by deforming the thin testa above gives rise to the 'macro-verrucae' seen on the surface: evidently of quite different

origin from that of the 'macro-verrucae' of Nymania. However, T. leroyana has fibres very similar to those of Naregamia.

Nymania has the simplest exotegmen, a single layer of long (to 265um) fibres with slightly oblique end walls. In T.S., it is columnar (2:1) and has the thickest (20um) walls, markedly thicker in the radial plane. Humbertioturraea has similar fibres, though much shorter (155um), with thinner walls and less columnar in T.S., but is remarkably multiplicative, consisting of about 35 hypodermal layers. In Calodecaryia the exotegmen is five to six layers thick, but the fibres are very variable in length and orientation and not obviously hypodermal and with relatively thin (3-4um thick) walls. Perhaps the most unusual exotegmen is that of Munronia with the longest fibres (320um) of which the upper two layers run longitudinally and the lower two to three transversely (Plate 13 & 14). More bizarre still is the ventral skirt-like extrusion of the tegmen which forms a bony, protective cap around the fleshy tissue. Apart from the shape, length, breadth, orientation and number of layers of fibres mentioned above, wall colour, lumina details and pitting characters (size, density, slit-like, circular or branched) also seem reasonably stable and potentially useful taxonomic characters. The exotegmen is all the more valuable for being robust and resistant to desiccation. Material from herbarium sheets can prove just as useful as that from spirit.

The endotegmen usually consists of thin-walled parenchyma. Together with the I.E., it is usually completely crushed (Calodecaryia, Humbertioturraea and Nymania). Cell details are detectable, but usually distorted in Munronia, Naregamia and Turraea. Turraea sericea is unusual in that the endotegmen is relatively well preserved with a very distinct and characteristic I.E. It is possible that, despite its labile nature,

this tissue may be of some use at the infra-generic level in that genus.

Aril and Sarcotesta. The historical use of these terms has recently been competently reviewed by Boesewinkel and Bouman (1984). The terminology used by Pennington and Styles (1975) and quoted in the introduction, that is of 'arillode' (and 'sarcotesta'), seems to be in the sense that van der Pijl uses 'Arilloid', i.e for a fleshy outgrowth of uncertain origin (as distinct from his use of 'aril': specific to fleshy outgrowths of the funicle ). 'Sarcotesta' is generally understood to refer to a generalized fleshiness of the seed-coat. However the terms arillode/arilloid seem superfluous here and the usage of Corner (1976) in calling any fleshy outgrowth an aril and prefixing it with its site of origin, is followed. In the Turraeeae arils appear only in Turraea & Naregamia where they are raphe-funicular in origin, appearing as large brightly coloured, fleshy pads (e.g. T.heterophylla) or thin, unpigmented adpressed ventral flaps (e.g. T.leroyana). They are easily removed and leave a long thin scar which extends from the chalaza towards the micropyle and clearly corresponds exactly with the raphe/pre-raphe. Anatomically, the tissue consists of a localized proliferation of the testal mesophyll clad in a modified testal epidermis. In the remaining genera the fleshy tissue does not proliferate as a localized outgrowth, is more generalized in origin and is best termed sarcotestal. In Calodecaryia it originates from the surfaces of the raphe, chalaza, around the micropyle and from parts of the ventral and lateral testa. In Humbertioturraea malifolia, the sarcotesta is similarly distributed and largely correlated with an enormous hilum.

The fleshy tissue of Munronia has a complicated topology but is

perhaps best regarded as a thick sarcotesta enveloped by an ingrowing outgrowth from the ventral rim of the tegmen.

**Infra-generic Variation in Turraea**

Due to lack of material, only Turraea was investigated with any thoroughness: eight species were studied (listed in the appendix). Great variation exists in the testal O.E. (especially in the disposition and extent of o.p.w. thickenings), in the exotegmen (in fibre shape, dimensions, wall-thickening patterns and pitting) and, to a lesser extent, the testal I.E. These provide many characters which seem to be constant within and characteristic of species. They may be of use in discerning species alliances. Characters of the testal mesophyll and endotegmen seem prone to artefact and, in the case of the former, are certainly far too variable within species and even within individual seeds for taxonomic use. Turraea as a genus seems to be characterized by its very short exotegmic fibres, barely longer than high, and a raphe-funicular aril. In this tribe these characters otherwise occur only in Naregamia.

**Delimitation & Affinities of Satellite Genera.**

Naregamia (Plates 6 & 7) is distinguished from Turraea, apart from its seeds, by its compound leaves. The exception is T. streyi which has staminal appendages and its rhachis is un-winged, characters not seen in Naregamia, nor in several other species of Turraea (Pennington & Styles, 1975). They go on to say ' In addition, the characteristic seed structure of Naregamia immediately separates it from Turraea. It is slender, curved, prominently truncate at the base and apex and the thick, bony testa has large, irregular, transverse ridges and is

puberulent. The seed of all species of Turraea is rather swollen and rounded, not truncate at base and apex, usually with a smooth shiny testa and always glabrous.' Although this is perfectly true of most Turraea species, it is clear that Pennington and Styles did not have the opportunity to examine much material of the Malagasy species. Several of these have slender curved seeds, with a thick, hard seed-coat and are truncate at least at the chalazal end. T. leroyana, as illustrated above has large bumps (macro- verrucae)/ridges and a papillate surface, distinctly similar to that of Naregamia and most unlike the normal state described above, quite accurately, for Turraea. In addition, it must be pointed out that Naregamia is the only satellite genus that shares short (<2:1)) exotegmic fibres and a raphe-aril with Turraea. The other genera are all long fibred and more or less sarcotestal. Naregamia now seems much less distinct. Although the genus can still be maintained using the differential morphological characters outlined above, as far as seed structure is concerned, the genus belongs in Turraea.

In seed anatomy, Naregamia is indistinguishable from Turraea in any character, being very close to T. leroyana (Plate 5) in the testal O.E. (thin, highly convex o.p.w.) and mesophyll (in dimensions and pigmentation) and in the strangely sinuate o.p.w. of the exotegmic fibres, curiously reminiscent of a 'roller-coaster'. T. leroyana though has largely lost (crushed?) the testal I.E., and no crystals are evident. In addition, the endotegmen is absent. Both are much in evidence in Naregamia (as they are in most Turraea species) which consequently seems more primitive than T.leroyana.

Humbertioturraea (Plates 8 to 11) is distinct from Turraea in its fleshy, indehiscent fruit (Turraea never fleshy and dehiscent), larger

seeds (three times as long as the largest in Turraea, straight embryo, larger hilum ( 15-20 % seed surface versus <5%), very thick seed-coat (<0.25mm versus 1mm ) and sarcotestal rather than raphe-arillate seeds. Its elongate testa cells are not usual in Turraea. The highly multiple hypodermis and exotegmen (35 layers) are unique in Turraeeae.

Leroy (1969) very convincingly shows how Humbertioturraea has closest affinity with Turraea section Rutaea Harms, since it shares the high number of ovary locules (8-20) which distinguishes this section. Additionally, several species of Rutaea (e.g T. wakefieldii Oliv., T. sericea and T. floribunda) are distinguished from the rest of the genus by a very thick pericarp and highly elongate staminal tube (up to 16cm in T. sericea and T. floribunda) both of which are also shared by the species of Humbertioturraea. Indeed, as Leroy points out, Rutaea and Humbertioturraea are indistingushable vegetatively, florally and in young fruit . However, the fruits of Humbertioturraea, in losing their dehiscence and becoming fleshy, seem to have lost all trace of the twin woody longitudinal bands which open each valve in Turraea and no sign of a distinct woody endocarp exists. Most of the protective function of the fruit has been taken on by the massively thickened coats of the enlarged seeds. Here, both integuments appear to be strongly multiplicative by the activity of intercalary meristems producing numerous additional layers of mechanical cells by periclinal divisions, clearly evident by the stacked nature of the cells in the testal hypodermis. In the process, the testal mesophyll and crystalline I.E. are crushed and barely detectable. The hilum is larger than mere scaling up from the size in Turraea would allow and may be an adaptation towards more rapid ovule growth, allowing more vascular bundles to enter. In short, there

is a strong case for stating that Humbertioturraea is derived from the ancestors of Section Rutaea of Turraea. The position of section Rutaea within Turraea can itself be regarded as advanced on the evidence of the characters it shares with Humbertioturraea. All of these are not otherwise known in Turraea or the tribe, and with the exception of thick pericarp, are rarely seen in the family as a whole.

Since the evolutionary position of Humbertioturraea with regard to Turraea seems clearly established, it now seems of particular use to examine the nature of seed fleshiness in this light. There has been some controversy over whether the sarcotestal condition is primitive and the arillate advanced (van der Pijl, 1969 ) or vice versa (Corner, 1976). In this instance, it seems that the sarcotestal condition in Humbertioturraea is derived from the presumably primitive funicular-raphe arillate condition in Turraea, presumably by the tendency towards succulent tissue in the testal mesophyll (which forms the basis of the succulent layers) spreading to the proximal integumentary tissue rather than being confined to the immediate neighbourhood of the vascular bundle as in Turraea. This seems to be an example of Corner's (1958) 'transference of function'.

If Humbertioturraea is considered derived from the ancestors of Turraea Section Rutaea, as it seems, then the straight embryo found in both species of Humbertioturraea investigated, must also be considered derived from the curved embryo otherwise prevalent in Turraea and the rest of the tribe. However, the curved embryo can itself be regarded as derived, since the condition in the rest of the family is straight. The condition in Humbertioturraea therefore, may represent a reversal in evolution. It is possible to speculate that the curved embryo, typical

of the tribe, is partly a function of the physical constriction of the very small seed-coat volume (typical of this tribe) in which the embryo develops, constraining it (to some degree) to become curved. With the dramatic increase in size of the seed-coat seen in Humbertioturraea, there can be no physical constraint on the embryo to become curved if the increase in embryo length does not parallel the increase in seed-coat length. Alternatively and perhaps more likely, the increase in seed-coat expansion that characterizes Humbertioturraea may be unequal. If it were largest on the proximal face, the inherent curvature of the seed would be 'ironed out'. The latter would also help to explain the disproportionate size of the increase in area of the hilum in Humbertioturraea if an origin from the ancestors of Turraea Section Rutaea is accepted. Finally, there is the possibility that Humbertioturraea is derived from a species of proto-Turraea with a straight embryo, though none is known in the modern species.

Similarly, the derivation of Humbertioturraea from Turraea can be used to give 'evolutionary direction' on the matter of exotegmic fibre length. The exotegmic fibres in the former are about four times as long as wide, whereas those in the latter are more usually only twice as long as broad and are amongst the closest in the Meliaceae to Corner's (1976,1:13) 'palisade' state. Exotegmic seed families can be divided into those with palisade exotegmen and those with fibrous exotegmen (which includes Meliaceae), according to Corner, but whether one is derived from the other, or whether both are of independent origin is uncertain. The evidence in this case suggests a palisade origin for the fibrous state.

Munronia (Plates 12-14) is one of the most morphologically distinct of the satellite genera in its mostly pinnate leaves (all but one Turraea simple), the petals united to the staminal tube (versus petals free), the bifid and stellate indumentum (simple), and the free tubular nectary which is barely detectable in Turraea (Pennington & Styles, 1975).

The genus is no less distinct in seed structure. Its exotegmic fibres are the longest in the tribe and quite unlike those of Turraea which are not much longer than they are broad. The transverse orientation of its lower fibre layer is very unusual in the family and the tegmic 'skirt' discussed above is quite unique. All these three character states can be viewed as highly derived. The evolutionary significance of the 'tegmic skirt' is obscure, but that of the long, cross-ply exotegmic fibres is presumably for greater structural strength in the digestive tract of the animal dispersal agent. Why this is greater than that seen in Turraea is difficult to comprehend unless one speculates that the inaccessibility of the succulent tissue (encased in the tegmic skirt) demands longer retention in the gut which in turn would favour a tougher seed-coat. Perhaps the longer a seed is retained in the gut, the greater the distance it is dispersed. This might be a useful attribute for 'island hopping' in S.E. Asia! On the other hand, Turraea virens in the same area has spread further than any Munronia species without the aid of this appendage.

Apart from the derived tegmic characters, the seed anatomy is remarkably conservative. The testal O.E., mesophyll and crystalline I.E. all appear unspecialized and can be viewed as tying in with the primitive morphological structures (typical of the family but not the tribe) of pinnate leaves and well-developed nectary.

Nymania (Plates 17 to 19) is unquestionably the most morphologically distinct genus in the tribe in its oblique-limbed flower and free filaments with versatile anthers. Its linear leaves and lack of a receptaculum pollinis are also unusual in Turraea and its inflated fruits are unique in the family (Pennington and Styles, 1975).

In seed structure, it is not quite so unusual, though it is unique in the tribe in its lacunar and multi-layered testal mesophyll. The presence of a crystalline testal I.E. and the the nature of the exotegmic fibres, the crushed endotegmen are quite usual in the tribe. The macro-verrucate and papillate-hairy seed surface suggests an evolutionary link with Turraea leroyana and Naregamia, but, in fact, they are not homologous, the macro-verrucae of Nymania arising wholly from the testal mesophyll lacunae and being quite unconnected with those of the latter which are of exotegmic origin. This is a clear example of the dangers of basing conclusions on morphological evidence without accompanying anatomical analysis.

The relationship with Calodecaryia, strongly suggested by the marked campylotropy is discussed under the latter.

Calodecaryia (Plates 15 & 16) is distinct from Turraea in its filaments, united for less than half their length (± completely united in Turraea) and also differs from most in its linear leaves and lack of marked receptaculum pollinis; but most of its distinction resides in the seeds (Pennington and Styles, 1975). These appear to lack completely a crystalline I.E. and are unusual in the multiple layered exotegmen. The simple testal hypodermis (O.E.), as the complete lack of crystals, is unique in the tribe. One of the most conspicuous features of the seed is its high curvature and campylotropy, unknown elsewhere in Meliaceae, apart from Nymania.

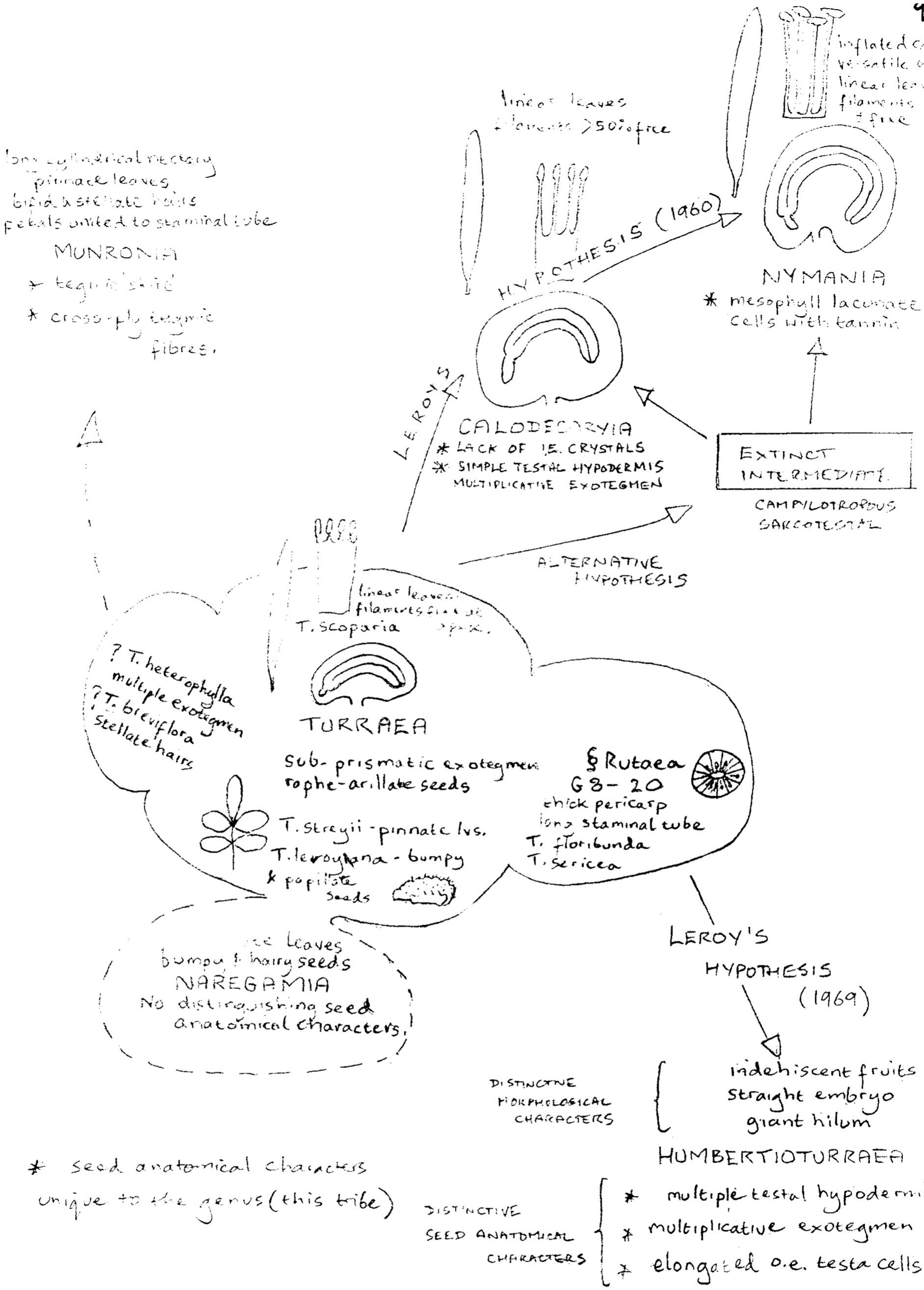



FIG. 3

SPECULATIVE RELATIONSHIPS OF THE SATELLITE GENERA TO TURRAEA

Leroy, in describing Calodecaryia, hypothesized that it represented an intermediate in evolution between Turraea and Nymania (Leroy, 1960). This seems reasonable enough, since, as he shows, this line of evolution shows increasing freedom of filaments together with increasing curvature of the embryo. Additionally , both Calodecaryia and Nymania share linear leaves and lack of a marked receptaculum pollinis, rare characters in the tribe, but also occurring, if not coinciding, in some species of Malagasy Turraea. However, seed anatomy tends to militate against this theory. Firstly, by any standards, the lack of a crystalline testal I.E., the presence of a multiple layered exotegmen and testal O.E. hypodermis in Calodecaryia are derived characters. If Calodecaryia were intermediate, surely Nymania would possess these features? Since Nymania does not, but possesses the character states here considered primitive in the tribe, it seems more fitting to speculate that both genera have diverged independently from a Turraea-like common ancestor with largely free filaments, linear leaves and lacking a receptaculum pollinis. This ancestor might have possessed campylotropous seeds, with a single layered exotegmen and a crystalline I.E.

In short, with the exception of Naregamia, the views of Pennington & Styles (1975) on generic delimitation in the tribe are entirely upheld and strongly reinforced by this survey. Seed characters diagnostic at the generic level are presented in table 2. The hypothesis that the Turraea seed is the ancestral model from which the satellites have evolved is completely tenable (see fig. 3 ).

**Tribal delimitation.**

The Turraeeae are well defined in the Meliaceae in their seed structure. Hemianatropy/campylotropy, with short (L.S.), ribbon like

(columnar in T.S.) exotegmic fibres, absence of pachychalazy, curved embryo and a high (1/3-2/3) endosperm to embryo volume ratio clearly mark them out.

The placement of Nymania has historically been somewhat contentious (see Pennington and Styles, 1975), but was intensively investigated there. They concluded after reviewing wood anatomy, chemistry and pollen as well as morphological characters, in the context of a monographic study of the entire family, that it clearly belonged in the Turraeeae. Subsequently, White (1986) has suggested it merits separate tribal treatment, although adducing no additional evidence. The seed anatomical data presented above, strongly favour its inclusion in the Turraeeae.

The placement by Harms (1896), on the basis of seed characters of Cipadessa in the Turraeeae is discussed under that genus.

## PHYLOGENETIC SPECULATION

The evolutionary polarity of most character states useful in delimiting genera has been discussed above under 'delimitation of genera'. It has generally been assumed here that character states usual in the rest of the Melioideae are primitive, the other states derived. Character states unique to genera (within the family) are considered derived. The unusual case of Turraea and Humbertioturraea, where the relationships between the two genera seems unequivocal, has been used for decisions on characters of controversial polarity, e.g. Seed fleshiness and fibre length. Sporne (1948), has been followed for the polarity of other characters, particularly those of gross seed structure (here see also Martin, 1947) e.g. Seed fleshiness, where these correlate with existing patterns.

| CHARACTER STATES / CHARACTERS | PRIMITIVE 0 | ADVANCED 1 |
|---|---|---|
| A. LEAVES | PINNATE | SIMPLE |
| B LEAVES | BROAD | LINEAR |
| C FLOWER SYMMETRY | ACTINOMORPHIC | BILATERALLY SYMMETRICAL |
| D FILAMENTS | UNITED | >50% FREE |
| E ANTHERS | BASIFIXED | VERSATILE |
| F INDUMENTUM | SIMPLE HAIRS | BIFID OR STELLATE |
| G FRUIT | DEHISCENT | INDEHISCENT OR INFLATED |
| H OVARY | ≤5-LOCULAR | 5-20 LOCULAR |
| I PETALS | FREE | UNITED TO STAM. TUBE |
| J SEEDS | SMOOTH | ROUGH |

| CHARACTER STATES / CHARACTERS | PRIMITIVE 0 | ADVANCED 1 |
|---|---|---|
| A. SEED FLESHINESS | ARILLATE | SARCOTESTAL |
| B. TESTAL O.E. | ISODIAMETRIC & TABULAR | LONGITUDINALLY ELONGATED OR HIGHLY CONVEX |
| C TESTAL O.E. | NOT HYPODERMAL | HYPODERMIS SIMPLE OR MULTIPLE |
| D TESTAL MESOPHYLL | NOT LACUNATE | LACUNATE |
| E TESTAL I.E CRYSTALS | PRESENT | ABSENT |
| F EXOTEGMEN 'SKIRT' | NOT 'SKIRTED' | SKIRTED |
| G EXOTEGMEN CELL LENGTH | SUB-COLUMNAR | FIBROUS |
| H EXOTEGMEN ORIENTATION | LONGITUDINAL ONLY | LONGIT. & TRANSVERSE |
| I EXOTEGMEN LAYER NUM | ONE LAYERED | MULTIPLE LAYERS & MULTIPLICATIVE |
| J EXOTEGMIC O.P.W. | TABULAR | SINUATE |

TABLE 3. SELECTED GENERIC CHARACTERS IN TURRAEEAE POLARIZED & ENCODED FOR CALCULATION OF ADVANCEMENT INDEX.

ABOVE TEN CONVENTIONAL MORPHOLOGICAL CHARACTERS

BELOW TEN SEED ANATOMICAL CHARACTERS

CONVENTIONAL MORPHOLOGICAL CHARACTERS:

| | NYMANIA | CALO-DECARYIA | TURRAEA * | NAREGAMIA | HUMBERTIO-TURRAEA | MUNRONIA |
|---|---|---|---|---|---|---|
| A | 1 | 1 | 1 | 0 | 1 | 0 |
| B | 1 | 1 | ½ | 0 | 0 | 0 |
| C | 1 | 0 | ½ | 0 | 0 | 0 |
| D | 1 | 1 | 0 | 0 | 0 | 0 |
| E | 1 | 0 | 0 | 0 | 0 | 0 |
| F | 0 | 0 | 0 | 0 | 0 | 1 |
| G | 1 | 0 | 0 | 0 | 1 | 0 |
| H | 0 | 0 | ½ | 0 | 1 | 0 |
| I | 0 | 0 | 0 | 0 | 0 | 0 |
| J | 1 | 0 | 0 | 1 | 0 | 0 |
| TOTAL | 7 | 3 | 2½ | 1 | 3 | 2 |

SEED ANATOMICAL CHARACTERS:

| | | | | | | |
|---|---|---|---|---|---|---|
| A | 1 | 1 | 0 | 0 | 1 | 1 |
| B | 1 | 0 | 0 | 1 | 1 | 0 |
| C | 0 | 1 | 0 | 0 | 1 | 0 |
| D | 1 | 0 | 0 | 0 | 0 | 0 |
| E | 0 | 1 | 0 | 0 | 0 | 0 |
| F | 0 | 0 | 0 | 0 | 0 | 1 |
| G | 1 | 1 | 0 | 0 | 1 | 1 |
| H | 0 | 0 | 0 | 0 | 0 | 1 |
| I | 0 | 1 | 0 | 0 | 1 | 1 |
| J | 0 | 0 | 0 | 1 | 0 | 0 |
| TOTAL | 4 | 5 | 0 | 2 | 5 | 5 |
| COMBINED TOTAL | 11 | 8 | 2½ | 3 | 8 | 7 |

TABLE 4. CODING OF CHARACTER STATES & CALCULATION OF CRUDE 'ADVANCEMENT INDICES' FOR THE GENERA OF TURRAEEAE: MORPHOLOGICAL & ANATOMICAL CHARACTERS CONTRASTED.

* WHERE GENUS LARGELY OF ONE CHARACTER STATE, BUT A SINGLE ABERRANT SPECIES OF THE OTHER STATE EXISTS, THE LATTER IGNORED, BUT, IF MORE THAN ONE SPECIES, GENUS MARKED '½'.

The polarities of character states being thus decided, are set down and encoded '0' for primitive and '1' for advanced in table 3. These are then applied to the genera of Turraeeae (table 4). The operation has been repeated for a similar number of conventional morphological characters. Totals of the encoded characters have been used to arrive at a simple 'advancement index', firstly to objectively compare genera for evolutionary 'advancement' and secondly to compare conventional morphological characters and internal seed characters. The results are as follows. By the combined score, Nymania is by far the most advanced at 11, followed at a respectable distance by Calodecaryia, Humbertioturraea (8) and Munronia (7), Turraea and Naregamia lag far behind (2.5 & 3). On conventional morphological characters alone, Nymania is by far the most derived, rating 7 out of 10 compared with its nearest contenders Calodecaryia and Humbertioturraea (3). Munronia (2) rates amongst Turraea and Naregamia as the most primitive. However, the indices based on seed anatomical characters alone tell a different story, Calodecaryia, Humbertioturraea and Munronia all ranking 5, Nymania lagging slightly at 4 with Turraea and Naregamia most primitive at 0 and 2 respectively.

These figures can only be used to give a broad indication, since for the sake of simplification, not all available characters were used and a different selection would inevitably result, with such a smaller range of characters, in comparatively large changes of up to 2 index points in either direction. This crude analysis does suggest that perhaps seeds can evolve at different rates from other plant organs. In Nymania, seeds are more conservative in terms of 'advancement' than their morphological counterpart, whereas in Munronia they are significantly more advanced. Whereas there is wide variation in indices in conventional characters,

those of seeds are much more constant, all the satellite genera having more or less the same rating, except Naregamia which comes very close to Turraea.

It is of interest that there were more generically important seed characters in this study than conventional morphological ones. Omitted here were: hilum size, endosperm %. embryo curvature and tropism. Davis and Heywood (1963) seem correct in stating that ' internal features of the seed, although more difficult to observe, are even more valuable than external characters'.

A number of valid criticisms can be levelled at this approach, not least over-simplification of coding and subjectivity in the selection of characters. It does have the advantage of repeatibility, however.

The primitive Turraeeae can be reconstructed using table 3, following the '0' column downwards. Not suprisingly, the list thus produced most nearly matches some present-day Turraea and Naregamia species.

The Turraeeae seed and the Meliaceae.

By the criteria of Martin (1947) and Sporne (1948), the Turraeeae seed, with its typically copious endosperm and exserted radicle (unusual in Meliaceae) can be regarded as amongst the most primitive in the family. The absence of the undoubtedly advanced unitegmic condition (common in the remaining tribes of the Melioideae) in the seed-coat and the presence of (hitherto unreported) short, sub-prismatic exotegmen (from which the fibrous state possibly derived according to Corner, 1976) adds weight to the idea that the primitive Turraeeae seed is the most primitive in the family. Against this must be set the fact that the embryo is predominantly curved and that the ovule and seed is predominantly hemi-anatropous. The comparatively conservative overall

seed construction in the tribe may be connected with the predominantly bushland habitat (sometimes forest edge or grassland), perhaps even the factor of supposed bird dispersal, since it can be argued that there has been little impetus towards a massive construction (the closest seen is in Humbertioturraea) to meet the forest (or primate) requirement. Rather, the seeds have remained simple and perhaps become simplified and reduced from the primitive Melioid condition. It is curious that strongly sculptured seeds occur only in this tribe and have arisen on two separate occasions. Again, this is best explained by the tribal tendency to open bushland habitats, since here, seed sculpturing is considered linked to wind dispersal (see Ecological Aspects, below) which in small trees is probably selected only in such a habitat.

## ECOLOGICAL ASPECTS.

In the absence of field observations on the subject, a discussion of Turraeeae dispersal ecology must remain largely speculative. According to Pannell and White (1985), Turraea heterophylla (Plates 2c & d) is probably dispersed by birds, its 'orange-red 'placentas' greatly enhance the conspicuousness of the small orange arils which contrast with the shiny black testas of the seed', as are the conspicuous red seeds of T.obtusifolia (Plates 2a & b) where 'the small white arils are completely concealed. The seeds have bright red shiny testas and are tightly packed together. Collectively they are conspicuous against the capsule. It is possible that the seeds ... mimic the more typically arillate seeds of other plants but nothing is known for certain'. On the other hand, T.pulchella & T.streyii (which I have not surveyed) have 'capsules, seeds and arils minute and inconspicuous and possibly dispersed by ants', whilst Nymania is possibly dispersed by wind.

The only field observations I am aware of are those of G. Nichols (pers. comm.) who has conducted a long-term study on animals which feed on the seeds of Turraea floribunda in Natal. According to him, they are consumed by at least 13 species of animal:

Birds: Sombre bulbul
Yellow-bellied bulbul
Terrestial bulbul
Black-eyed bulbul
Speckled mousebird
Cape white-eye
Black-bellied glossy starling
Red-eyed dove (feeding off the ground and later regurgitating)
Red-fronted tinker barbit
Golden-rumped tinker barbit
Purple-crested lowry (minor consumer)

Mammals: Vervet monkey
Duiker (minor consumer)

Variation in seed presentation in Turraea

The species referred to above by Pannell and White are all atypical of the genus. The usual mode of seed presentation in Turraea is that seen in , for example, T. cornucopia Styles and White ined. and T. robusta (see Plate 3). Here the seeds are clustered around the placenta in the centre of the fruit. The testa of each seed is dark brown, or black and conspicuously enveloped by a contrasting fleshy raphe-aril coloured dull or bright orange. T. obtusifolia (and T. mombassana) are atypical in that the main attractive function is taken on by the bright

red testa, the arils being small, white and completely concealed (Pannell and White, 1985). This may represent an adaptation against 'aril predation' since according to G. Nichols (pers. comm.), some of those animals feeding on T. floribunda take the aril and leave the main body of the seed in the fruit. At the other end of the spectrum of seed presentation, T. heterophylla, in common with a small number of equatorial forest undershrub species (these may represent a secondary colonisation from the usual, non- forest habitat.), has its seeds displayed along the length of unusually long fruit valves (see Plate 2c and Cheek, 1989b). Although the raphe-aril is well developed, the main attractive function is taken by the fruit septa which appear orange and succulent. This may represent an adaptation towards greater showiness necessary in a habitat where light levels and concentrations of potential dispersal agents are lower.

The inflated, bladdery capsule of Nymania is clearly adapted to wind dispersal in the semi-desert bushland of the Karoo. Though superficially quite out of keeping with the usual capsule in Turraeeae (indeed, Meliaceae), many analogies exist in other groups, perhaps the most striking parallel being that of Helleborus vesicarius Auch. ex Boiss. (see Mathew, 1986) a species from steppe country (resembling the Karoo in physiognomy; windswept with scattered clumps of low vegetation.) with wind dispersed, inflated fruits (like those of Nymania: see Plate 20), whilst its congeners have small, dehiscent follicular fruits. The verrucate seeds with papillae/hairs may well facilitate rolling over the soil surface or conversely may function to trap grains of sand between the trichomes thus helping to weigh down and bury the seed (Manders, 1986 on hairy Protea seeds). It now seems likely that these characters

must have some functional significance since papillate/hairy seeds with verrucae of different origin also occur in Naregamia and Turraea.

Bird dispersal would accord well with the thick, glossy seed-coat and cuticle with reduced surface sculpturing of most Turraea species. Such characters would facilitate an undamaged passage through a gut and account for the conspicuous presentation and lipidic 'aril' of seeds of these species. Conversely those of Naregamia and Turraea leroyana with their thin-walled and sculptured epidermides may be unsuited to bird dispersal. This speculation together with their poorly developed aril perhaps signifies ant or wind dispersal. The large, weighty, fleshy berries of Humbertioturraea are too large for birds (excepting the extinct Aepyornis) and are presumably dispersed by lemurs. The formidably thickened seed walls would surely otherwise provide far more protection than necessary: a passage through a bird's gut is less likely to be fraught than a mammal's (see Trichilieae discussion). The seeds of Calodecaryia and Munronia do not seem to match any known dispersal syndrome and defy ecological conjecture.

## SUMMARY

This study highlights the limited value of seed micromorphological characters in a fleshy-seeded, woody tropical group and illustrates the danger of drawing conclusions on affinities based on micromorphology without associated anatomical investigation. Attention is drawn to the utility of seed anatomy in investigating generic limits. Whilst the delimitation of other satellite genera in the family is reinforced, that of Naregamia is considerably weakened.

Work is still needed to broaden the basis of the survey in Turraea in order to investigate infra-generic groupings and to look for further links with the satellite genera.

# CHAPTER SIX

# MELIEAE

## INTRODUCTION

The Melieae consist of two closely-related genera with bipinnate or pinnate leaves which have glands at the base of the petiole, hermaphrodite flowers, indehiscent fruits with a woody endocarp and "a number of interesting anatomical features not recorded elsewhere in the Meliaceae, in particular clusters of minute vessels with spiral thickening of the walls" (Pennington and Styles, 1975).

The tribe is centred in the Old World tropics. Melia consists of one species in Indomalesia with possibly two closely related ones in South and East tropical Africa. Forms of Melia azedarach, the Indomalesian species, are widely cultivated and naturalized throughout the warm parts of the world (Mabberley, 1984). Azadirachta consists of two species in the Indo-malesian region, with one, A. indica A. Juss., widely cultivated and sometimes naturalized elsewhere in the tropics (Pennington and Styles, 1975).

The first investigation of seed anatomy in this tribe was by Netolitzky (1926) of Melia azedarach, subsequently re-investigated by Nair (1959), who traces the development of the two integuments of the seed-coat, but does not note the presence of crystalline cells in the seed-coat (testal I.E.) or the thickenings of the testal O.E. periclinal walls or the exotegmic fibres. However, he does indicate the presence of a 'tanniniferous inner epidermis of the inner integument'. This species was investigated again by Vaughan (1970) but his description is

even more deficient. Finally, this species was examined by Corner (1976,1:190) who investigated the development of the seed-coat, confirming the presence of the usual Meliaceae pattern and accounting for most of the characters of the seed-coat described here excepting the 'tanniniferous' part. Corner points out that earlier workers "may not have studied mature seeds. The species may be variable, or there may have been confusion with M. dubia, the fruits of which are similar". Corner also investigates 'Melia dubia Cav.' (= wild forms of the cultivated M. azedarach L., Mabberley 1984) which he shows to have noticeably different anatomy from the material he describes as 'M. azedarach'.

Azadirachta was investigated by Nair and Kanta (1961) who trace the development of the two integuments but who do not investigate the mature seed-coat (and hence miss the crystalline I.E.). However, the last stage that they illustrate can readily be matched with that of a mature seed-coat (the inner part of the testa with its 'three layers of loosely arranged cells' is very distinctive) and helps to confirm the identification of testa and tegmen, which are distinguished in both genera by the usual Meliaceae markers (Chapter Four). Vaughan (1970:156) figured the seed-coat competently, but did not note the crystals in the testal I.E.

A S.E.M. study of the seed-coat micromorphology was not carried out since a light microscopical survey suggested little variation and S.E.M. studies in other tribes had shown S.E.M. characters to be of little value in genera with fleshy fruits.

Fortunately it was possible to obtain adequate material of both Azadirachta (A. indica) and Melia (three accessions under three different species names) for anatomical investigation.

RESULTS

Melia dubia Cav. (= wild form of M.azedarach)

This description based on Cheek 1561

Collector's notes: "Fruits fully grown, green to yellow."

Corner 1976,1:190 "Seeds 1 per loculus, in the very hard endocarp, 1-3 per fruit, c.12x3mm, oblong, elliptic in section, acute at the chalazal end, flattened towards the short funicle, dark brown, smooth, exarillate. Testa well developed with conspicuous palisade (O.E.) and more or less crushed mesophyll, not lignified, c. 9-10 cells thick on the sides of the seed, 15-20 cells thick in the elongate exostome-raphe; O.E. as a palisade of prismatic cells with thickened outer and inner yellowish walls (faintly punctate-striate) and brown middle part (? thick walled); mesophyll composed of small, tangentially elongate, sub-stellate cells with brown contents; I.E. unspecialized. Tegmen crushed or absorbed except for a single layer of large more or less hexagonal cells with brownish walls, not lignified; endostome as a small plug of crushed brown cells, unlignified. Vascular bundle only in the raphe, dividing at the chalaza into 7-9 branches shortly recurrent to the base of the endosperm, apparently perichalazal along the raphe. Hypostase not evident. Endosperm oily.

"There is no fibrous exotegmen. Whether I have interpreted the exotestal palisade -cells correctly must be decided from earlier stages than were available. At first sight the exotesta seems to be composed of three layers of cells but in surface-view as well as in section, the radial walls can be traced as continuous lines from the outside to the inner side of the complex. The nature of the yellowish thickened outer and inner ends of the cells I could not determine. A few palisade cells,

particularly along the raphe, had the brown middle part of the cell clearly delimited with thick walls, but most cells had merely glairy contents.(Ceylon; ripe fruits in alcohol.)".

GROSS MORPHOLOGY

Seeds nil-one per locule, placentation axile, attached towards distal end of fruit. Fruits baccate, oblate-ellipsoid, 12-20mm long, 11-15mm broad. Pericarp glossy yellow with thickly scattered corky lenticels. Mesocarp thick (2.5-3.5mm) and fleshy. Thick, woody, dark brown endocarp (1.5-2mm thick) evenly developed around each locule (to 6), whether ovules aborted or not. Usually 1-3 fertile locules per berry. Seeds dark brown, glossy, narrowly ellipsoid, beaked at each end. Distal beak formed by the chalaza, the proximal, curved beak the funicle-exostome: not noticeably fleshy. Seeds 10mm long, 2.5mm broad.

ANATOMY

SEED-COAT

Cuticle: to 7um thick. Reticulately patterned, murae along anticlinal walls of O.E.

O.E. Single (-two) layer(s) of radially columnar cells with very thick o.p.w. (35-40um thick)and i.p.w.(15-20um thick). Anticlinal walls much thinner; 2um thick. Lumina without contents or colour, walls lustre-less yellow brown. i.p.w. thickening sometimes restricted to angles. Cells 120-140um tall, 18-25um wide. Hexagonal in paradermal section.

Mesophyll and I.E. (latter not noticeably differentiated from former) of 4 to 7 layers of small, brown, prostrate c. quadrangular cells, 10-14(-20)um wide and 7-10um tall, walls thin, colourless, lumina with

PLATE 25

MELIA AZEDARACH

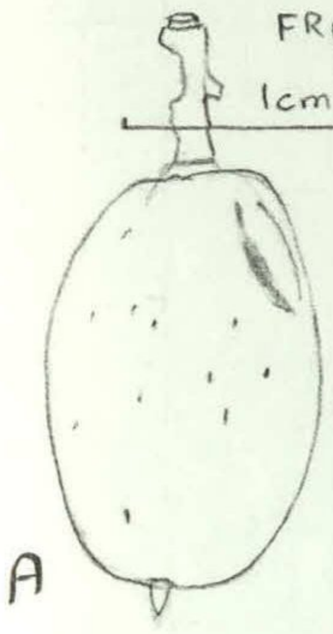
A-G FRUIT AND SEEDS: VARIOUS VIEWS. NOTE LIGNIFIED PUTAMEN THAT ENCAPSULATES ALL FIVE SEEDS IN THE FLESHY, INDEHISCENT, FRUIT.

H SEED-COAT ANATOMY: NOTE THE SHORTLY COLUMNAR TESTAL O.E. WITH HIGHLY THICKENED O.P.W., THE TANNINIFEROUS TESTAL MESOPHYLL, THE PERSISTANT AND CRYSTALLINE TESTAL I.E. & THE LAYER OF LIGNIFIED EXOTEGMIC FIBRES.

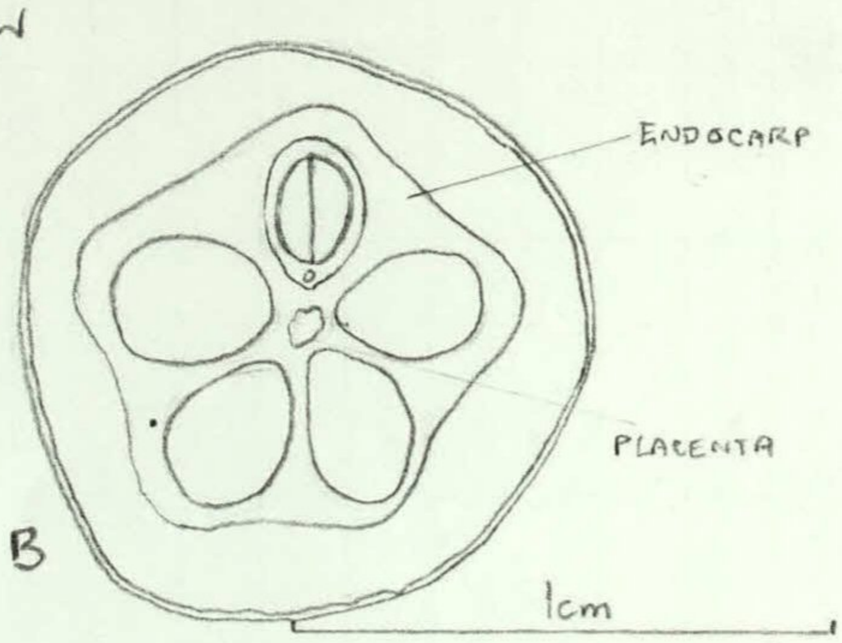
# Melia azedarach. L.



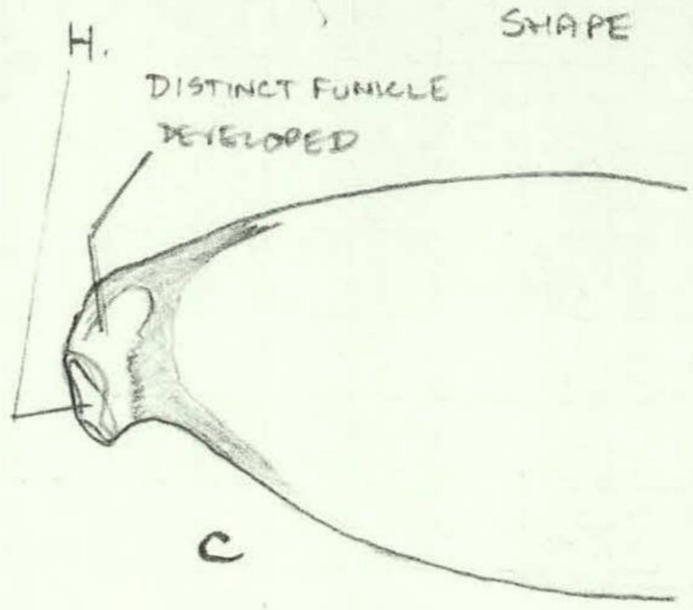
FRUIT: LATERAL VIEW




FRUIT T.S.




SEED: VARIATION IN SHAPE



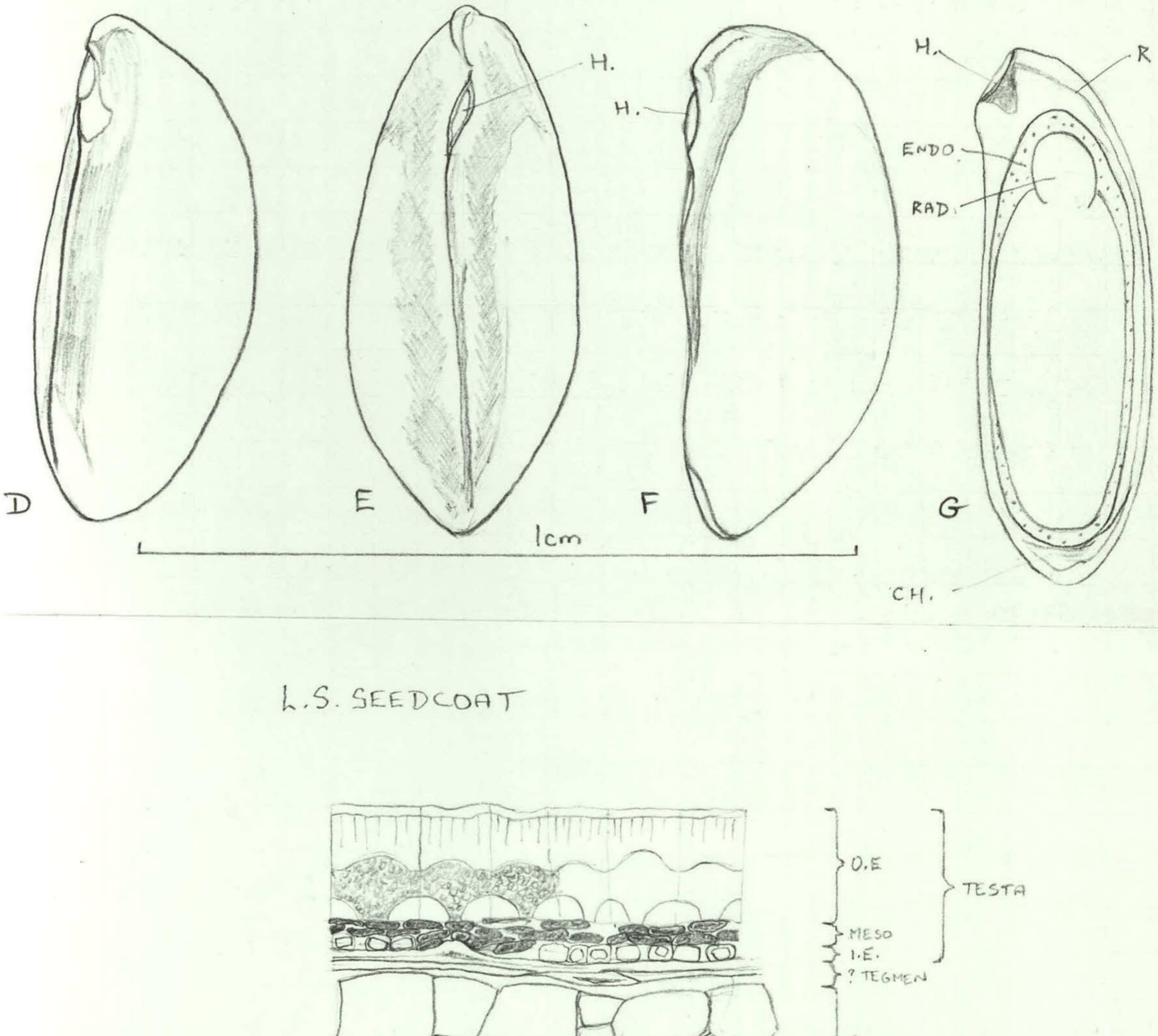

SEED:

VENTRAL/LATERAL VIEW

VENTRAL VIEW

LATERAL VIEW

L.S. SEED




L.S. SEEDCOAT

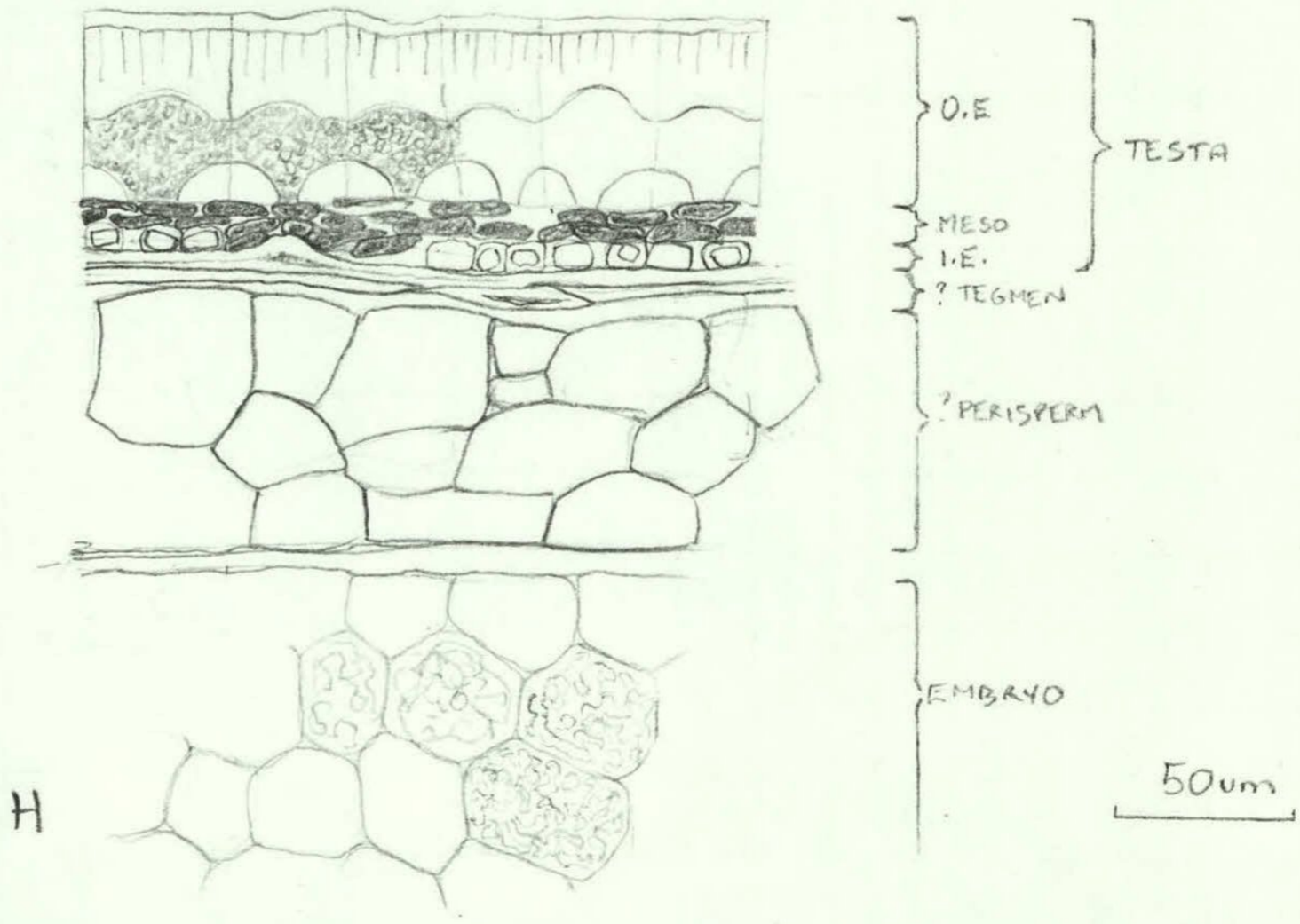


PLATE 26

'MELIA DUBIA'

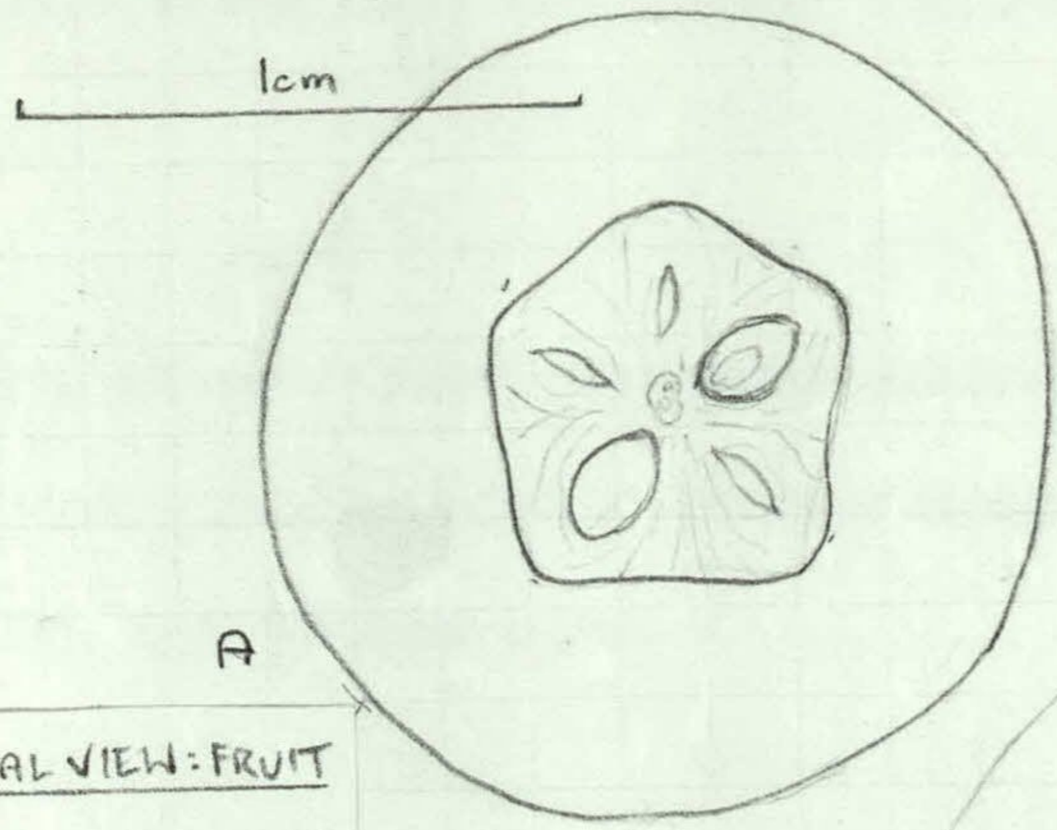
A-C FRUITS, WHOLE & IN SECTION. NOTE THAT THREE OF THE FIVE LOCULES ARE STERILE.

D-E SEEDS IN MACRO-SECTION. NOTE 'BEAK', FUNICLE & CHALAZA AT POLES (cf. AZADIRACHTA, PLATE 28) & EXSERTED RADICLE.

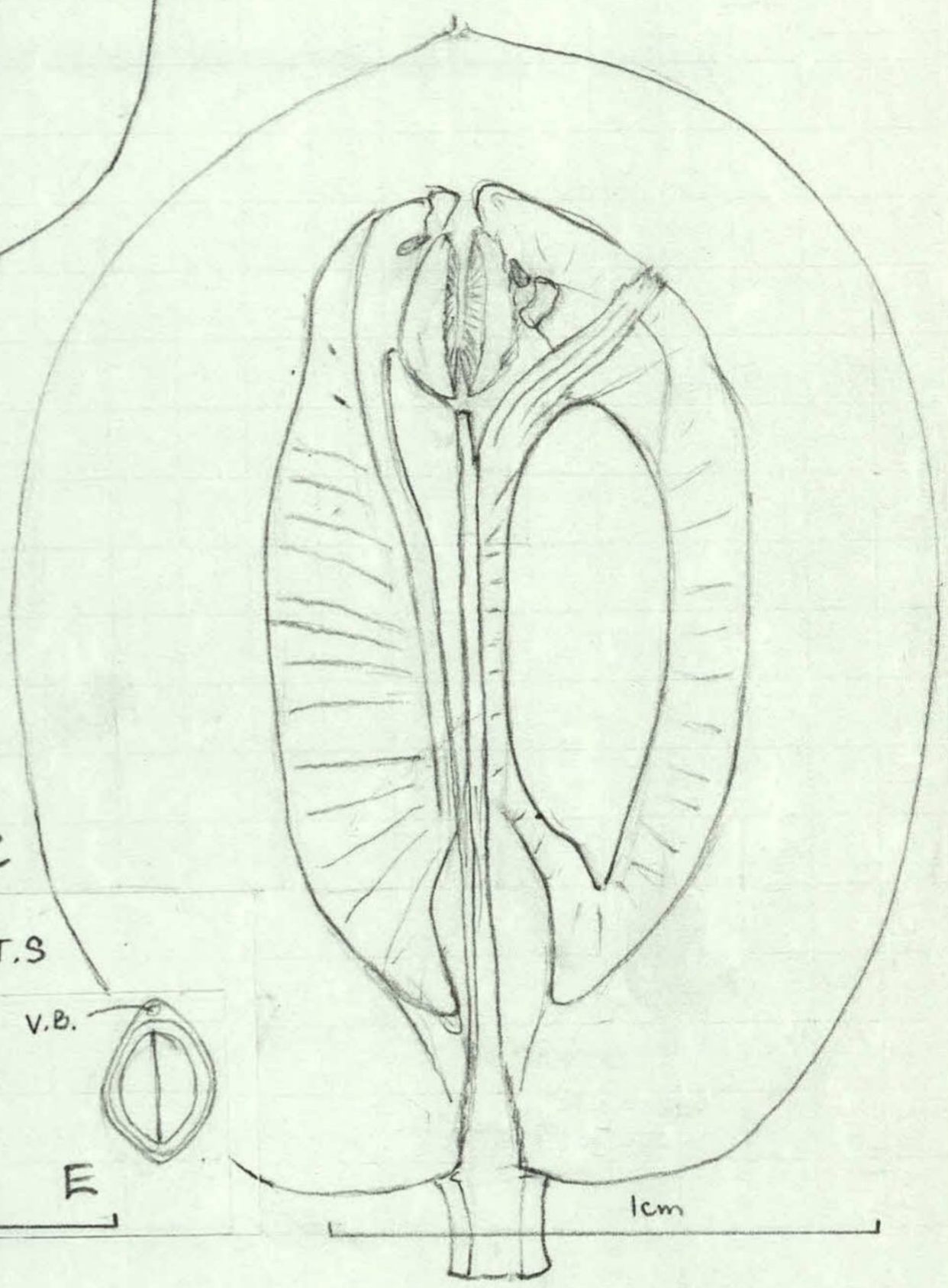
F-G L.S. SEED-COAT. NOTE HIGHLY COLUMNAR TESTAL O.E. WITH VERY THICK PERICLINAL WALLS, TYPICAL OF THE GENUS. THE TESTAL MESOPHYLL HAS UNUSUALLY NUMEROUS LAYERS OF VERY SMALL PARENCHYMATOUS CELLS AND THE TESTAL I.E. AND TEGMEN ARE GREATLY REDUCED.

Melia dubia Cav. Cheek 1561

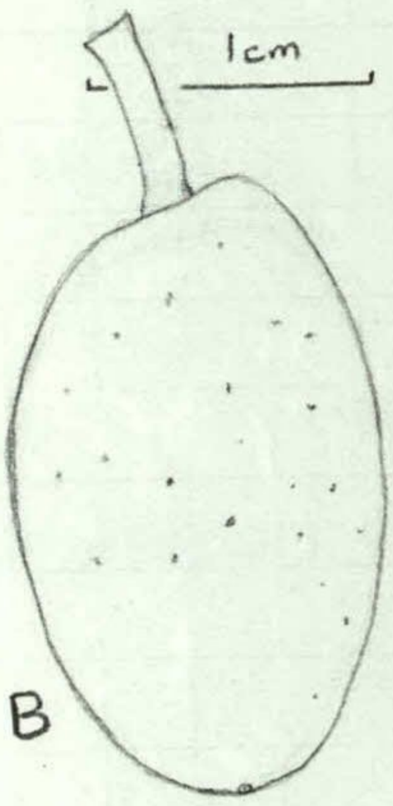
FRUIT. T.S.

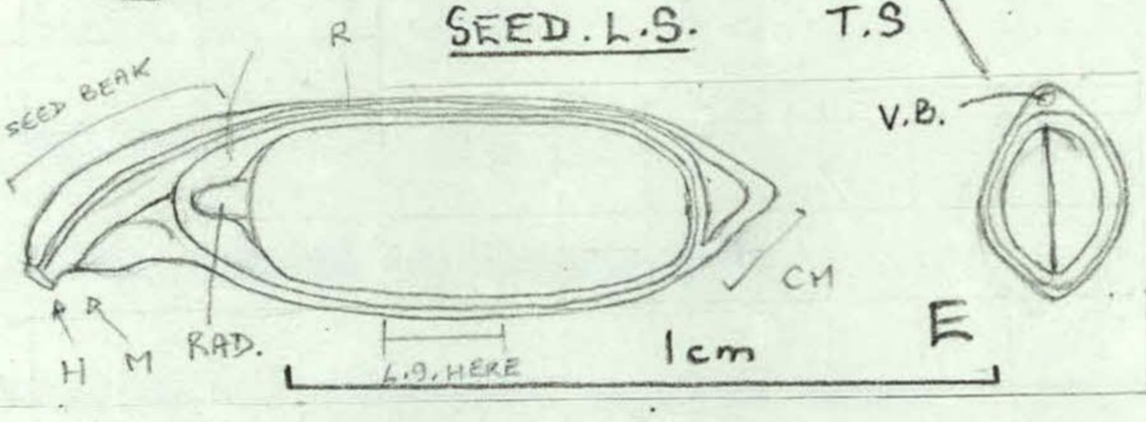



FRUIT
SUB-MEDIAN L.S.



LATERAL VIEW: FRUIT



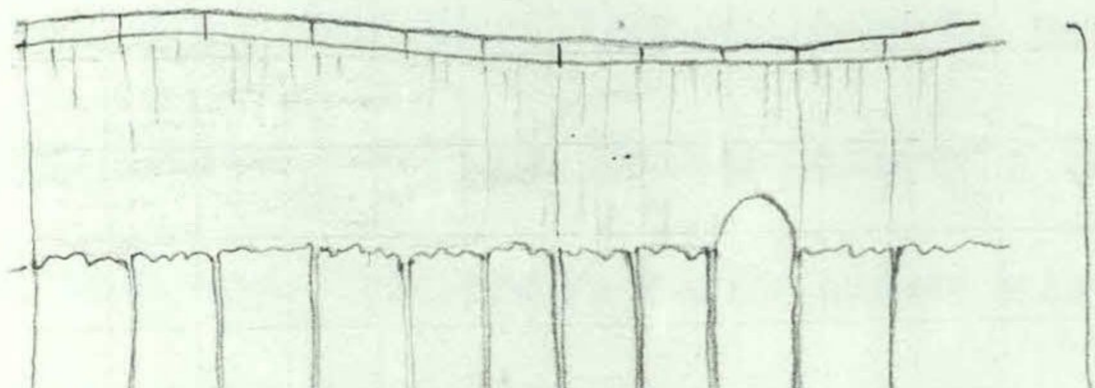




SEED. L.S.

T.S

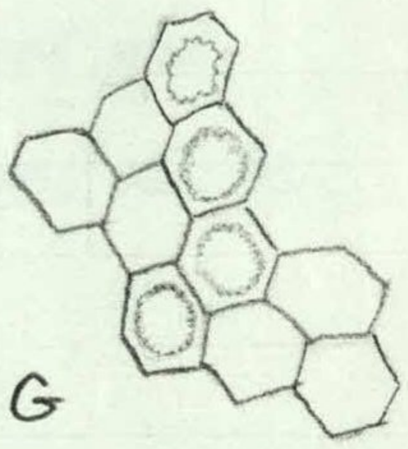
L.S SEEDCOAT / PERISPERM




SEED COAT.

TEGMEN / PERISPERM

O.E. TESTA
- PARADERMAL




50um

dark brown granular contents. Cells densely packed. Those of lowest layer frequently invaginate (by c.5um) the perisperm below.

PERISPERM

About 7 layers of prostrate, extended quadrangular, thin (c.1um)-walled cells. Walls and contents highly transparent, without colour. Cells 10-14-25um high and 28-85um wide.

ENDOSPERM

To 500um thick.

EMBRYO

To 1200um thick.

Melia azedarach L.

This description based on Cheek 994

Collector's notes: " Berries yellow when ripe."

Netolitzky(1926):"Melia azedarach. EBERT beschreibt sechs verschiedene Schichten: eins und drei bernsteingelb homogen, Zellen ganz verdickt, feinst gepunktet, vollig "kutinisiert"; Schichte zwei mit geschlangelten Radialwanden und Phloroglucotannoiden als Inhalt; Schichte funf aus rundlichen, isolierten Steinzellen. End und Embryo ohne Starke, mit Ol und Aleuron. EBERT erwahnt weder Kutikularhaut noch Sekretzellen."

Nair (1961):"During post-fertilization stages the integuments and nucellus undergo considerable changes and modifications. At the time of fertilization, both the integuments are three layered. While the outer

epidermal cells of the outer integument slightly elongate radially, the other two layers divide actively to produce 6 to 7 layers of cells. The tanniniferous inner epidermis of the inner integument alone persists as the inner seed-coat and the other two layers are crushed and absorbed."

Vaughan (1970,156): "Testa. The testa consists of thin-walled parenchyma cells containing pigment, and its outer epidermis has a thick outer tangential wall".

His figure of the seed-coat T.S. shows the shortly columnar testal O.E., and the small pigmented prostrate cells of the testal mesophyll, but omits the rest.

Corner (1976,1:190): "Seeds 3.5x1.6mm, 1 per loculus, 1-5 per fruit, oblong, brown, smooth, exarillate, with very short funicle, each enclosed in a fibrous-woody coccus (transverse fibres). Testa 2 cells thick; O.E. composed of somewhat tabular thin-walled cells with polygonal facets, not lignified; I.E. as a layer of small crystal-cells with lignified walls. Tegmen 5-6 cells thick; O.E as a compact layer of longitudinal fibres -200u long, lignified, pitted; mesophyll consisting of 3-4 layers of large thin-walled cells, eventually crushed; I.E. as a layer of shortly radially elongate cells with brown walls, not lignified. Vascular bundle only in the raphe, not perichalazal. Endosperm oily."

GROSS MORPHOLOGY

Seeds 0-1-2 per locule, placentation axile, distal to fruit. Fruits baccate, yellow, oblate ellipsoid , 11-14mm long, 8-12mm broad. Pericarp glossy yellow with occasional corky lenticels. Mesocarp thick (1.5-2.5mm) and fleshy. Thick (to 0.5mm) woody endocarp evenly developed around each locule, whether ovules aborted or not. Usually 2-5 fertile

locules per berry. Seeds morphology as M.dubia Cav.: dark brown, glossy, narrowly ellipsoid, beaked at each end. Distal beak formed by the chalaza . Proximal beak by the raphe-exostome: not noticeably fleshy. Seeds 6.5-8.5mm long, c.3mm broad.

ANATOMY

TESTA

Cuticle reticulately patterned in tangential plane, murae along anticlinal walls of O.E. Scattered verrucae. Rather thick, 8um.

O.E. Single layer of shortly radially columnar cells with very thick o.p.w. (together with cuticle, constitutes half total cell height.) and large thickenings in angle of anticlinal wall and i.p.w.. Anticlinal walls comparatively thin (1um), o.p.w. 20-25um thick and i.p.w. thickening to 10um thick at max.. Thickening deep yellow. Long, fine, hair-like pits, about 6 per cell in L.S., traverse o.p.w. from lumina to cuticle. Lumina always deep red, contrasting vividly with yellow walls. Overall dimensions: 28-42um wide, 41-56um high.

Mesophyll one to six layers thick. Very variable, this range over 3 to 4mm length of testa. Thickest near raphe. Cells prostrate, ellipsoid (T.S. and L.S.); walls and lumina uniformly middle brown. 14-22um wide, 4-6um high.

I.E. Single, sometimes intermittent layer of translucent, sub-cuboidal cells, each with a single crystal. Cells 10(-15)um wide and c.8um wide.

TEGMEN

Highly reduced, effectively to one or two layers of weak fibres (exotegmen). Endotegmen almost completely crushed. Where it persists,

PLATE 27

MELIA VOLKENSII

A-D FRUITS. NOTE LARGER SIZE THAN MELIA AZEDARACH AND PRESENCE OF ONLY A SINGLE SEED PER FRUIT.

E SEED. NOTE BEAK AT FUNICULAR END.

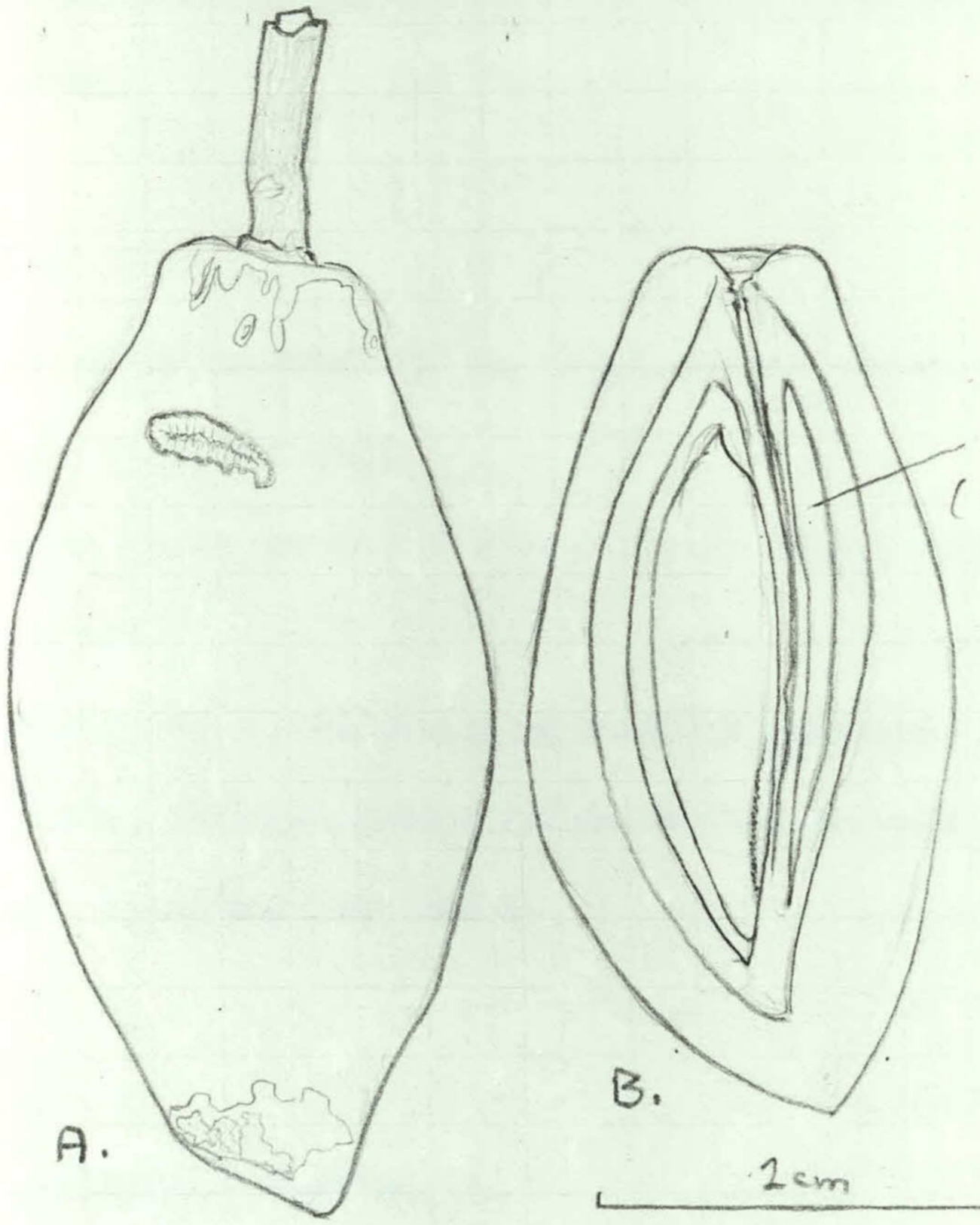
F SEED-COAT ANATOMY. NOTE COLUMNAR TESTAL O.E. WITH VERY THICK PERICLINAL WALLS- CHARACTERISTIC OF THE GENUS. THE TESTAL I.E. AND TEGMEN ARE POORLY DEVELOPED, AS IN MELIA DUBIA, BUT THE TESTAL MESOPHYLL DIFFERS GREATLY: THE CELLS ARE AN ORDER OF MAGNITUDE LARGER AND HIGHLY AERENCHYMATOUS.

# Melia volkensii



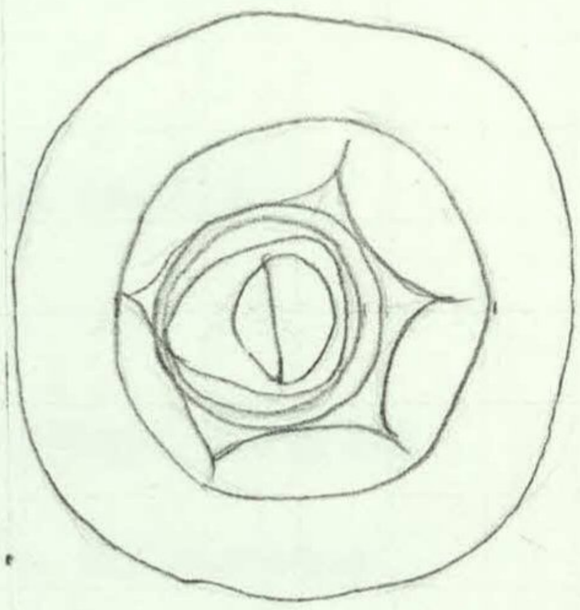
FRUIT: LATERAL VIEW

FRUIT: L.S.




FRUIT: T.S.

1. ONE-SEEDED



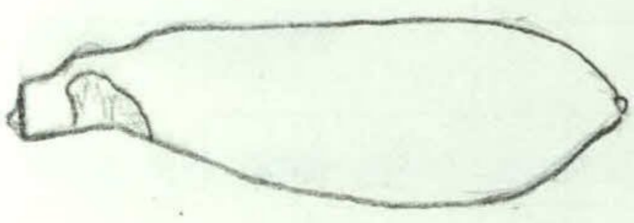
C.

2. STERILE



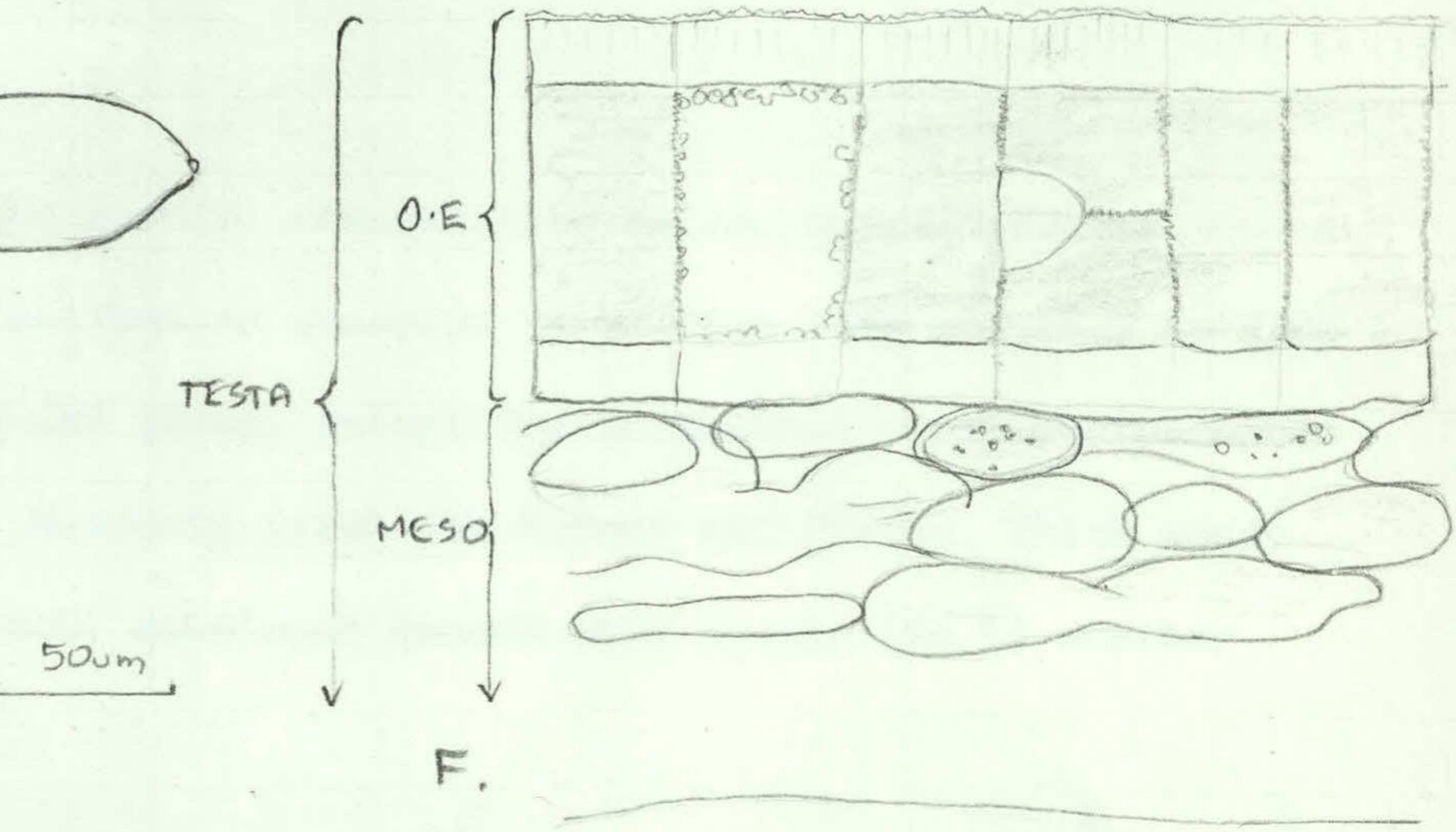
D.

SEED (RECONSTRUCTED) LATERAL VIEW



E.

SEED COAT L.S.




F.

apparently of large 90-100um, cuboidal, thin-walled cells without contents.

PERISPERM

Two to four cells thick.Cells large, angular, thin walled isodiametric to slightly tangentially extended, 15-40um wide and high. Lumina colourless.

ENDOSPERM

In T.S. forms a layer 500um thick around cots. at shortest axis, 250-300um at major axis.

Epidermal cells barely distinct, with fewer contents and smaller (-28um) size.

8-14 cells thick, slightly extended ellipsoid, 30-45um long, 25-35um wide. Lumina conspicuously filled with coarsely granular, colourless contents, staining for lipid.

Melia volkensii Guerke

This description based on Hughes 239

Collector's notes: not available.

GROSS MORPHOLOGY

Seeds nil to one per locule, placentation axile, apical. Fruits baccate, truncate fusiform to obovoid. 34 to 41mm long and 18.5 to 22mm wide. Pericarp thin and glossy except for occasional corky excrescences prevalent at poles. Mesocarp thick (to 4.5mm) and fleshy. Thick woody endocarp (to 4mm thick) developed around each locule (to 5) whether

ovules aborted or not; detatches cleanly from mesocarp, fusiform, smooth. No lobing (as M.azedarach) except at distal tip. Usually only one fertile locule per fruit ( effectively a drupe ). Some fruits (admittedly smaller) are seedless. Seeds glossy brown, narrowly ellipsoid with a short beak at each end; very difficult to extract whole from the intransigent endocarp. The shorter distal beak chalazal; proximal beak longer, slightly hooked, surmounted by hilum. To 22mm long, 6mm broad.

ANATOMY

TESTA

Cuticle: 3um thick. Irregular.

O.E. one (to two) layers of columnar cells. Cells 28-42-50um wide, (280-)420um high, outermost periclinal walls 14-18um thick with fine radial pits, innermost periclinal walls 14-18(-20)um thick. Periclinal wall thickenings sometimes occur also at i.p.w. of upper cells where epidermis is bilayered, and o.p.w. of lower cells. Thickenings amber coloured. Anticlinal (radial) walls very dark brown, 2 to 3um, indistinct. Lumina filled with translucent, pale brown protoplasmic contents (sometimes dark and finely granular.)

Mesophyll varies from 7-8 cell layers (c.150um) to (near raphe) 20 layers (c.540um) thick. Cells prostrate ellipsoid in T.S., but often radially elongate in L.S. Upper 1 to 2 layers generally larger (30um high and 55um wide) and thicker (2-3um)-walled than smaller (to 9um high) cells of aerenchymatous lower layers, which have many intercellular 'arms' in tangential plane.

I.E. not distinguished.

TEGMEN

Indistinct. Probably represented by crushed layer c.15um thick below aerenchymatous mesophyll.

PERISPERM

To 9 cells (c.280um) thick, thin-walled (c. 1um), no contents. Upper cells cuboidal, 30-40um; inner layers of cells progressively larger and more radially elongate: to 120um wide and 70um high. Lower boundary of zone marked by layer of crushed cells.

ENDOSPERM

About as thick as perisperm, to 250um, 15 layers, of radially extended (to isodiametric) quadrangular to hexagonal cells, with thin walls and dense, finely granular protoplasm. 30-40um wide, 10-18um high.

Azadirachta indica A.Juss.

This description based on Cheek 3.19.15

Collector's notes:"Drupes abundantly borne; glossy yellow, thick-skinned, foetid and juicy at maturity".

Nair and Kanta (1961): "When the embryo-sac is ready for fertilization there are four to six layers and ten to twelve layers of nucellar cells on the sides and chalazal end respectively. During post-fertilization stages the nucellar are consumed by the growing endosperm and in a mature seed only two or three layers of cells are present in the periphery.

Both the integuments contribute towards the formation of seed-coat. In a mature seed, the outer seed-coat consists of a thick-walled epidermis

PLATE 28

AZADIRACHTA INDICA

A-F FRUIT AND SEED. VARIOUS VIEWS. NOTE SUB-TERMINAL HILUM & HORSESHOE-SHAPED CHALAZA.

G-H SEED-COAT ANATOMY. NOTE RECTANGULAR (L.S.) TESTAL O.E. WITH THIN PERICLINAL WALL AND DISPERSED TESTAL MESO-PHYLL AND I.E., LATTER VERY UNUSUAL: THICKENED AND PITTED WALLS.

# Azadirachta indica Juss.



FRUIT:
LATERAL VIEW

1cm

A

SEED: ADAXIAL SIDE
DISPLAYING CHALAZA
& HILUM.

FRUIT: L.S.
WITH DETAIL

1cm

B

FRUIT: T.S. WITH
DETAIL

1cm

C

SPACE

V.B.

ENDOCARP.

TESTA

1cm

CH

R.

H

D

M

MESOCARP

REMNANT OF
SEED-COAT

COT.

SPACE

ABORTED LOCULE (EMPTY)
ENCLOSED IN WOODY
ENDOCARP

RAD.

PYRENE: L.S., DISPLAYING
VASCULAR RIDGE (PLACENTA) &
SEED ATTATCHMENT SITE

REVERSE

E

F

PLACENTAL CREASE

EXCEPTIONAL SEED-COAT:
UNCRUSHED (NEAR CHALAZA)

TYPICAL SEED-COAT: CRUSHED

O.E
MESO
I.E
TESTA

CRUSHED
TEGMEN

O.E
ENDOSPERM

CRUSHED
ENDOSPERM

G

H.

50um

and three layers of loosely arranged cells. The cells of the inner integument undergo tangential elongation and become the inner seed-coat".

Vaughan (1970): "The testa is composed of thin-walled parenchyma cells containing pigment, and then groups of loosely arranged thick-walled rounded cells, some 20-25um in diameter".

GROSS MORPHOLOGY

Seeds single; placentation axile, apical. Fruits drupaceous, ellipsoid, proximally truncate, distally pointed, 16-19mm long, 11-13mm broad. Pericarp glossy yellow without corky areas. Mesocarp 1.5 to 2.5mm thick, translucent, succulent. Endocarp woody, straw-coloured, thin (0.25-0.5mm thick), thinnest around the two infertile (each usually with remains of aborted seeds) locules. Seeds 11.5-12mm long, 4.5-5.5mm broad obliquely obovoid-ellipsoid, pointed at micropylar end, seed-coat very thin, pale to medium matt-brown, distinctly darker and thicker at chalaza. Micropyle obscure, small at tip of seed; hilum 2-4mm from micropyle, circular to elliptic, c.1mm diam., opposite vascular aperture in endocarp; raphe short (2-3mm), broad (c.1mm); chalaza large (to 5-6mm longitudinally, 4mm to width of seed transversely), crescentic, scutate or ellipsoid. Embryo with exserted radicle and cots. collateral; invested with very thin (<0.1mm) endosperm.

ANATOMY

TESTA

Cuticle 1um thick, even.

O.E. Usually crushed beyond description. Where spared, tangentially extended quadrangular cells, 22-28um wide, 14-17um high, o.p.w. 3-4um thick, slightly convex, lumina and walls pale brown.

Mesophyll similarly crushed, 3-5 layers thick. Where uncrushed, prostrate ellipsoid cells with very pale brown protoplasm. Cells c.14um high, 21um wide.

I.E. One layer thick. Cells ellipsoid (L.S.and T.S.), shortly tangentially extended, 17-24um wide, 14-18um high. In paradermal view, isodiametric. Walls thick with simple pits, 6-7um thick. About 70% of cells with a single luminal, prismatic crystal. Distinct in that usually only uncrushed layer of entire seed-coat and that cells do not continuously abut each other, occupying 75% or less of field. Unusually, cells often in several tangential planes.

TEGMEN

Almost completely crushed except near chalaza, where 8 cell layers (about 70um) thick. Cells thin-walled with thin protoplasm, tangentially elongated; about 70um long and 8.5um high.

ENDOSPERM

To 4-5 cell layers (c.125um) thick. Cells colourless, isodiametric to randomly extended pentagonal-heptagonal, each cell containing 1-2 large oil droplets in very finely granular protoplasm. Walls lustrous white, 1-2um thick. Cells 28-30um broad, 28-38um long.

Epidermis (last layer to be lost) quite distinct, of tangentially extended quadrangular cells.

EMBRYO

To 6000um thick.

CHALAZA

Little crushing evident and many more cells thick than rest of seed coat. O.E. well preserved in character, as testal; mesophyll much thicker (210um) than in testa, of 2 parts; upper mesophyll as testal, but of 10 layers (c.85um thick) and many air-spaces, lower mesophyll of compact, angular parenchyma interspersed with tangential vascular bundles ( zone about 126um thick). Below, a zone of 2-3 layers of thin-walled angular parenchyma with dark contents, confluent with I.E. of testa. Continuous with tegmen, but thicker (105um), a zone of 6-8 layers with similar thin-walled, empty cells, but higher and not as tangentially elongated.

DISCUSSION

**Anatomical characters: assessment of taxonomic value**

Testa. The O.E. and cuticle both seem to be of taxonomic use at the generic level. The former is the best developed and the single most important taxonomically important layer in the seed-coat, varying from species to species and perhaps even at the infra-specific level (cf. testal O.E. of '*M. dubia*' and *M. azedarach*, plates 26F and 25H). The cells vary considerably in both shape and in periclinal wall-thickening.

Lumen pigmentation is also variable but less taxonomically useful in that it is liable to vary with the precise degree of maturity.

Mesophyll. This tissue varies from two to eight layers thick and seems to vary considerably from one species to another in number of layers, dimensions and contents. These differences seem reasonably constant within species.

The I.E. is lost at maturity in two of the three Melia collections but provides a useful diagnostic character for Azadirachta indica.

Tegmen. The tegmen appears completely crushed in one species of Melia, in another is indeterminate and although fibres or fibroid cells are visible in M. azedarach and A. indica they do not provide the wealth of taxonomic characters that they do in other tribes of the Melioideae.

**The genera: variation, delimitation and affinities**

Melia (plates 25-27) is perfectly distinct from Azadirachta indica (plate 28) on seed-coat anatomical characters alone. Whilst all three accessions of Melia have a highly columnar testal O.E., the cells extremely large and with both outer and inner periclinal walls highly thickened, those of A. indica are rectangular in L.S. with only a moderate o.p.w. thickening. They are of the usual familial proportion in relation to the dimensions of the testal mesophyll. Azadirachta indica is different from the Melia species investigated in its testal I.E., since as well as having the usual calcium oxalate crystal (characteristic of the testal I.E. of most Meliaceae) the cell wall is very unusual in the family in being both lignified and pitted. Where the testal I.E. is detectable in Melia (M. azedarach) the cell wall is unpitted.

The two genera also differ in the gross structure of their seeds. Whilst in both species of Melia investigated here there is a long funicular-raphe 'beak' at the end of the seed, and the chalaza is small and inferior, at the opposite pole the raphe running the length of the seed, in Azadirachta, the hilum is sub-terminal, the funicle virtually non-existent , the raphe very short and the chalaza occurs mid-way along the seed and is short and horseshoe-shaped. There is no difficulty distinguishing these two genera on seed structure.

The infra-specific variation in Melia azedarach as represented by Corner (compare his figure [1976,2:327 and 328] of 'M. dubia' with 'M. azedarach') is so immense as to compel scepticism: no other species investigated in this study has varied to such an extent in its seed anatomy. However, re-investigation of cultivated material under these same names from a different source (his from Ceylon, that here from East Africa) agrees with his descriptions, especially that of 'M. dubia', though some discrepancy, compatible with the different origins, does exist. His description and figure of the highly columnar testal O.E. with very and almost equally thick periclinal walls in 'M. dubia' as compared with more cuboidal (L.S.) cells and less thickened i.p.w. for 'M.azedarach' agrees with that here although the material illustrated here of the latter is more columnar and has thicker periclinal walls than his (perhaps immature). Similarly, he figures the testal mesophyll of 'M. dubia' as 9-10 layers thick and a crystalline I.E. as absent compared with M. azedarach with no testal mesophyll and a distinct and crystalline I.E. as absent compared with a M. azedarach with no testal mesophyll and a distinct and crystalline I.E. which agrees with the findings here except that a thin mesophyll of two layers of orange-brown cells (tannin?) is present in the material investigated

here of M.azedarach. Clearly, the unusually large amount of infra-specific morphological variation in this cultivated species (see Mabberley, 1984) is matched by that of the seed anatomy. It would be interesting to investigate other components of the variation e.g. "M.japonica".

Melia volkensii Guerke has greatest similarities with the 'M. dubia' (i.e. wild forms) element of M. azedarach but has markedly less narrowly columnar testal O.E. cells, a few-celled (three versus more than nine layers) mesophyll with cells at least ten times as large and with prominent intercellular 'arms'.

## TRIBAL DELIMITATION

Despite the undoubted proximity of these genera based on morphological and wood anatomical characters, there is little seed structural evidence to link these two genera together apart from the fact that they share the same basic Meliaceous seed organization, lack of any fleshy appendage and have a weakly developed tegmen. Predominantly bitegmic, non-fleshy seeds in indehiscent fruits with bony endocarps are characteristic of some Trichilieae and it may be that the affinities of the Melieae lie there. Of all genera, Ekebergia shows greatest similarity in seed structure to those of the Melieae, but convergent evolution cannot be ruled out.

## PHYLOGENETIC SPECULATION

It is possible in Melia to relate some of the variation in seed-coat anatomy to 'evolutionary advancement'. Since both species investigated here have five-locular ovaries, it seems logical that that in which all five develop a seed (M.azedarach: plate 25) is the more primitive,

whilst that which develops only one and has a thicker endocarp , is more advanced, by a process of reduction. Correlated with this line is a loss of the testal O.E. and tegmen. This seems to be an example of the transition from a bitegmic to a unitegmic (by loss of the tegmen) seed-coat occuring within a single genus.

## ECOLOGICAL ASPECTS

Owing, no doubt, to their being highly widespread by introduction and naturalization in the tropics, both A. indica and M.azedarach, and especially the latter, have generated a considerable amount of literature relevant to their fruit dispersal. As is pointed out by Pannell and White (1985), from which much of the information below is drawn, most of this relates to plants outside their natural range. A. indica is recorded as being dispersed by bats and also by baboons in Ghana (Lieberman et al. 1979) and I have observed large fruit bats eating the fruits in Southern Madagascar. In Africa, outside its natural range, Melia azedarach is recorded as being eaten by animals as diverse as mousebirds, grey loeries and pouched rats, though bats are probably the most important dispersers in cities in Natal (Pannell and White, 1985). In Northern Australia (within its natural range according to Mabberley, 1984), the fruits of this plant are eaten and the seeds possibly dispersed by fruit pigeons (see e.g. Crome, 1975). Although the evidence is far from complete, it may be that these species have 'non-specialist' fruits, dispersed by a wide range of animals.

In contrast to the foregoing, Melia volkensii is restricted to the drier parts of Eastern Africa and there is no literature pertaining to its dispersal, although the fruits are recorded as being eaten by giraffe ( fide collectors ). Since it might be expected that the

digestive system of a giraffe is longer and more hazardous to a seed than that of most birds and bats, it is possible that the thicker endocarp of Melia volkensii (compared with that of the two species considered above) represents the result of selection by their postulated dispersal agent. Similarly, a single, large-seeded fruit might have selective advantage over one containing five smaller seeds united by their endocarp in that the resulting seedling would probably have less sibling competition and larger reserves - these might (perhaps) be crucial factors in establishment in the more xeric environment that this species inhabits.

## THE VAVAEEAE

This tribe, containing a single genus, Vavaea, of five species, occupies an isolated position within the Melioideae, possessing morphological, anatomical and palynological characters of the sub-family, but in a distinctive combination enabling it to be easily distinguished from all other genera according to Pennington and Styles (1975), who place it between the Turraeeae and Trichilieae on vegetative and gross seed-structural characters. However, they relate that the wood anatomy is unlike either of those tribes, but closer to Sandoricum (Sandoriceae), sharing predominantly solitary vessels and very heterogeneous ray tissue.

No investigation appears to have published of seed anatomy. Although I have investigated and prepared a description of the seed anatomy of Vavaea tubiflora Pennington (from T.D.P. 8050), I have not drawn a plate and so have refrained from discussing this interesting genus here.

# CHAPTER SEVEN

# TRICHILIEAE

## INTRODUCTION

The Trichilieae as redefined by Pennington and Styles (1975) are not as clearly demarcated as the Turraeeae, the differential characters there employed being far from diagnostic if taken individually . Genera within the tribe usually have a cylindrical staminal tube, anthers inserted on the margin of the tube, nectary poorly developed, seeds usually without endosperm. The wood anatomy is particularly distinctive, however. Fibres are nearly always non-septate; apotracheal terminal parenchyma is usually present, while paratracheal parenchyma is usually vasicentric, aliform and confluent.

The tribe is centred on the large genus Trichilia and the nine closely related satellite genera recognized by Pennington and Styles. It is convenient, for the purposes of this discussion, to recognize an additional genus, Heynea (included in Trichilia by Pennington and Styles). Trichilia has most species in tropical America where c. 68 occur (Pennington and Styles, 1981), 19 species occurring in Africa (de Wilde, 1968; Cheek, 1989b); Pterorhachis has one or two species in Cameroun and Gabon, Pseudobersama is monotypic and found in coastal East Africa; Walsura has c.7 spp. (14 spp.- T. Clark, pers. comm.) in the Indo-Malesian region; Malleastrum has 12 species described from Madagascar and the Comores; Lepidotrichilia has one species in montane Africa and three species in Madagascar; Astrotrichilia comprises c. 14 species in Madagascar, Owenia c. six species in N. and E. Australia;

Ekebergia is widespread in Africa with four species, Cipadessa one species in the Indo-Malesian Region ( Mabberley, Fl.Mal.MS; others from Pennington and Styles, 1975). Heynea has 2 species in S.E. Asia (Bentvelzen, 1962 as Trichilia).

The first investigation of seed anatomy in this tribe was of Trichilia emetica Vahl by Netolitzky (1926), subsequently re-investigated by Vaughan (1970). Since then, Corner (1976,1:192) has gone on to investigate in more detail an unidentified species of Trichilia from Bolivia, and recently Boesewinkel (1981) has executed a model investigation of the development and mature structure of the seed-coat of Trichilia grandifolia Oliv. from Saõ Tomé. The latter confirms the presence of the normal pattern of Meliaceous seed-coat construction in the tribe and is of particular interest for the light it sheds on the development of chalazal unitegmy. The only other genus hitherto investigated is Cipadessa, an embryological study being made by Narayana (1958), the mature seed-coat being described by Corner (1976,1:188). These further confirm the the validity of using the usual `markers' in anatomical interpretation, namely the inner epidermal cells (I.E.) of the testa each with a rhombic crystal of calcium oxalate and the upper layers of the tegmen with lignified, longitudinally directed fibres.

A S.E.M. study of the seed-coat micromorphology of the Trichilieae was not carried out since a light microscopical study of the outer epidermis (paradermal sections) suggested little of interest here and S.E.M. studies in Turraeeae and Guareeae had shown these to be of little value in genera with heavily fleshy fruits and seeds. The taxonomically useful seed sculpture of the exceptional species of Turraeeae were first detected using a hand lens.

Fortunately, it was possible to obtain representative material of each genus in the tribe, in four of which it was possible to investigate several species. All but two genera (Owenia and Lepidotrichilia) appear predominantly bitegmic. Unitegmy occurs in some or all species of Trichilia, Walsura, Malleastrum, Lepidotrichilia and Owenia; polyphyletic pachychalazy is at least partly responsible.

For the purpose of the discussion it is convenient to divide the tribe into two groups of genera: those with non-fleshy seeds, usually with fleshy (at least slightly) and indehiscent fruits (generally berries and drupes) and those with fleshy seeds, usually from leathery, dehiscent capsules. The former have thick, often highly stratified seed-coats with well-developed vascular systems, whereas the latter appear reduced, probably as a consequence of the indehiscent fleshy fruit type accompanied by a woody endocarp. They sometimes (Cipadessa and Astrotrichilia) consist of only six cell layers in total and they tend to be more highly crushed, and less complicated, with fewer taxonomic characters than the first group, so much so that it is difficult to compare the two.

## RESULTS

### Trichilia monadelpha (Thonn.) J.J.De Wilde

This description based on Keay, F.H.I. 25359 (as T.heudelotii Planch.)

Collector's notes: 'Capsules mauve, seeds black, aril scarlet'.

#### GROSS MORPHOLOGY

Fruits loculicidally dehiscent capsules, 3 valved, obovoid-spherical, 18-19.5mm long, 15-20mm broad, with a small (1x1mm) apical stipe. Pericarp puberulent (hairs to 0.3mm), leathery, 2-3mm thick. Endocarp of

longitudinal fibres separated into two discrete lenses (T.S.) per locule, to 0.75mm thick. Seeds 1-2 (collateral) per locule, (2-)3 locules and 2-5 seeds per fruit; fertile seeds 7-10mm broad, 13-15.5mm long (sterile seeds, to 2 per capsule, to 12x5mm), at maturity on placental (not raphe) vascular bundle: to 13.5mm long and 0.3x0.75mm broad (ellipsoid in T.S.). Seeds ellipsoid; if geminate, with lateral facet(s) and triangular in T.S.; bi-coloured: c.70% of seed-coat fleshy and orange red, c.30% black and hard in an irregular dorsal elliptic area c.10mm long, c.6mm broad.

ANATOMY

Orange fleshy seed-coat.

Cuticle: very thin (<0.5um), colourless, even.

Epidermis single layer of tangentially extended prostrate quadrangular cells (L.S. and T.S.), 7-10um high and 18-40um wide in paradermal view, isodiametric or slightly randomly extended polygonal, 6 or 7 sided, 22-40um diameter. Walls c.1.5um thick dense orange-brown as are lumina, the two almost indistinguishable.

Mesophyll of c. 20 (560 um) layers of randomly orientated elliptic parenchymic cells with thin (c. 1um) walls and grey granular protoplasm surrounding a large oily lumen, colourless or pale brown. Cells 28-35 X 20-25um. Lowermost 3-5 layers of mesophyll without lipidic contents.

Intermittent single layer of longitudinal fibres to 100um long, prostrate elliptic in T.S., 10um high, with yellowish pitted cells 3um thick and dense orange-brown, apparently tanninized lumina.

Below this, 3-7 layers of prostrate elliptic cells 10 X 25um lumina filled with 5-11 apparently tanniniferous bodies.

Vascular bundles occur intermittently throughout all the lower layers of cells.

PLATE 29

A TRICHILIA EMETICA: FRUIT AND SEEDS. NOTE 'ARILLATE' SEEDS WHICH CLOSER INVESTIGATION SHOWS TO BE LARGELY SARCOTESTAL. IN FRESHLY OPENED FRUITS (RIGHT), THE 'ARIL' REMAINS WHITE, SLOWLY BECOMING RED ON EXPOSURE.

B TRICHILIA SP 1. (MADAGASCAR): NOTE SUPERPOSED SEEDS (NOT SEEN IN AFRICAN SPECIES, BUT OCCURRING IN PSEUDOBERSAMA) AND SLIGHTLY WARTY FRUITS.


A
B

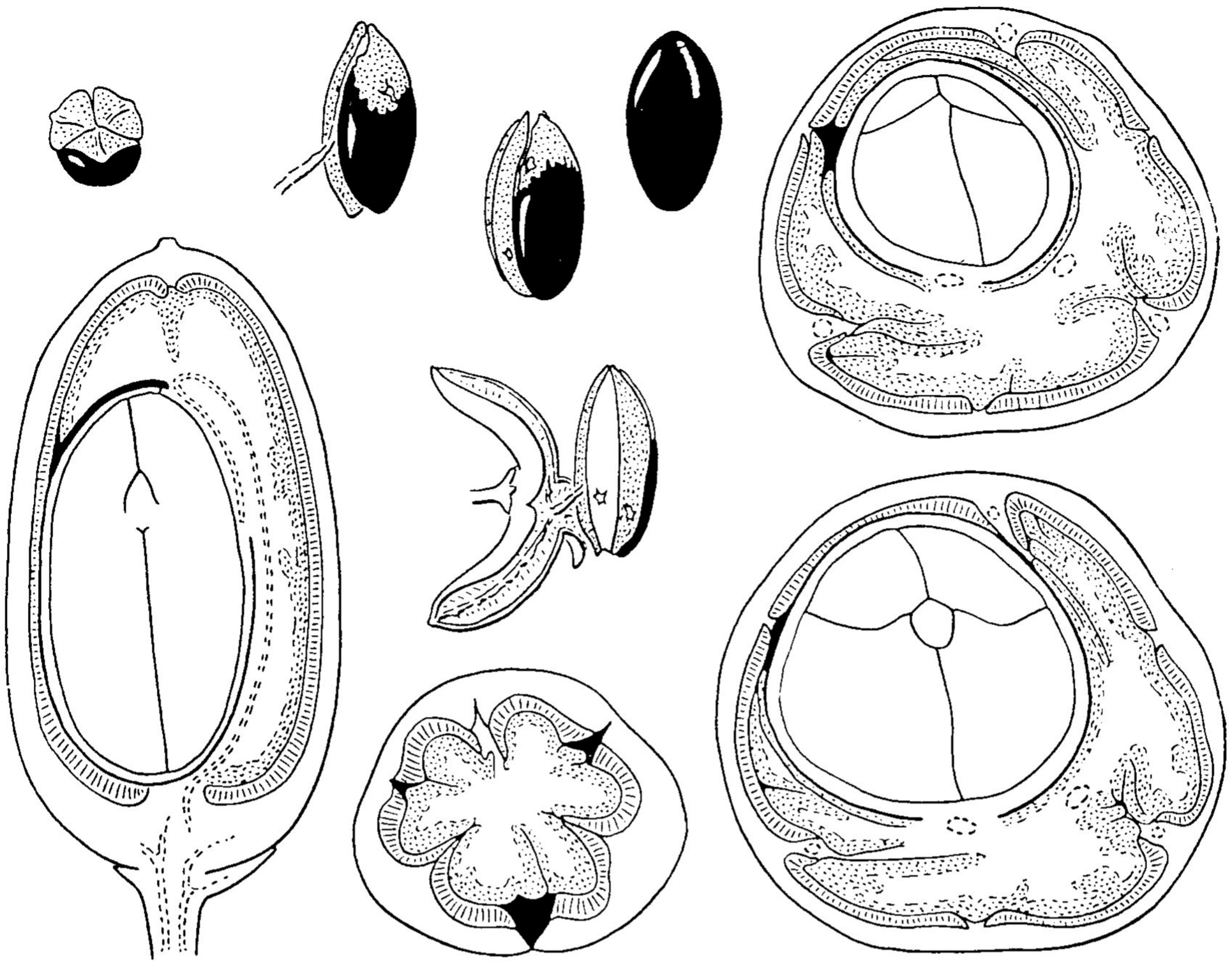
PLATE 31

TRICHILIA SP. (BOLIVIA)

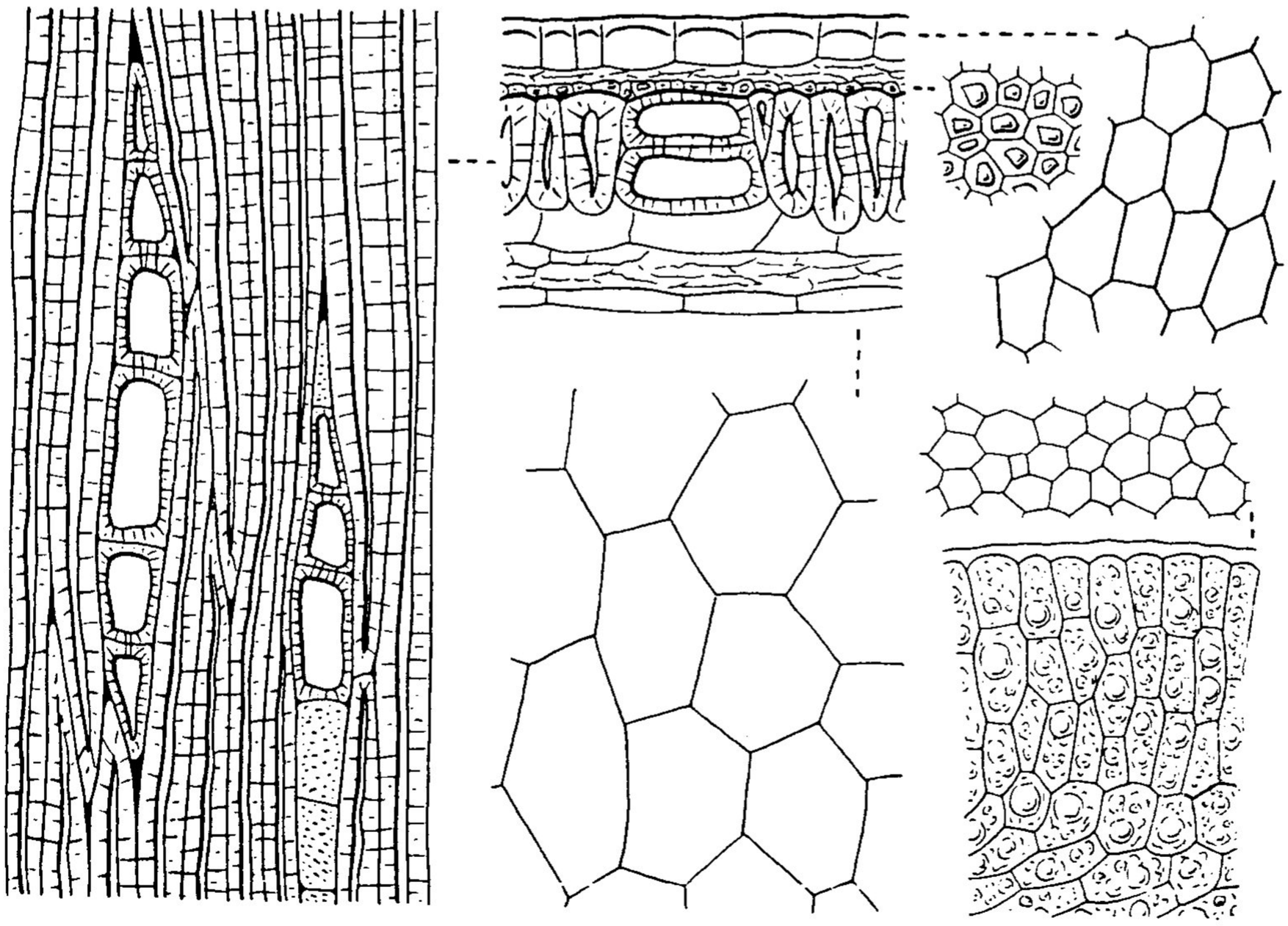
(FROM CORNER,1976,2: 330 & 331)

UPPER: FRUIT AND SEED. NOTE RAPHE-FUNICULAR ARIL.

LOWER: SEED-COAT ANATOMY. NOTE BITEGMIC CONSTRUCTION, AND TYPICAL MELIACEOUS SEED CHARACTERS: TESTAL I.E. WITH CRYSTALS AND LONG, LONGITUDINAL, LIGNIFIED AND PITTED EXOTEGMIC FIBRES.



390 *Trichilia* sp. (Bolivia). Capsule and seeds, the red part of the aril stippled, the undeveloped ovules embedded in stellate recesses in the aril, the v.b. of the columella of the capsule acting as a funicle; one seed with the aril removed to show the white raphe, × 2. Unopened capsule in l.s., × 6; in t.s., × 10, at three levels from that of the radicle upwards, the cocci striated, the red cortex of the aril stippled, showing the compound nature of the aril and the loculicidal dehiscence.



391 *Trichilia sp.* (Bolivia). Seed-coats in t.s., with facets of exotesta, endotesta, exotegmen and endotegmen; cortex of the aril (lower right); × 225.

PLATE 32

TRICHILIA CAPITATA

A-D FRUIT. NOTE SEEDS COLLATERAL.

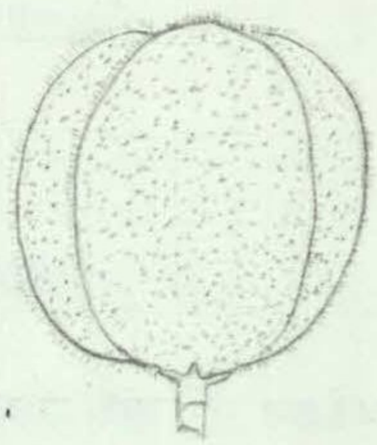
E-I SEEDS WITH FUNICULAR-RAPHE-ARIL

J-K SEED-COAT ANATOMY: NOTE LONGITUDINALLY EXTENDED AND HIGHLY THICKENED TESTAL O.E., PITTED & THICKENED CELLS OF TESTAL MESOPHYLL, UNUSUAL EXOTEGMEN CONSTRUCTION (cf. PLATE 35 A & B: PSEUDOBERSAMA).

# Trichilia capitata



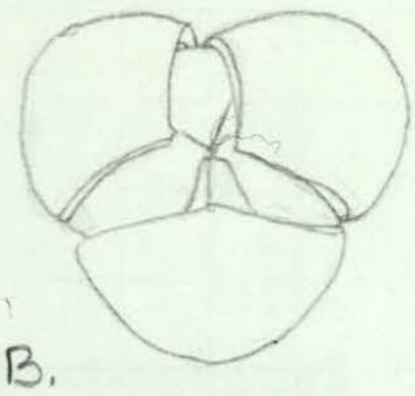
Fruit. Pre-dehiscence
Lateral view



A.

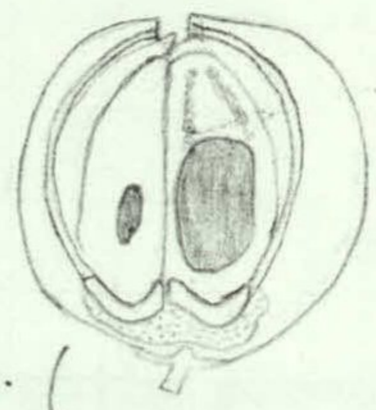
5mm

Plan view. Dehisced



B.

Fruit. Lateral view
One valve removed



C.



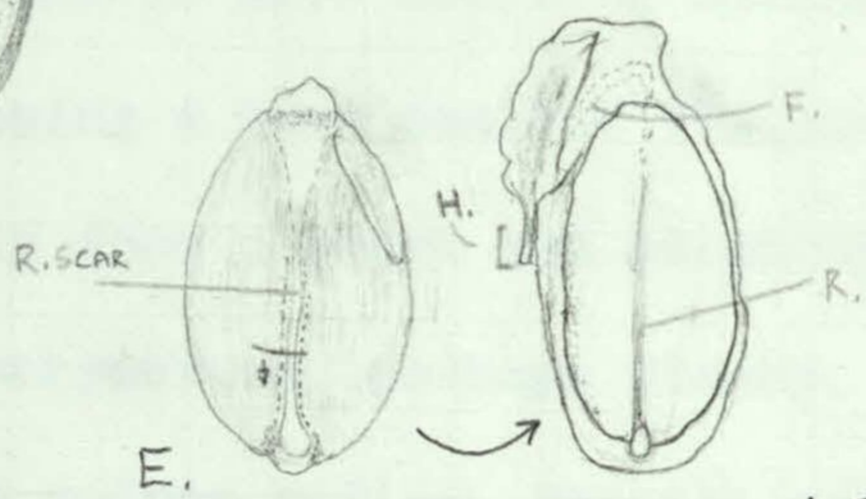
FRUIT LOCULE: INTERNAL VIEW



D.

5mm

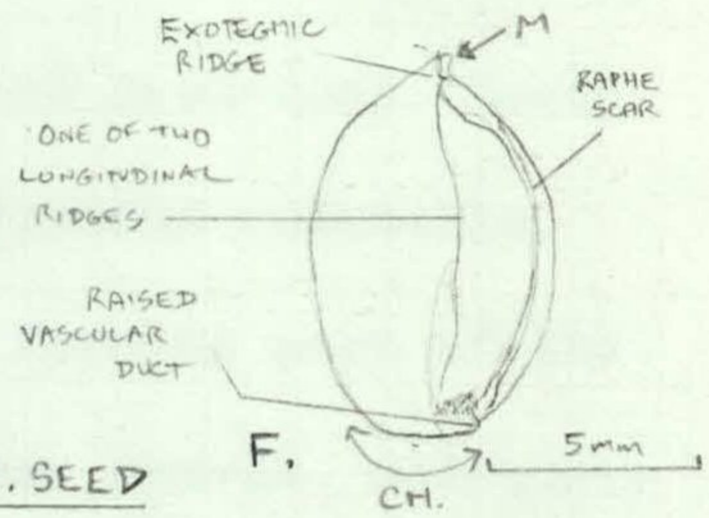
L: SEED VENTRAL VIEW WITH RAPHE-FUNICULAR ARIL REMOVED & TURNED OVER (R).




E.

5mm

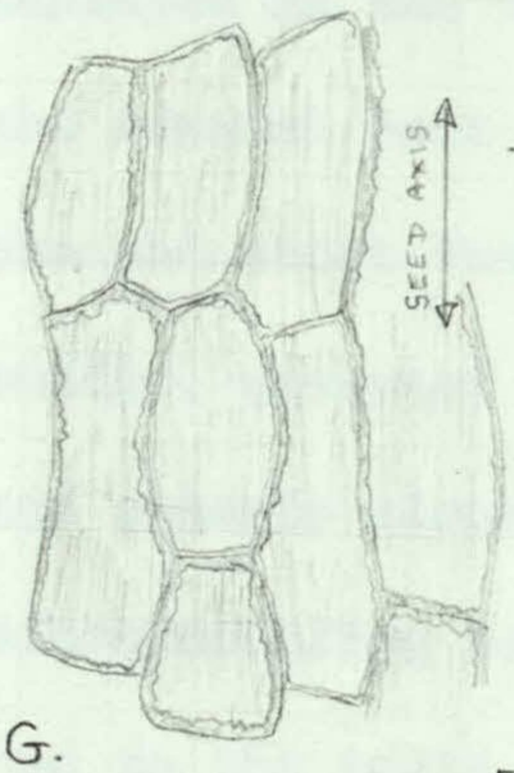
SEED: ARIL' REMOVED. LATERAL VIEW.




F.

L.S. SEED

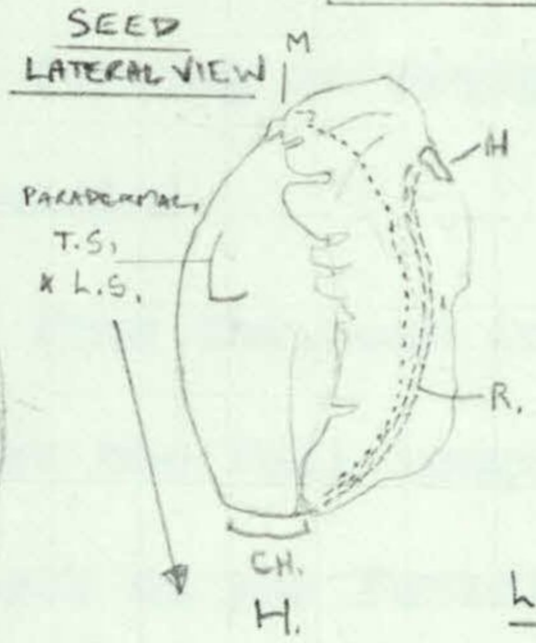
PARADERMAL VIEW. O.E. TESTA



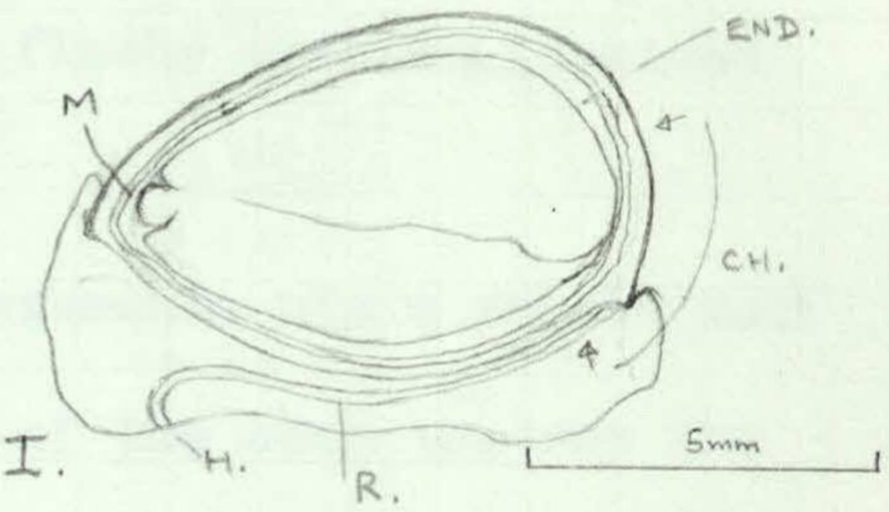

G.

50um

SEED LATERAL VIEW

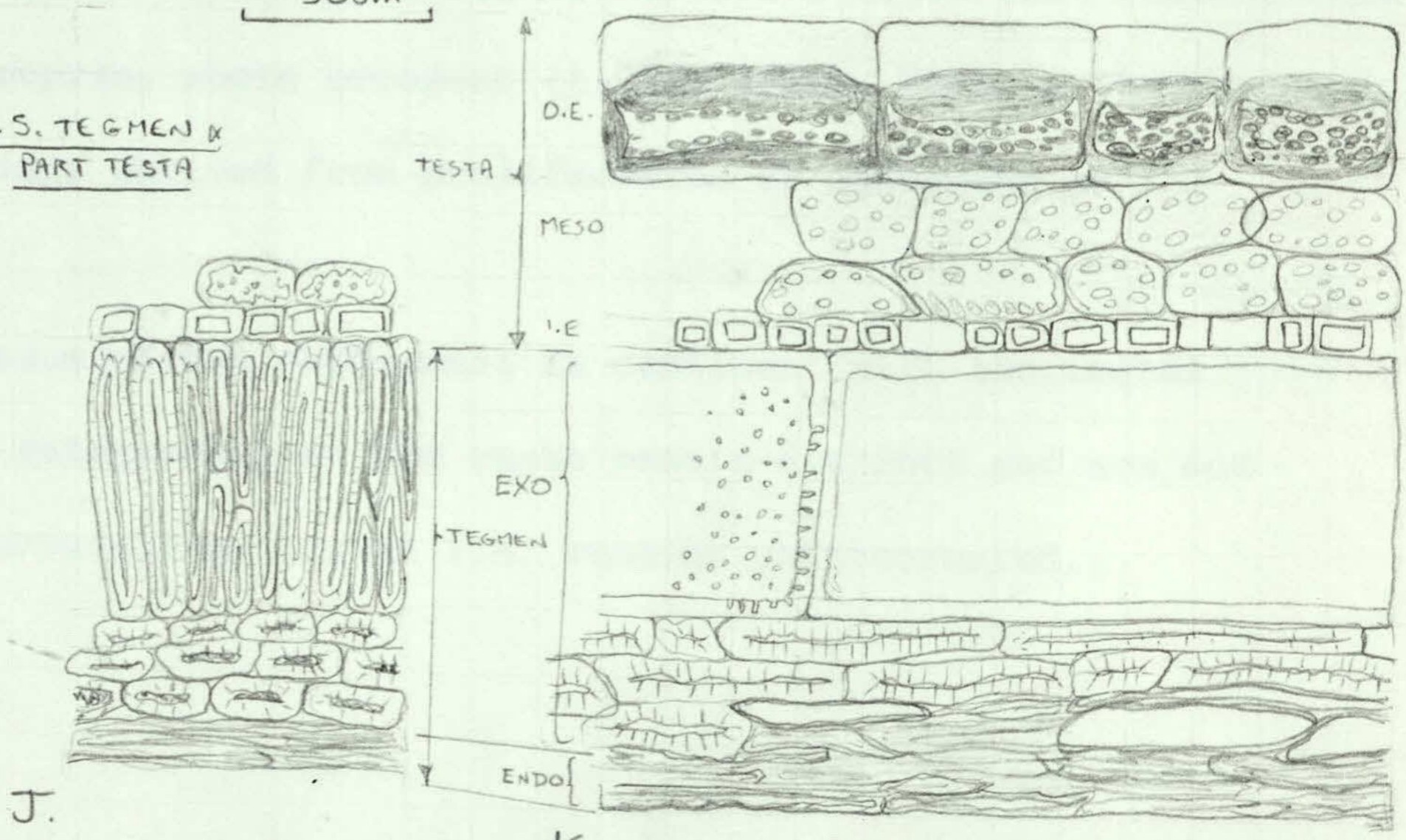



H.




L.S. INTEGUMENTS

T.S. TEGMEN & PART TESTA




J.

K.

Trichilia capitata Klotzch

This description based on J.D.Chapman 6338

Collector's notes: 'Fruit abundant, bunched together, short stalked (c.0.75mm), mostly c.1.3cm diam., tri-locular, the ripe seeds black with an orange covering'.

GROSS MORPHOLOGY

Fruits dehiscent by 3 valves, sub-spherical to slightly obovoid; dull green, 10-12mm diam., 10-12mm long. Calyx persistent. Pericarp villous, c.1mm thick, inner third to half of lignified endocarp. 3 locules, each with two collateral seeds one or both aborting during development leaving a large raphe-aril, enveloping a much smaller flattened seed-coat. Seeds pendulous-axile, apparently from a short and parenchymatous columella. Inner septa thin and parenchymatous, perhaps fleshy, forming part of the seed mass displayed as the valves reflex. Fertile seeds approx. obliquely ellipsoid, the adaxial part forming an orange fleshy cushion (derived from the raphe and short funicle).

The raphe bundle, exserted from the seed integuments via a raised duct at the chalaza extends almost the full length of the seed towards the micropyle before doubling back as the funicle and joining the placenta; it is attached to the testa by a thin strip c.0.1-0.3mm wide running from chalaza to micropyle, where broadest (1.25mm wide). Here it terminates in a transverse ridge derived from proliferation of exotegmen at the micropyle.

The fleshy tissue of the raphe-aril is confluent with the testal mesophyll. The integuments at the raphe remain distinct and are not chalazal: the crystalline testal I.E. remains uninterrupted.

Seed-coat glossy chestnut brown, marked by two irregular longitudinal lines flanking the raphe (corresponding with rim of raphe-aril flap). Seed-coat of two integuments, c.0.25mm thick. Chalaza a shallow saucer, 2.75mm diam. at proximal pole of fruit, blunt end of seed, marked internally by deep brown colouration, externally by shallow irregular folding and darker colour. Micropyle at opposite, pointed end of seed; not detectable superficially except by coinciding ridge at end of raphe.

Perisperm not detected, endosperm a thin (0.1-0.2mm thick) white layer surrounding the embryo. Embryo of two collateral, flattened plano-convex cotyledons, each 5mm long, 4mm broad, and 1.25mm thick. Radicle c.1.2mm long, 1.1mm wide, exserted

ANATOMY

TESTA

Cuticle: thin, even c.1.5um thick.

O.E. a single layer of prostrate, rectangular to square cells 35-50um high (TS and LS). In paradermal view, longitudinally extended, polygonal cells (± 2:1), c.63um long, 35um wide, with scattered isodiametric cells, these becoming dominant in ventral areas. Periclinal walls thick, apparently bi-coloured: outer cream, inner ruby red (sections c.20um thick). O.p.w. 30-36um thick, i.p.w. 6-10um thick. Inner surfaces convex, outer anticlinal boundaries sunken slightly. Lumina with reddish brown granules.

Mesophyll 2(-3) layers of prostrate ellipsoid (or rounded polygonal by mutual compression) cells. 30-50um wide, 17-21um high. Very pale brown, apparently without contents. Walls thick, 1.5um or more, apparently pitted, perhaps lignified.

I.E. single layer of small cuboidal to prostrate rectangular cells, 10-21um wide, 9-14um high. Walls thin, lumina colourless, occluded by a single colourless prismatic crystal up to 14um wide.

TEGMEN

Exotegmen of 3-5 layers of prostrate fibrous cells.

Cells of uppermost layer (erratically 2 cells thick) much the largest. In L.S. long rectangular, 210-560um long, (30-)75(-95um) high, pitted wall c.4um thick. In TS, very narrowly columnar, 11-18um wide, apparently with a double ± colourless thickening occluding the lumina, outer thickening markedly pitted.

Lower 2-3 layers of fibres smaller, shorter and non-columnar. 30-140um long, c.15um high in LS., prostrate, rounded rectangular 21-30um wide in TS. Walls ± colourless, c.3um thick, pitted. Lumina small with dark pigment.

Endotegmen almost completely crushed, but sometimes cell walls detectable. Amorphous brown layer 17-45um thick.

Pseudobersama mossambicensis(Sim)Verdcourt

This description based on Cheek et al. 1603.

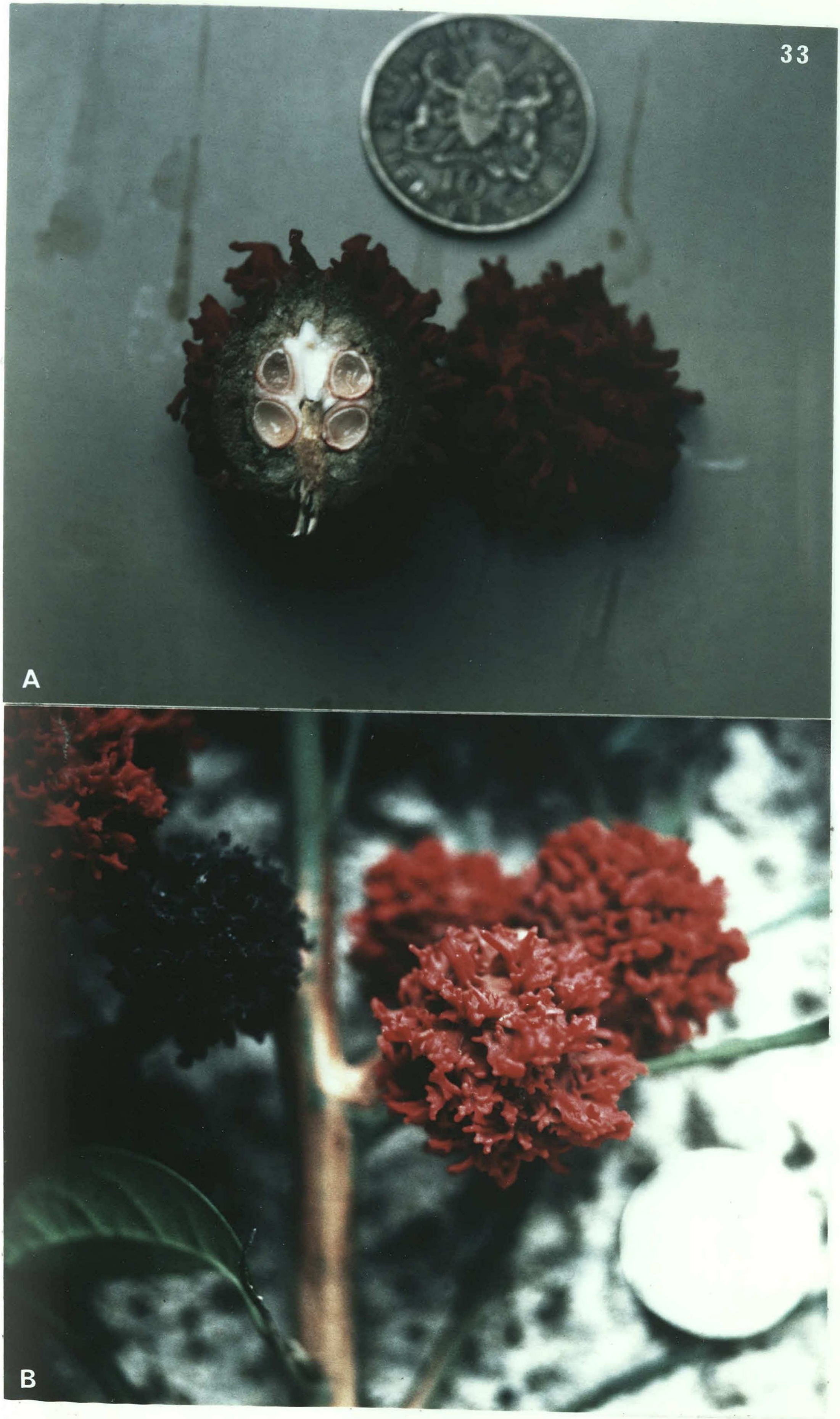
Collector's notes: 'Fruits vivid red , easily mistaken for 'Litchis'! Valves extremely thick and woody, covered by wrinkled, horny excrescences, dehiscing only slightly at first. Seed-coat very dark chestnut brown, proximal part encased in yellowish succulent layer. Marcescent fruits from previous season on some trees, without seeds'.

PLATE 33

PSEUDOBERSAMA

A FRUIT, L.S. NOTE SUPERPOSED SEEDS AND VERY THICK PERICARP.

B WHOLE FRUITS. NOTE BRIGHT RED AND HIGHLY ORNAMENTED FRUIT SURFACE (SLIGHTLY IMMATURE) X 1.25.



A

B

PLATE 34

PSEUDOBERSAMA

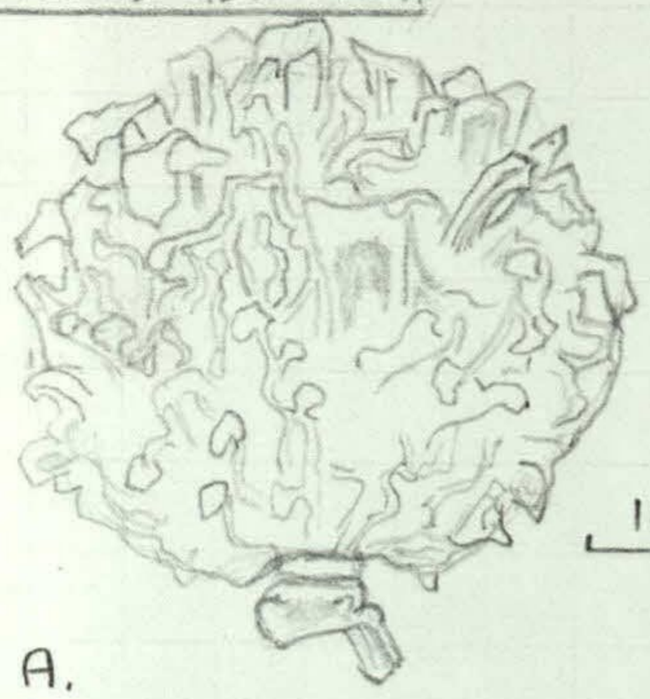
A-C FRUITS. NOTE THICK PERICARP, 5-LOCULAR, SUPERPOSED SEEDS.

D-L SEEDS. NOTE FUNICULAR-RAPHE-ARIL WITH HAIR-PIN

VASCULAR BUNDLE.

# PSEUDOBERSAMA MOSSAMBICENSIS

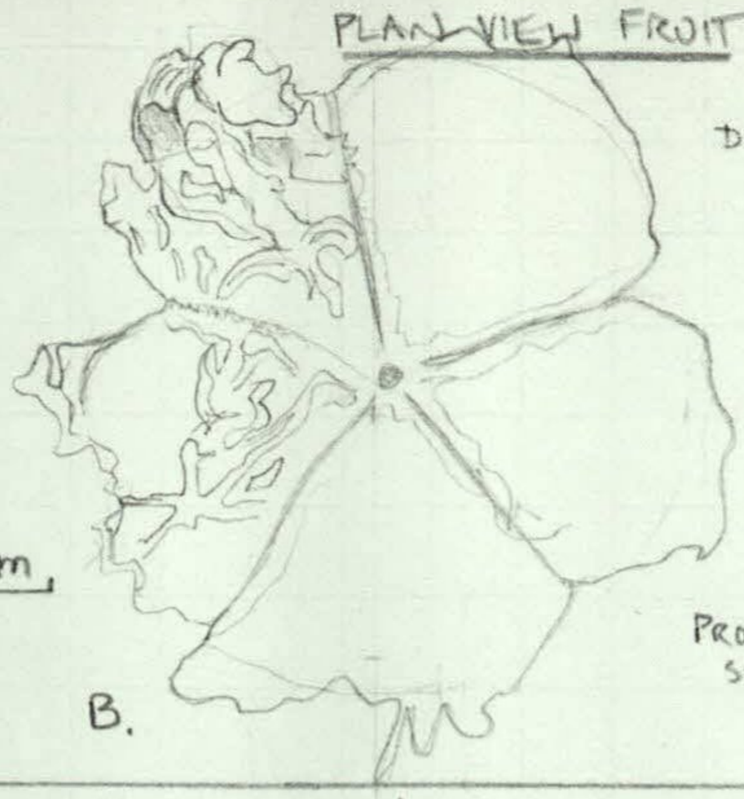
LATERAL VIEW FRUIT



A.

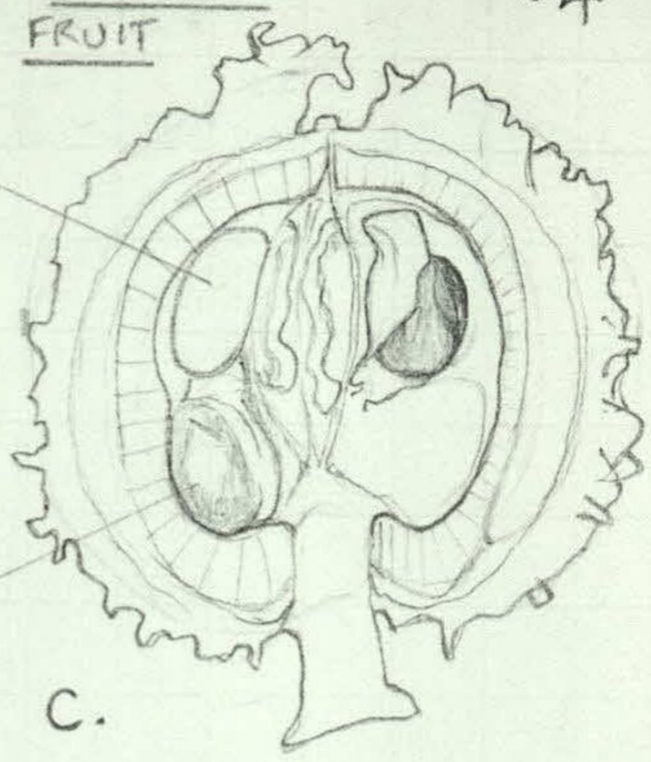
1cm

PLAN VIEW FRUIT



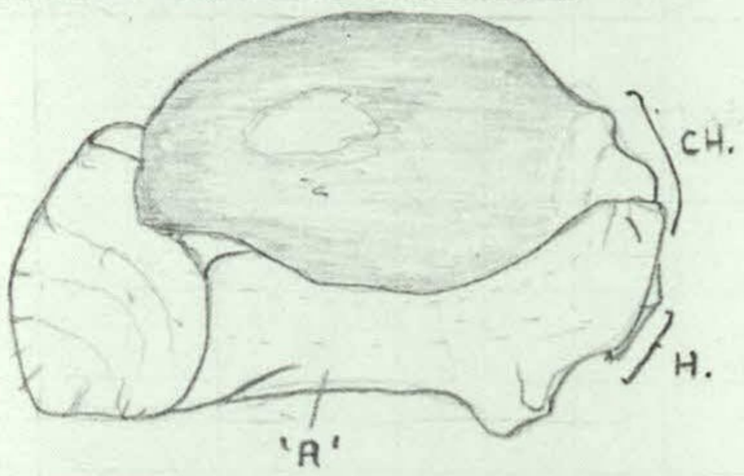
B.

SUB-L.S. FRUIT



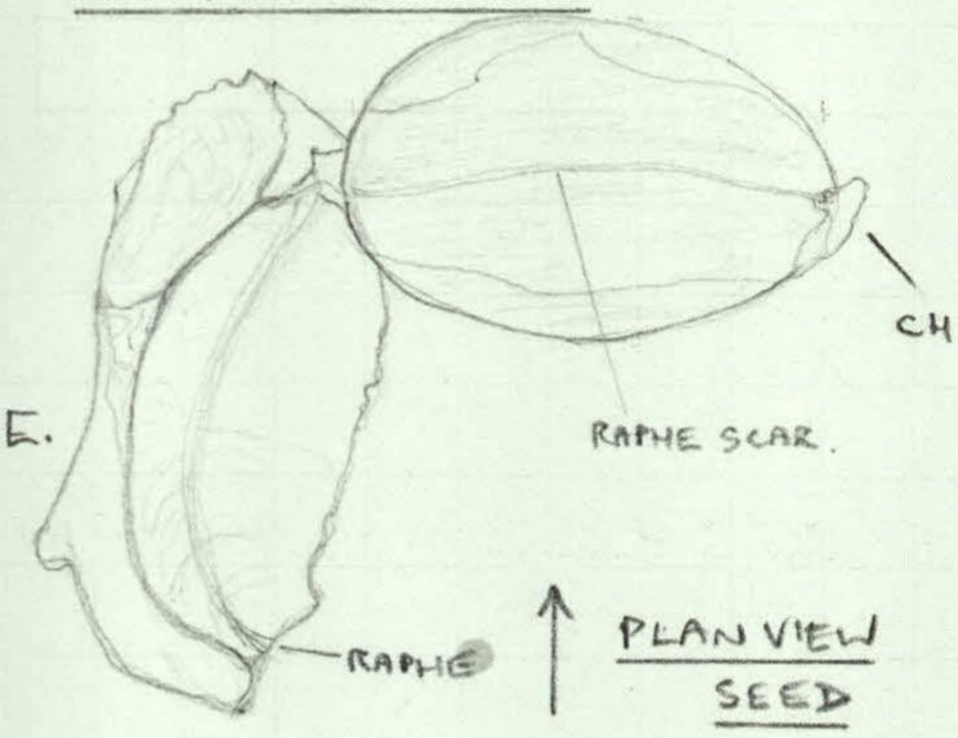

C.

LATERAL VIEW SEED: PROXIMAL




D.

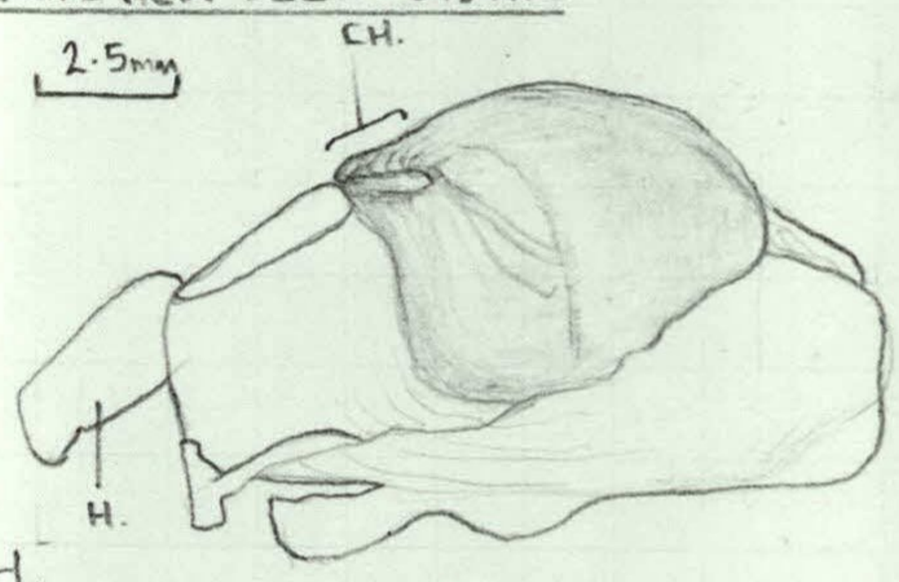
'ARIL' PART-DETATCHED



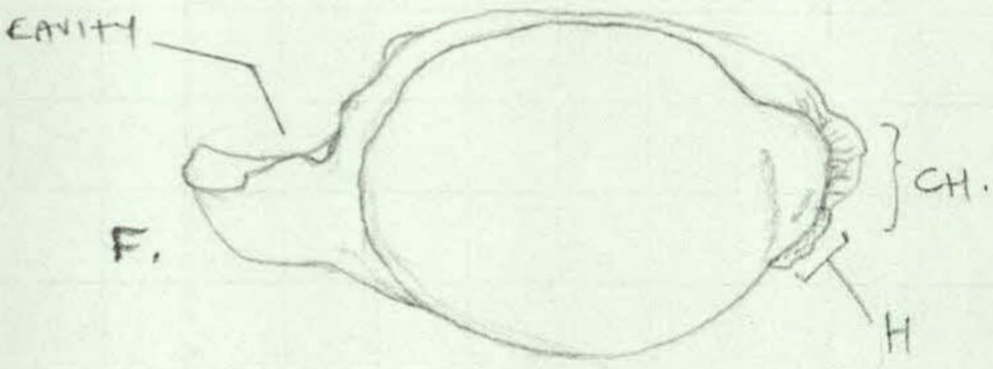

E.

PLAN VIEW SEED

LATERAL VIEW SEED: DISTAL

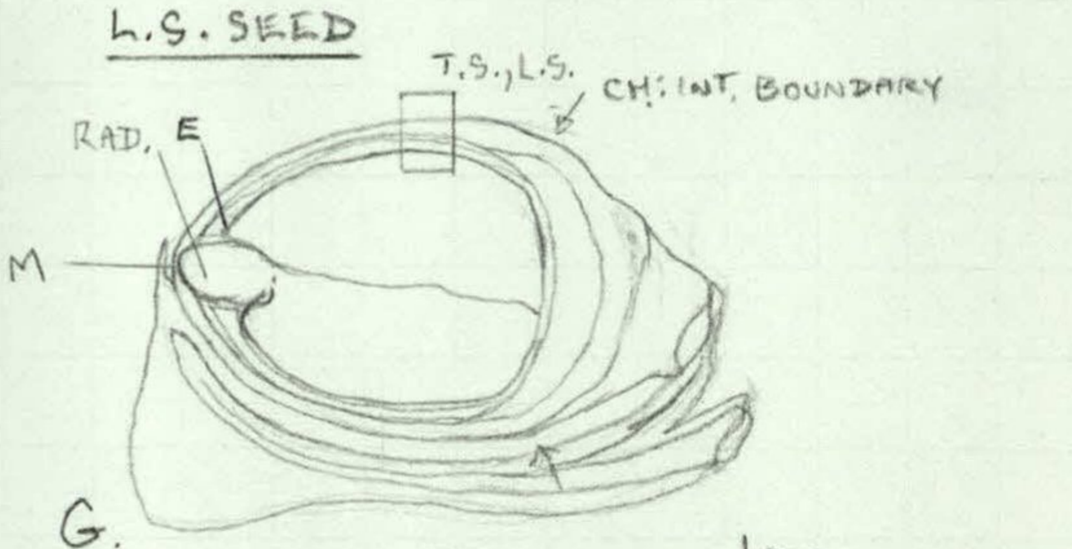



H.

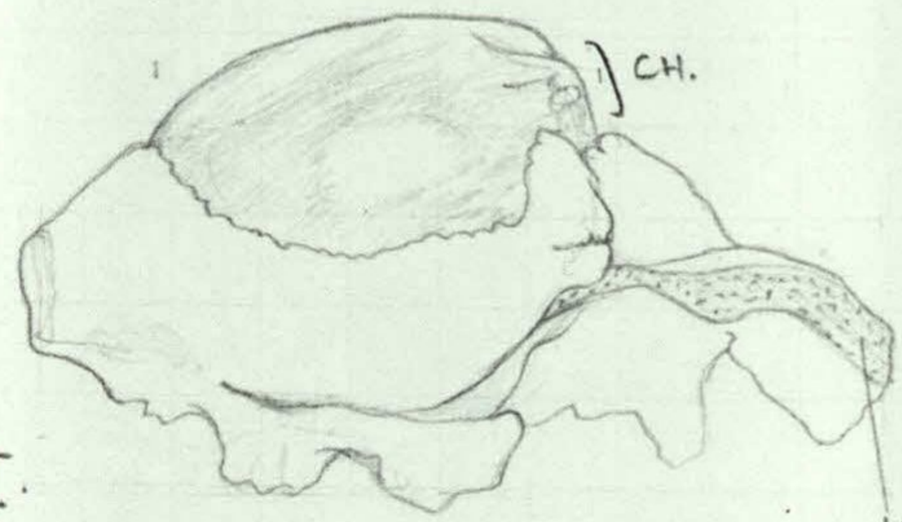



F.

L.S. SEED

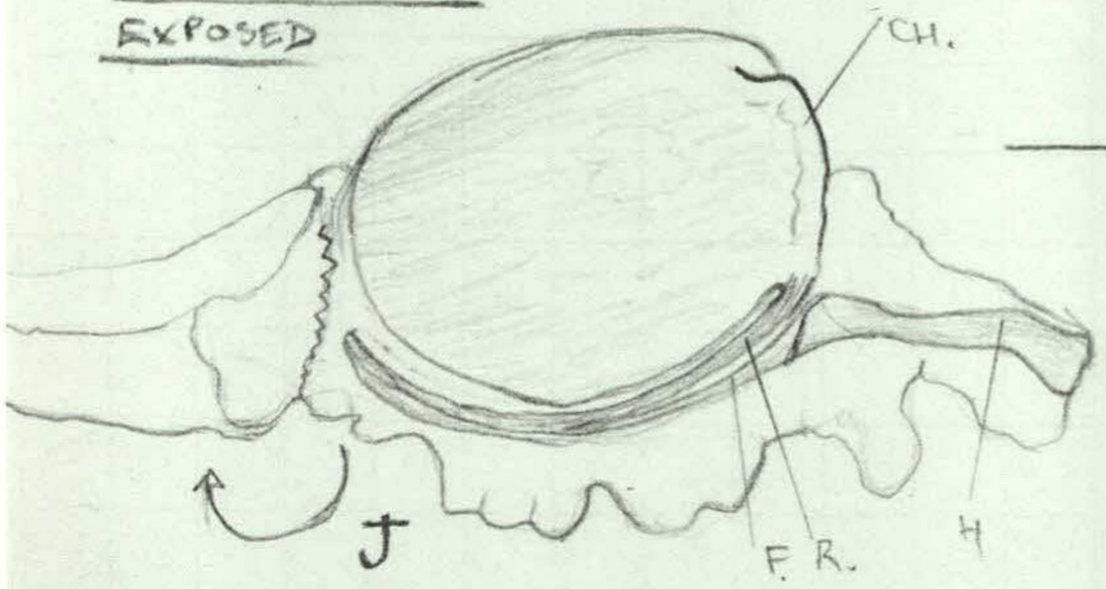



G.



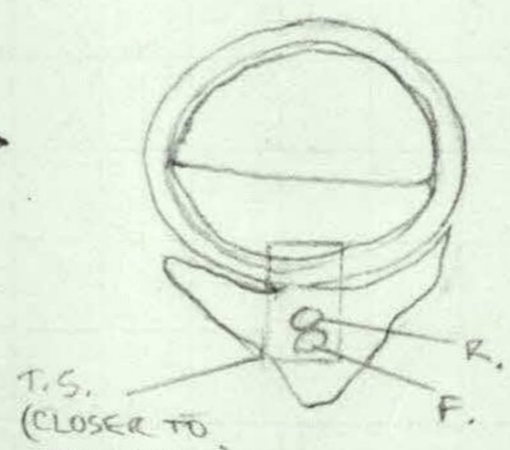

I.

LATERAL VIEW SEED. VASCULAR SUPPLY EXPOSED



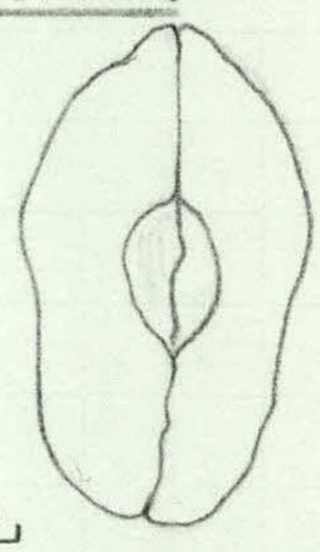

J

T.S. SEED




K.

FRUIT SEPTAE EXCISED LATERAL VIEW.




L.

PLATE 35

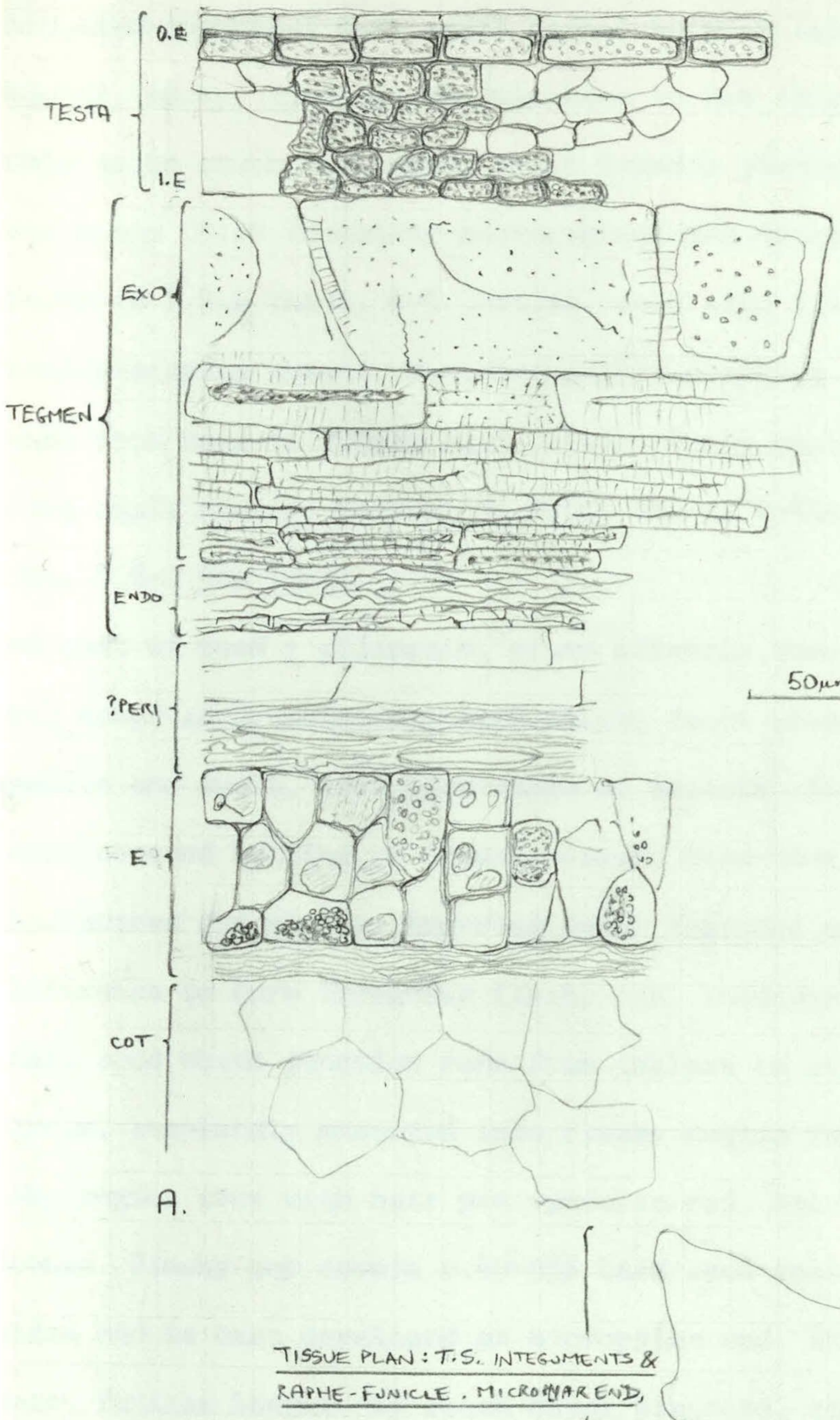
PSEUDOBERSAMA

A-D SEED-COAT ANATOMY. NOTE STRIKING SIMILARITY WITH THAT OF TRICHILIA CAPITATA (PLATE 32).

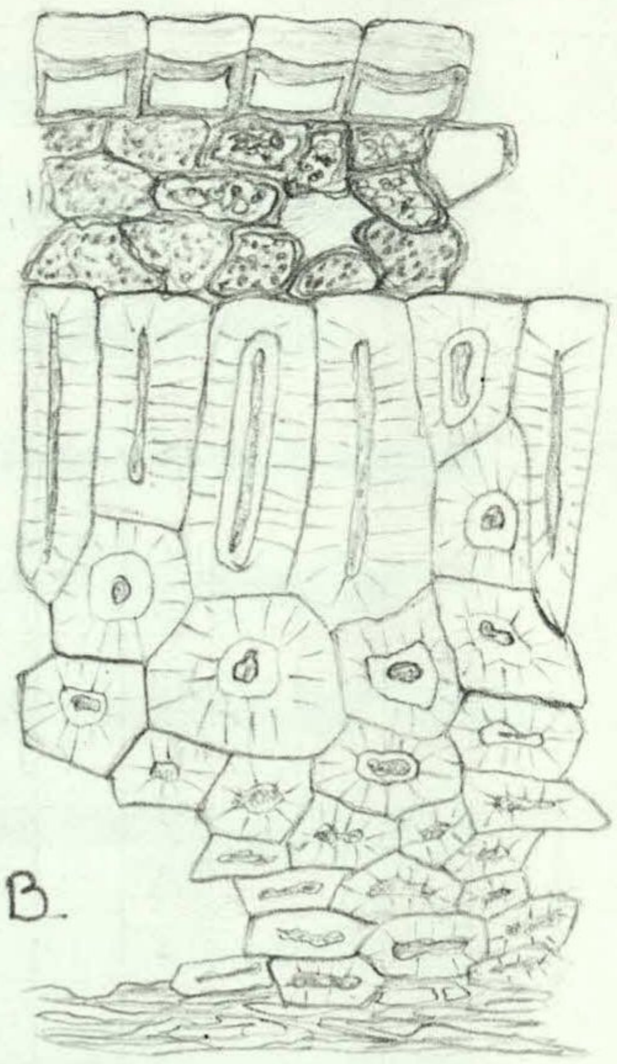
# PSEUDOBERSAMA MOSSAMBICENSIS



L.S. INTEGUMENTS & SUB-INTEG. TISSUES.

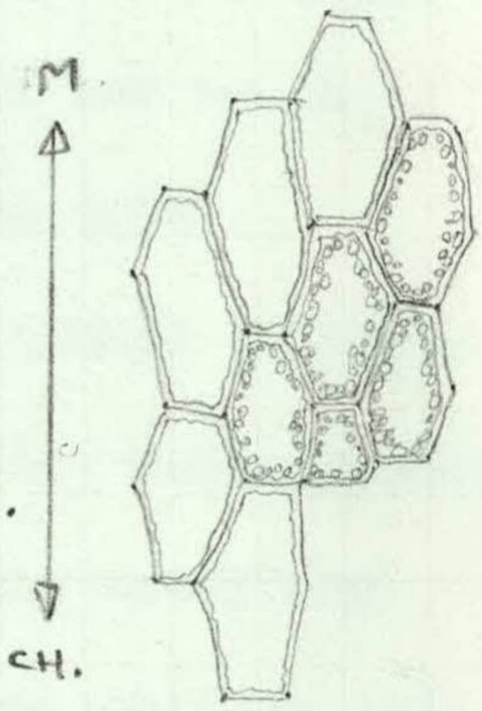



T.S. INTEGUMENTS



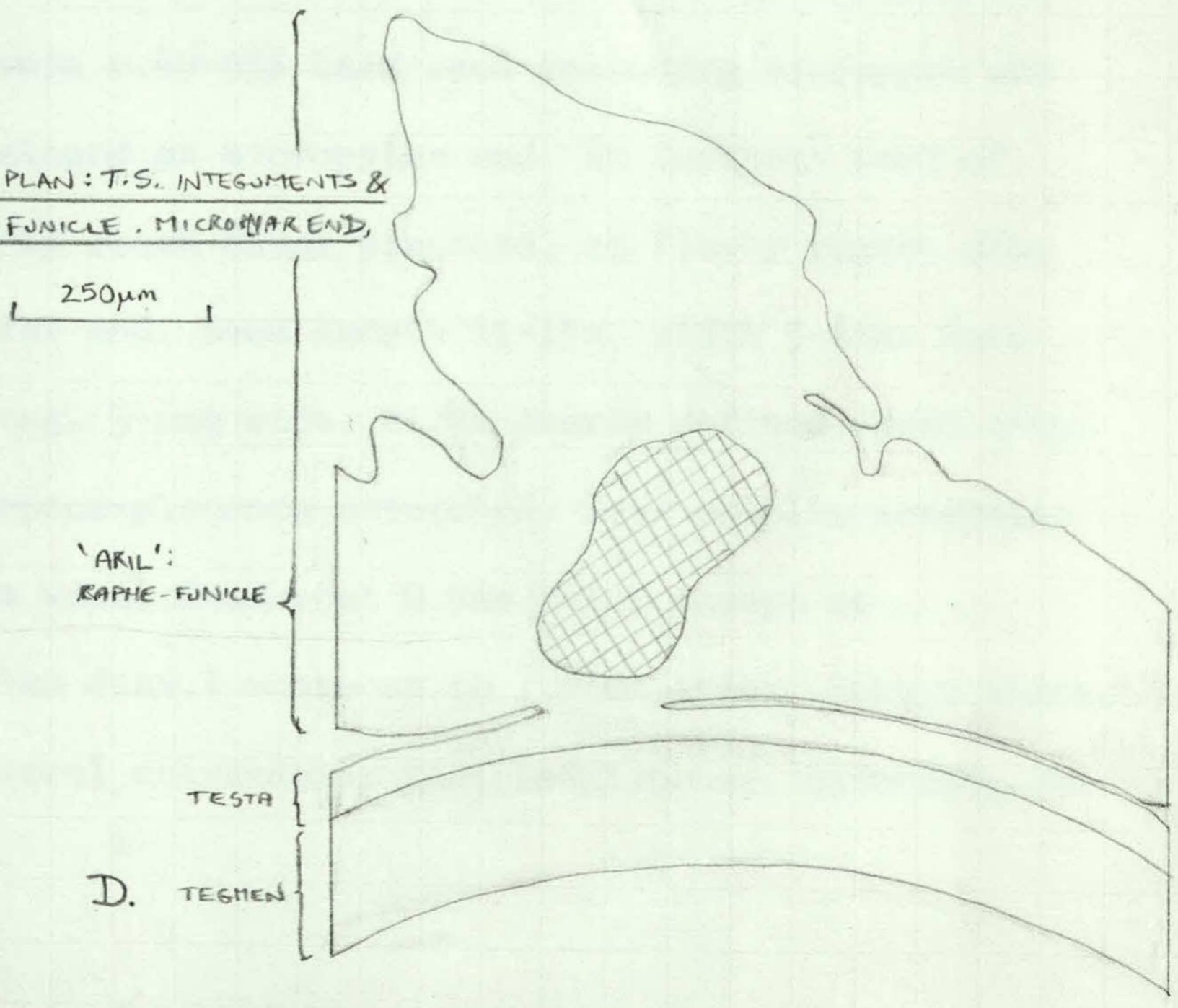

50µm

PLAN VIEW OF O.E. TESTA




TISSUE PLAN: T.S. INTEGUMENTS & RAPHE-FUNICLE. MICROPYLAR END.

250µm



GROSS MORPHOLOGY

Fruits sub-spherical with small distal boss. 5 valves covered by irregular, warty, lamellar excrescences to 5mm long, in some fruits so densely as to cover the septa. Fruit breadth 31-40mm, length 30-40mm. Valves c.9mm thick including excrescences and discrete sclerified endocarp to 2.5mm thick. 4-5 locules, each with (1-)2 superposed seeds. Central placentae absent, vascular supply breaking into 5 diverging strands from base to supply each locule. Septa parted at centre of fruit leaving small cavity. Pedicel in fruit short, 2-4mm. Peduncle with 1-4 fruits, 1.8-2.5cm long.

Hard part of seed ± ellipsoid, often slightly dorsi-ventrally (w.r.t. fruit) compressed, sometimes with slight facet where adjoins its locule companion and small, irregular ridge at chalaza. Micropyle inconspicuous, usually covered by flap of fleshy tissue. Seed-coat thick and tough, cuticularized and glossy. Exserted raphe together with funicle proliferates to form irregular fleshy cup, insecurely attached at raphe to main seed which junction runs from chalaza to micropyle. Raphe bundle discrete, completely exserted into fleshy region from main seed body. Fleshy region thus with hair pin vascular rod, attached at chalaza and placenta. Fleshy cup covers c.40-55% hard seed including micropyle and chalaza and is best developed at micropylar end. In furthest seed of locule, funicle longer, to reach basal placenta, so fleshy region also well developed at chalazal end. Seed length 11-15m, width 5-6mm. Hard portion of seed 8-9mm long, 5-6mm wide. Hilum poorly defined, seed often detaches with part of septum-placenta attatched. Scar usually irregular, c.1-3mm long and 1-1.5mm wide. Seed-coat 0.5mm thick except at saucer-shaped chalaza (4mm diam.) where up to 1.25mm thick. Embryo white, of 2 plano-convex collateral cotyledons; radicle glabrous, exserted, 2mm

long, 1mm wide. Endosperm thin, greyish white, sub-membranous, thickest near radicle.

ANATOMY

TESTA

Cuticle: 3(-7)um thick, colourless, even.

O.E. single layer of cells, prostrate rectangular in LS, square in TS. 20-28um high and 20-22um (TS) or (22-)40um (LS) wide. In paradermal plane, longitudinally extended hexagonal, about twice as long as broad. O.p.w. 6-10um thick, i.p.w. and anticlinal walls 1-2um thick. Walls red brown. Cell contents of brown, granular inclusions.

Mesophyll: 3-10 layers thick with thinly scattered, small airspaces. Cells prostrate, shortly elliptic, 20-27um wide and c.15um (outer layer) to 10um (lowest layer) high. Walls c.1um thick, lumina with dull grey or brown cytoplasmic contents, often with brown nodular (tanniniferous?) inclusions.

I.E. single layer of small, prostrate elliptic cells, 10-12um high and 11-3um wide. Apparently without crystals. Walls apparently sometimes thickened. Lumina empty or with grey contents. This layer tightly adhering to exotegmen below, section fractures occurring in testal mesophyll rather than testa-tegmen boundary.

TEGMEN (equatorial region)

Exotegmen four to eight layers of short to long, longitudinally directed fibres. In T.S., upper layer columnar, to 70um (-105um) high and 14-28um wide, but sometimes isodiametric (often nearly so near raphe), c.32um square. In L.S., upper layer sub rectangular to square. Near chalaza, 3-4 times longer than broad. Towards micropyle, columnar. Walls 4-10um thick, very pale straw , heavily pitted. Apparently two layers of thickening,

outer thickest with pits, inner thinner (best seen in isodiametric cells of middle layer) without pits. Lumen very small, orange brown contents.

Cells of lower layers generally of much smaller dimensions, in TS uppermost 1-3 isodiametric, 25-40um diam.; lowest layers becoming broader than tall (prostrate), 7-10um high, 13-40um wide. In longitudinal section, fibre length ( 90-114um) fairly uniform, apart from lowest layer 68-95um long.

Mesophyll crushed to an amorphous medium brown layer 9-15um thick.

PERISPERM? (L.S.)

Two layers of cells surviving above. Thin-walled, prostrate rectangular in L.S., without cell contents, anticlinal walls slightly oblique. 14um high, 94-120um wide. Layers of crushed cells below, yellow brown, 10-15um thick.

In T.S., cells cuboidal, 14-20um wide, c.15um high.

ENDOSPERM(L.S.)

2-3 layers of isodiametric to shortly radially extended cells 22-35um tall and 17-24um wide each filled with ± colourless plastids.

EMBRYO(L.S.)

Very thin-walled isodiametric cells, 5-6 sided, 50-64um diam..

RAPHE-FUNICLE

Raphe-funicular aril connected to main seed by thin strip (160um wide) of tissue, linking chalaza with micropyle, derived from testal mesophyll which confluent with arillar mesophyll. Despite raphe, tegmen notably

distinct from testa: perichalaza absent. Hair-pin vascular bundle 200-350um diam., discrete, without branches.

Epidermis: single layer of prostrate, angular ellipsoid to spherical cells (T.S.,L.S.), cell contents absent, walls medium brown, 3um thick. o.p.w. markedly convex, with cuticular ridges in parallel lines or spiralled, 3/um. In paradermal view, 5-7 polygonal, isodiametric to shortly extended polygonal, 20um diam. to 35um long and 28um wide, ± randomly orientated.

Mesophyll: Thin-walled, angular, isodiametric to extended polygonal cells to 21um wide and 56um long, walls c.1um thick, colourless. Numerous lipid globules, 4-6um diam. at periphery of each cell.

Pterorhachis zenkeri Harms

This description based on Letouzey s.n.

No collector's notes available.

GROSS MORPHOLOGY

Fruits strongly 3(-4) lobed and valved dehiscent capsules with short terminal rostrum (1.5-2mm long) and marked fluting/ridging forming coarse surface reticulum with remnants of stellate indumentum, 15-17mm broad, 14.5-17mm long. Pedicels 4-5.5mm long, stellately hairy, persistent calyx. Pericarp 0.9-1.25mm thick, cartilaginous-woody, septa parting with valves. Central vascular column 9-11mm long, c.1.25mm diam., seeds attached at base.

Seeds slightly ovoid ellipsoid, sometimes slightly orange-segment shaped by mutual compression, 9-10.5mm long, 6-8mm broad. Seed-coat glossy chestnut brown, 0.2-0.3mm thick. Micropyle at distal (w.r.t. fruit) end of seed, on obtuse point with black plug. To 0.4mm diam.. Issuing from basal chalaza (3-4mm diam.), a thin (0.1-0.3mm), regularly vascularized,

PLATE 36

PTERORHACHIS ZENKERI

A-C FRUITS: 3-LOCULAR, SLIGHTLY ROSTRATE AND WITH AN IRREGULARLY RIDGED SURFACE.

D-G SEEDS: NOTE CHALAZAL-ARIL WITH PRE-RAPHE GAP, PRE-RAPHE FURROW (E), SHORT FUNICLE, AND SUB-ORTHOTROPOUS ORIENTATION OF SEED (F).

H L.S. ARIL.

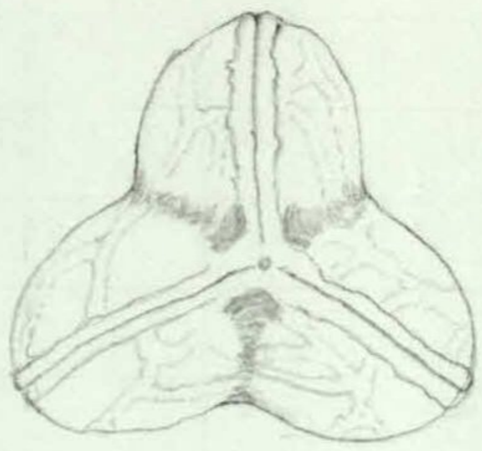
# PTEROCARPUS ZENKERI

FROIT, LATERAL VIEW



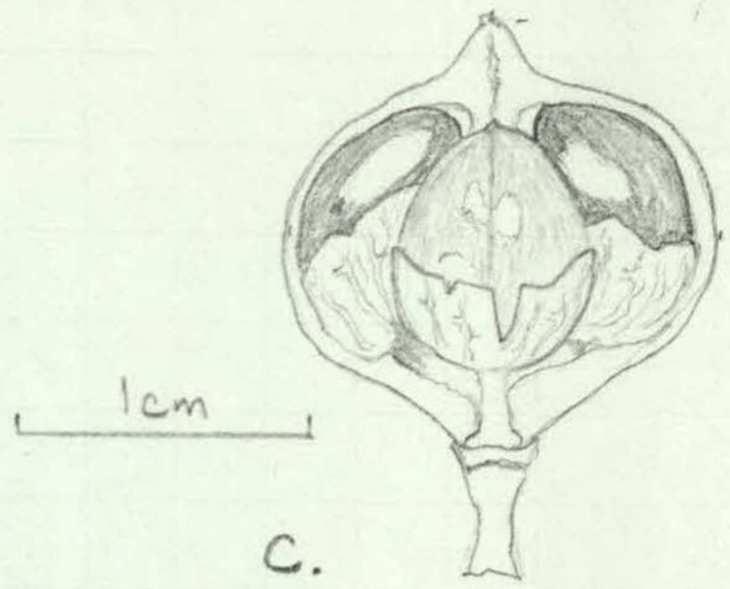

A.

PLAN VIEW



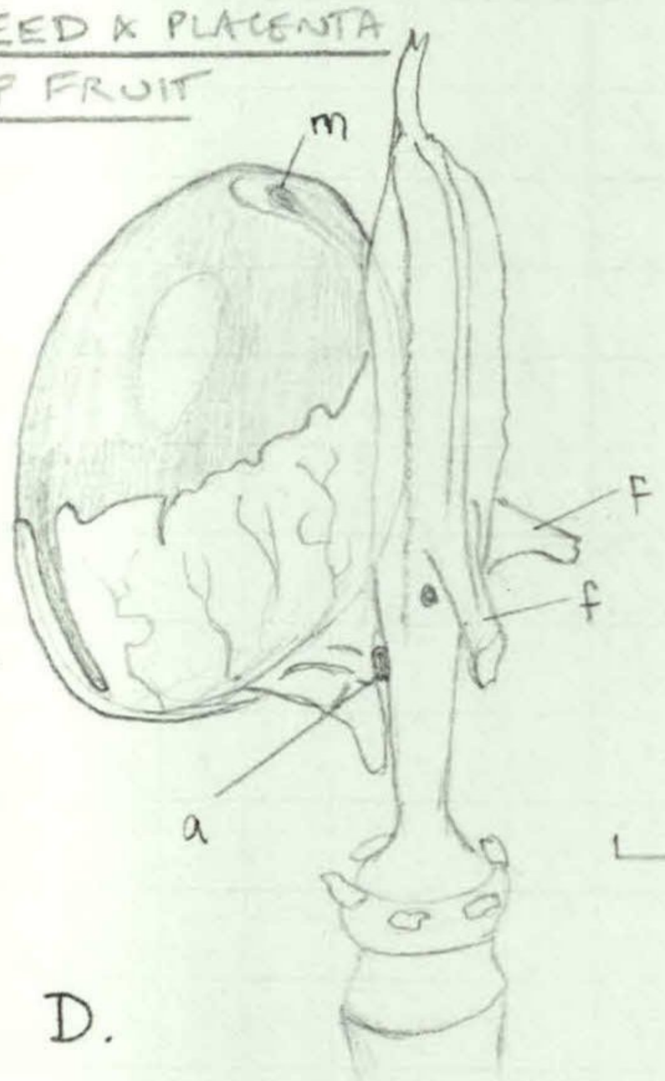
B.

FROIT, LATERAL VIEW, 2 VALVES REMOVED TO EXPOSE SEEDS



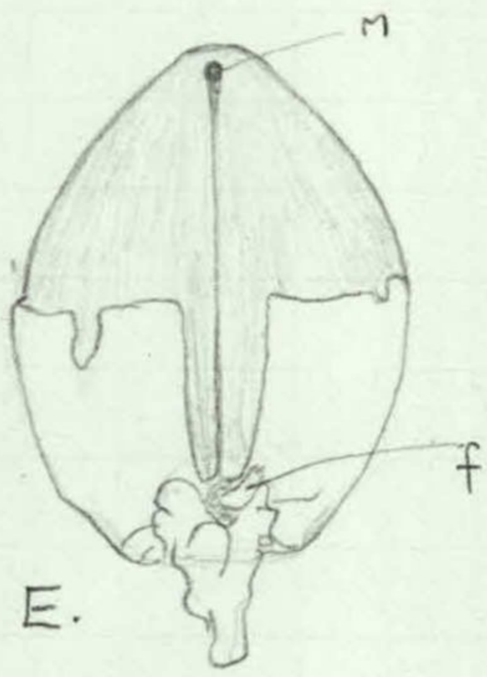

C.

SEED & PLACENTA OF FRUIT




D.

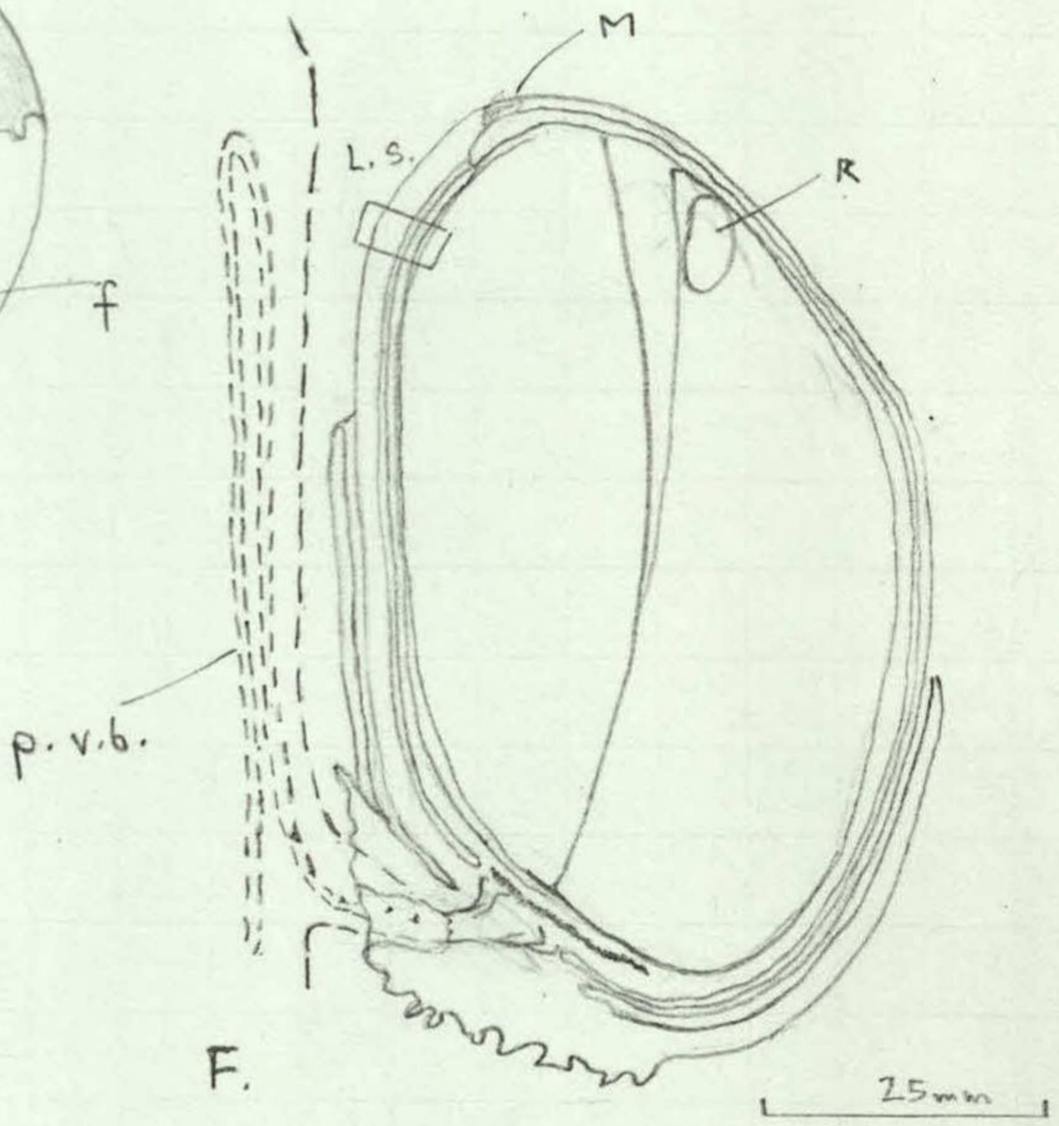
VENTRAL VIEW, SEED




E.

1cm

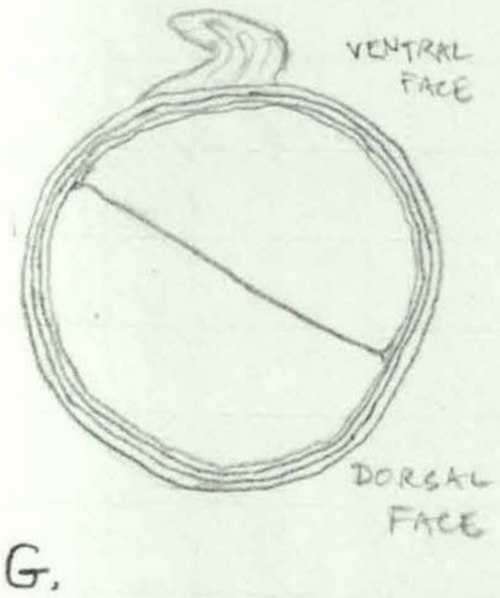
MEDIAN L.S, SEED




F.

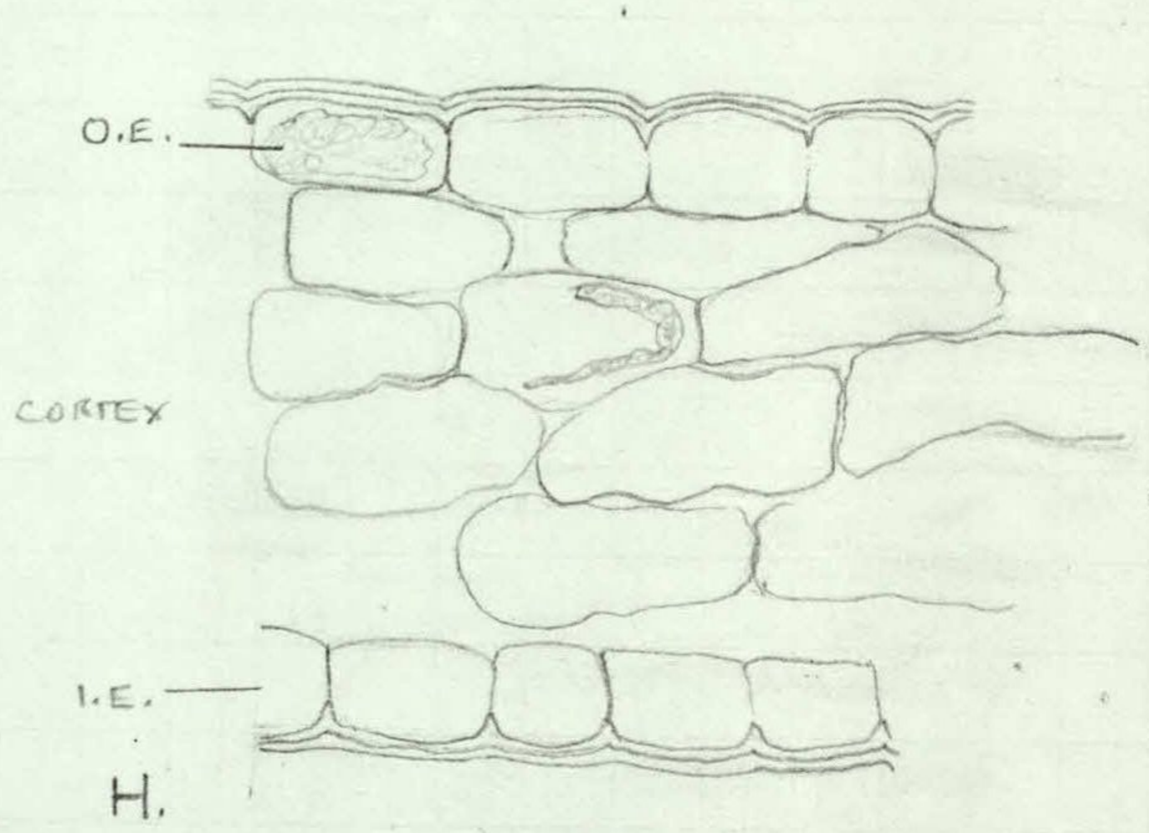
2.5mm

T.S. SEED




G.

L.S. 'ARIL'




H.

PLATE 37

PTERORHACHIS ZENKERI

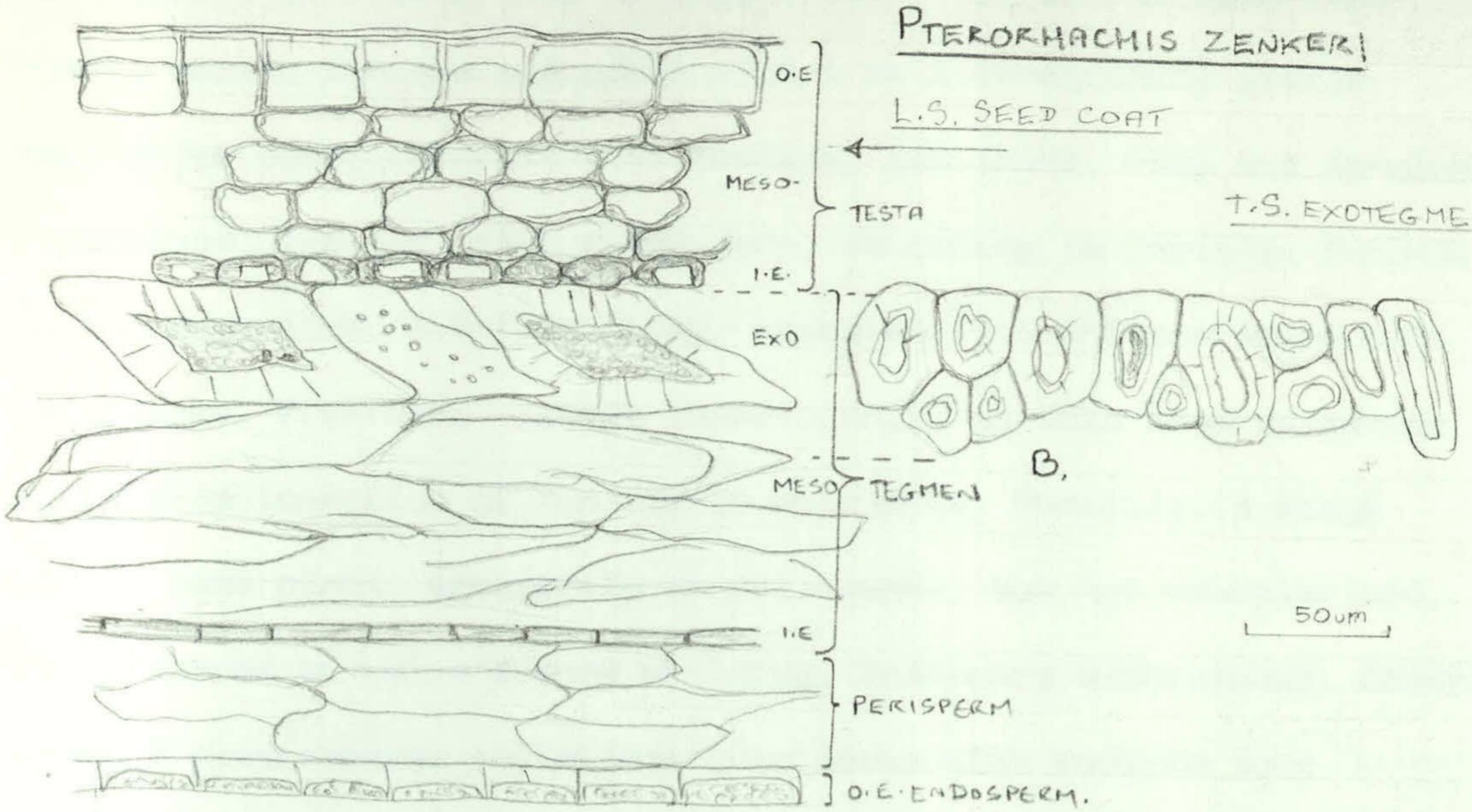
A-D SEED-COAT ANATOMY. NOTE EXOTEGMEN: SUB-PALISADE (A).

PRE-RAPHE VASCULAR BUNDLES (C).

PTERORHACHIS ZENKERI

L.S. SEED COAT

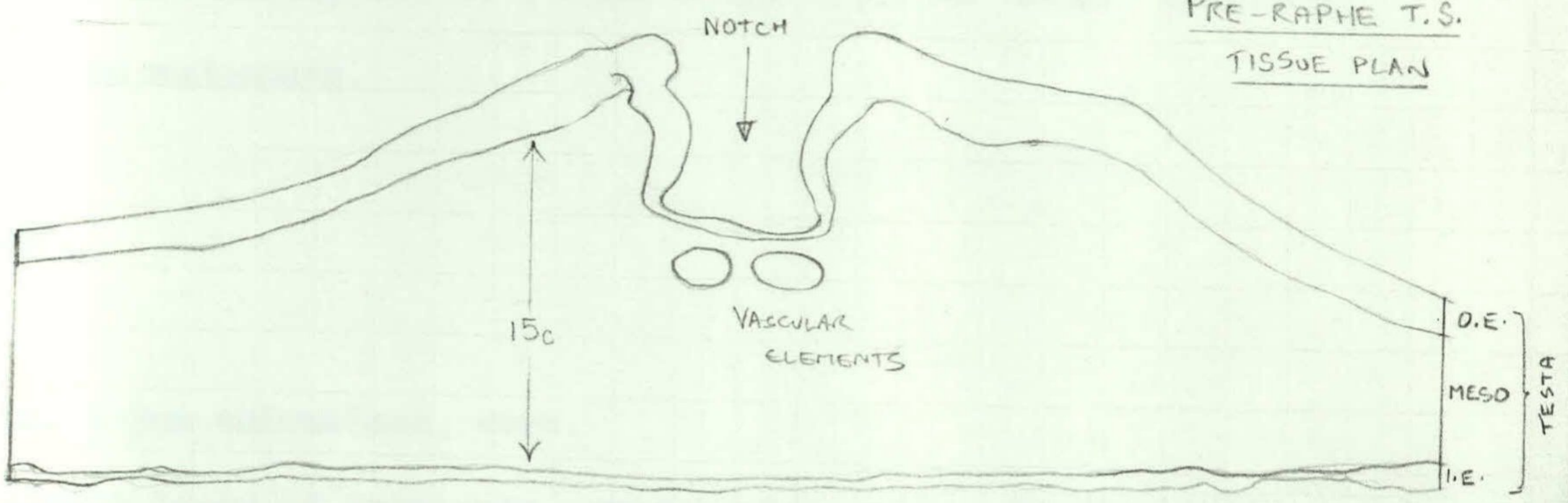
T.S. EXOTEGMEN




A.

PRE-RAPHE T.S.

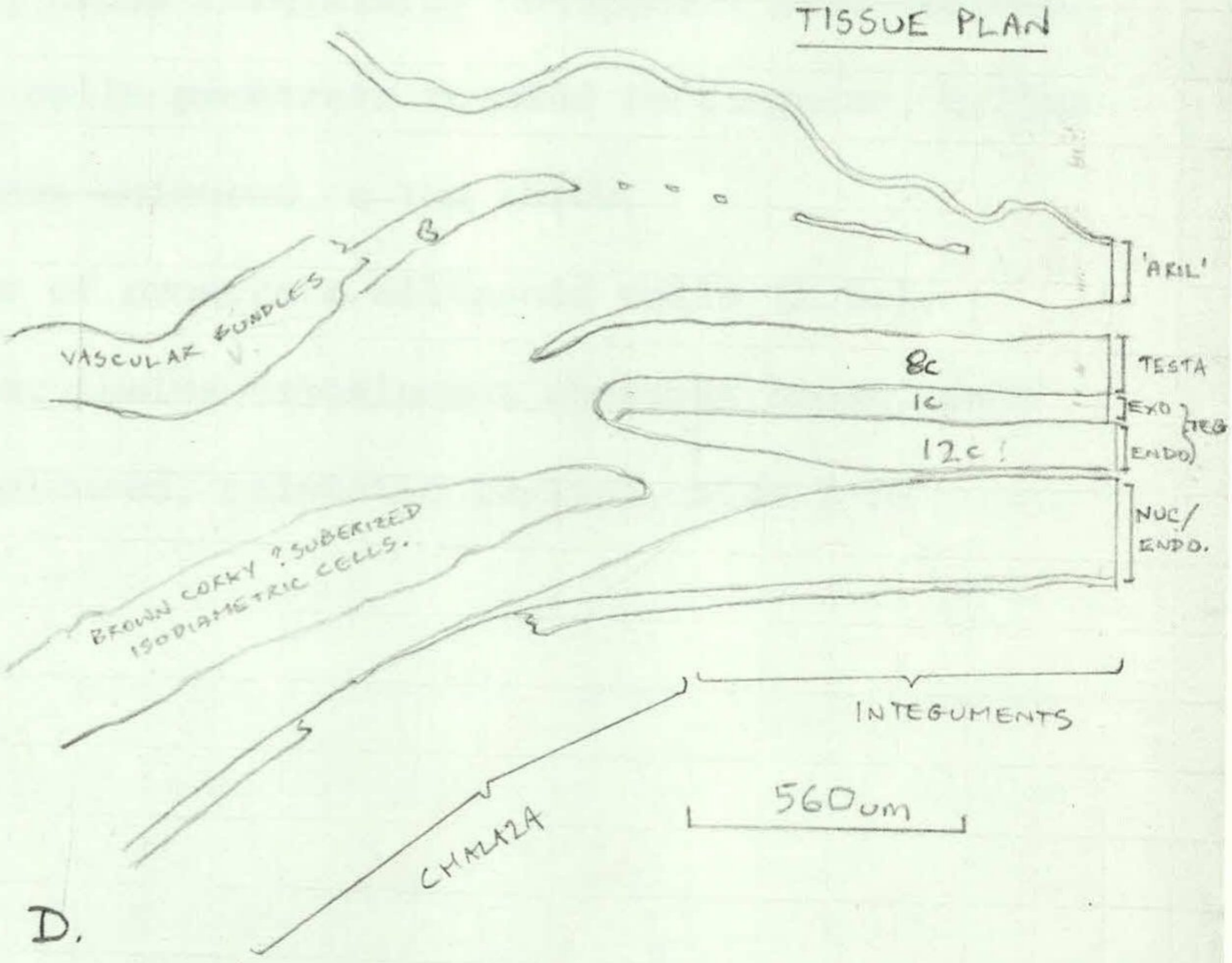
TISSUE PLAN




C.

L.S. TRANSITION ZONE

TISSUE PLAN




D.

pale yellow-orange fleshy flap envelopes lower 1/3-2/3 of seed-coat (c.4-7mm), margin sinuous and often with 1 or 2 irregularly placed notches, 2-3mm deep; thickest over chalaza, 3mm thick. Flap not developed over pre-raphe, leaving notch c.6mm deep, extending to funicle. Funicle stout, c.0.5mm thick, 0.8-1.5mm long, inserted into chalaza where most readily breaks. Pre-raphe visible superficially as thin seam extending ventrally from insertion of funicle to micropyle. Dorsally, a ridge extends in same plane, apparently an anti-raphe, but not vascularized, evidently formed by valve suture moulding. Endosperm membraneous. Embryo straight, 2 plano-convex collateral cotyledons with radicle just included, below micropyle, c. 1.25mm long, c.0.75mm broad, glabrous, c.0.3mm from endosperm.

ANATOMY

TESTA

Cuticle: 1-3um colourless, even.

O.E. single layer of prostrate, rectangular cells, 20-25um high, 25-35(-50)um wide. O.p.w. pale-medium brown, 10um thick. Anticlinal and i.p.w. thin, straw-coloured, c.1um thick. Lumina with sparse granular contents. In paradermal view, cells irregularly hexagonal, isodiametric.

Mesophyll 3-5 layers thick, cells prostrate rounded rectangular, c.15um high, 25-45um wide. Walls straw-coloured, c.1um thick.

I.E. single continuous layer of prostrate ellipsoid cells (L.S.), 10-12um high and 20-25um wide. Lumina translucent chestnut brown, each containing a single, straw-coloured, prismatic crystal, side 7-10 (-15)um.

TEGMEN

Exotegmen a single layer of shortly longitudinally extended fibroid cells. In L.S., rectangular rhombic with lustrous, pitted, straw walls 10-15um thick and scanty dark brown contents. Cells 84-150um wide, heavily pitted, 42-65um high. In transverse section, shortly columnar, 18-25um wide.

Mesophyll 3(-4) layers of thin-walled parenchyma with very thin contents. Cells prostrate narrowly elliptic, T.S. and L.S., ± isodiametric in paradermal plane. 90-140um wide (T.S. and L.S.), 13-25um high. This zone usually slightly crushed and distorted (this collection).

I.E. single layer of distinct , small, brown, prostrate, rectangular cells (T.S. and L.S.) 30-40um wide, 6-8um high, poorly distinguished with 2-3um thick, medium brown walls and medium brown contents.

Walsura pinnata Hassk.

This description based on TDP 7815.

Collector's notes: ' Fruit in erect axillary or terminal panicles, fawn when nearly ripe, pericarp leathery-fleshy, usually 1-seeded. Seed surrounded by fleshy whitish-membrane, exuding clear sticky fluid. Fruit looks like that of Lansium domesticum'.

GROSS MORPHOLOGY

Fruits indehiscent, ellipsoid to obovoid capsules to 27mm long, 18mm broad, with persistent calyx, and short, 0.6mm pedicel and matt surface. Pericarp rather thick, (1.25-2mm), apparently slightly succulent (oozing fluid), endocarp reduced to a thin non-mechanical layer. Valve sutures not detected. Fruits bi-locular, largely occupied by the single fertile

PLATE 38

WALSURA PINNATA

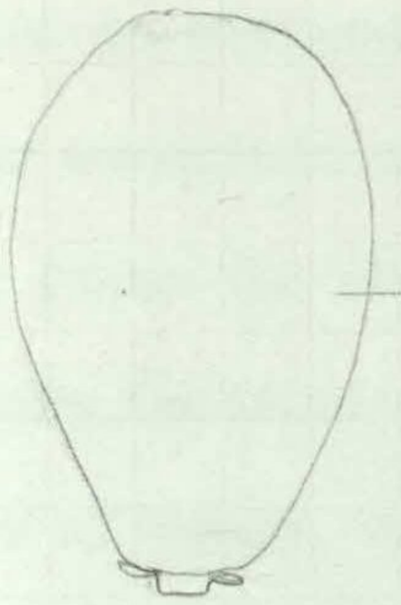
A,B,E & F INDEHISCENT, SINGLE-SEEDED FRUIT.

C,D,G-M SEEDS & ATTACHMENT TO FRUIT. NOTE EXTENDED HILUM, FUNICULAR-PRE-RAPHE ARIL WHICH ENWRAPS AND ADHERES TO TESTAL O.E.

N SEED-COAT ANATOMY. NOTE UNUSUAL TESTAL O.E. THICKENING AERENCHYMATOUS TESTAL MESOPHYLL, EIGHT-LAYERED AND 'CROSS-PLY' EXOTEGMEN.

# WALSURA PINNATA

LATERAL VIEW FRUIT



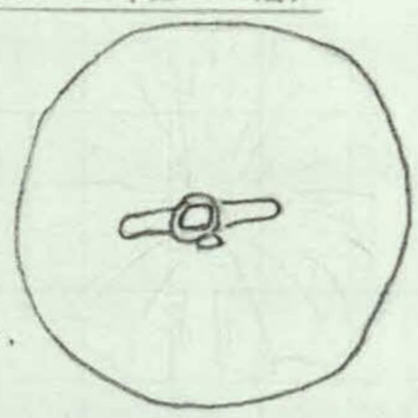
A.

FRUIT T.S.

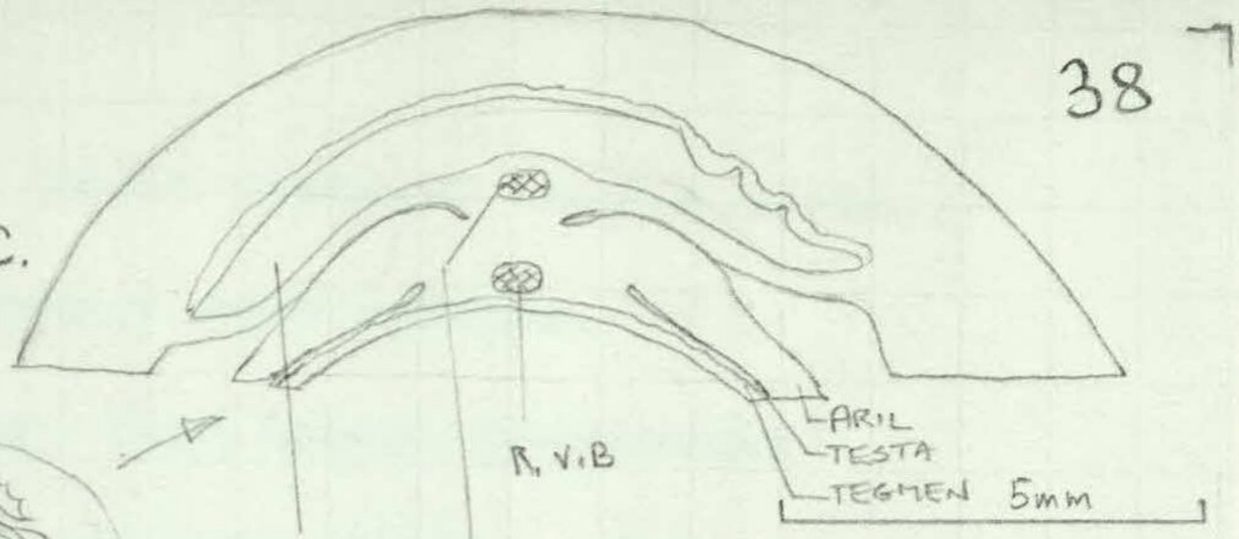


B.

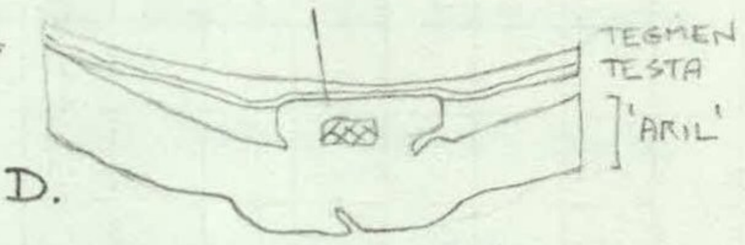
FRUIT PLAN VIEW

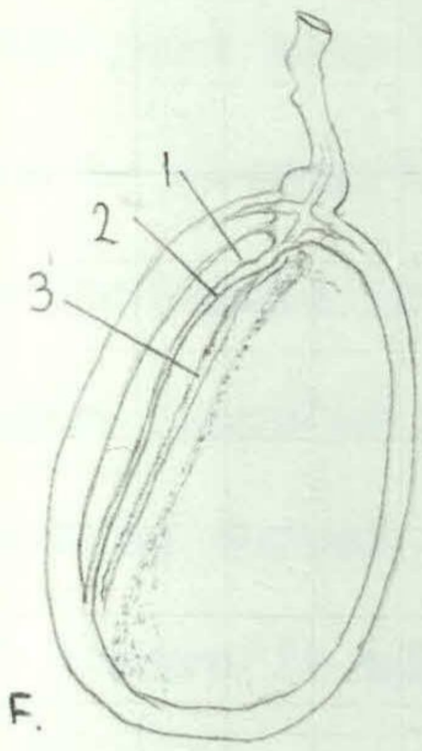


E.




TISSUE PLANS

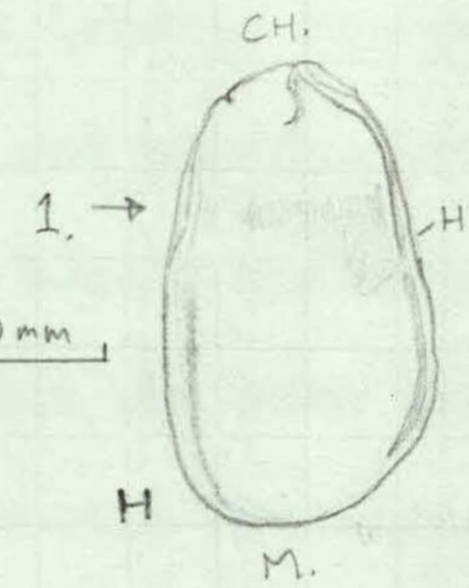


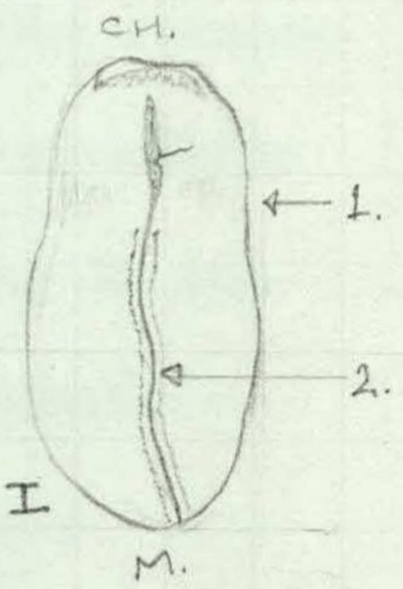

10 mm

FRUIT L.S SEED REMOVED

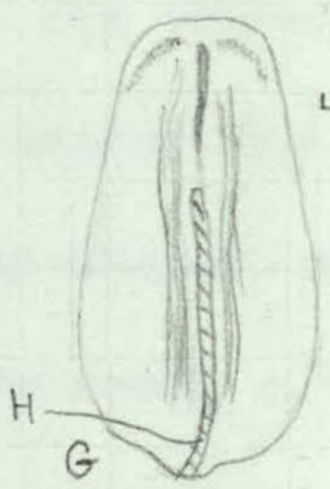
LATERAL VIEW SEED




DORSAL VIEW SEED.

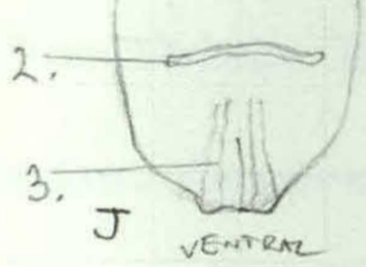



VENTRAL VIEW SEED

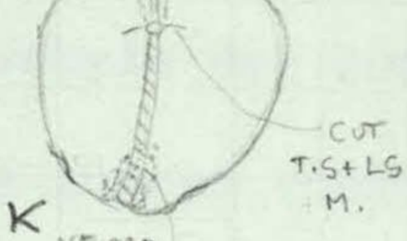


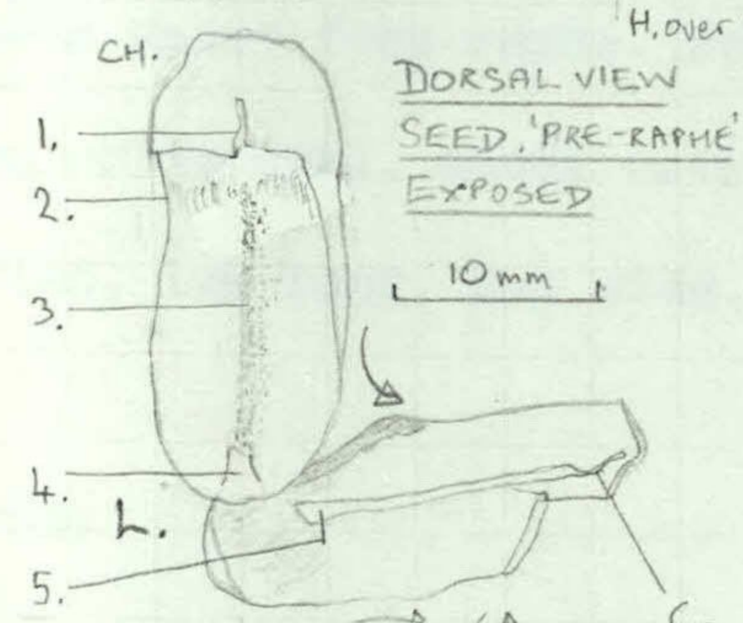

10 mm

SEED. CHALAZAL END




MICROPYLAR END

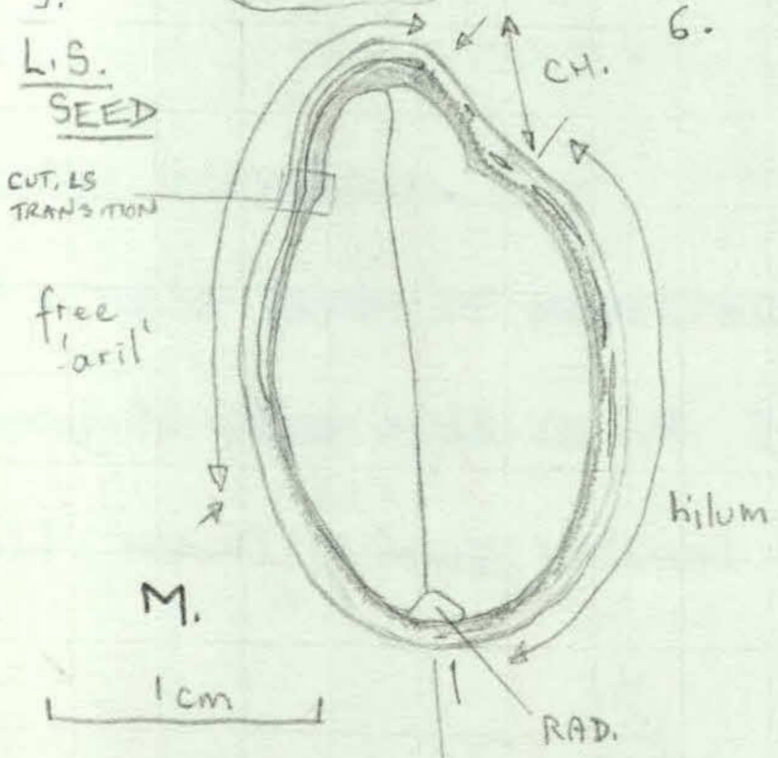


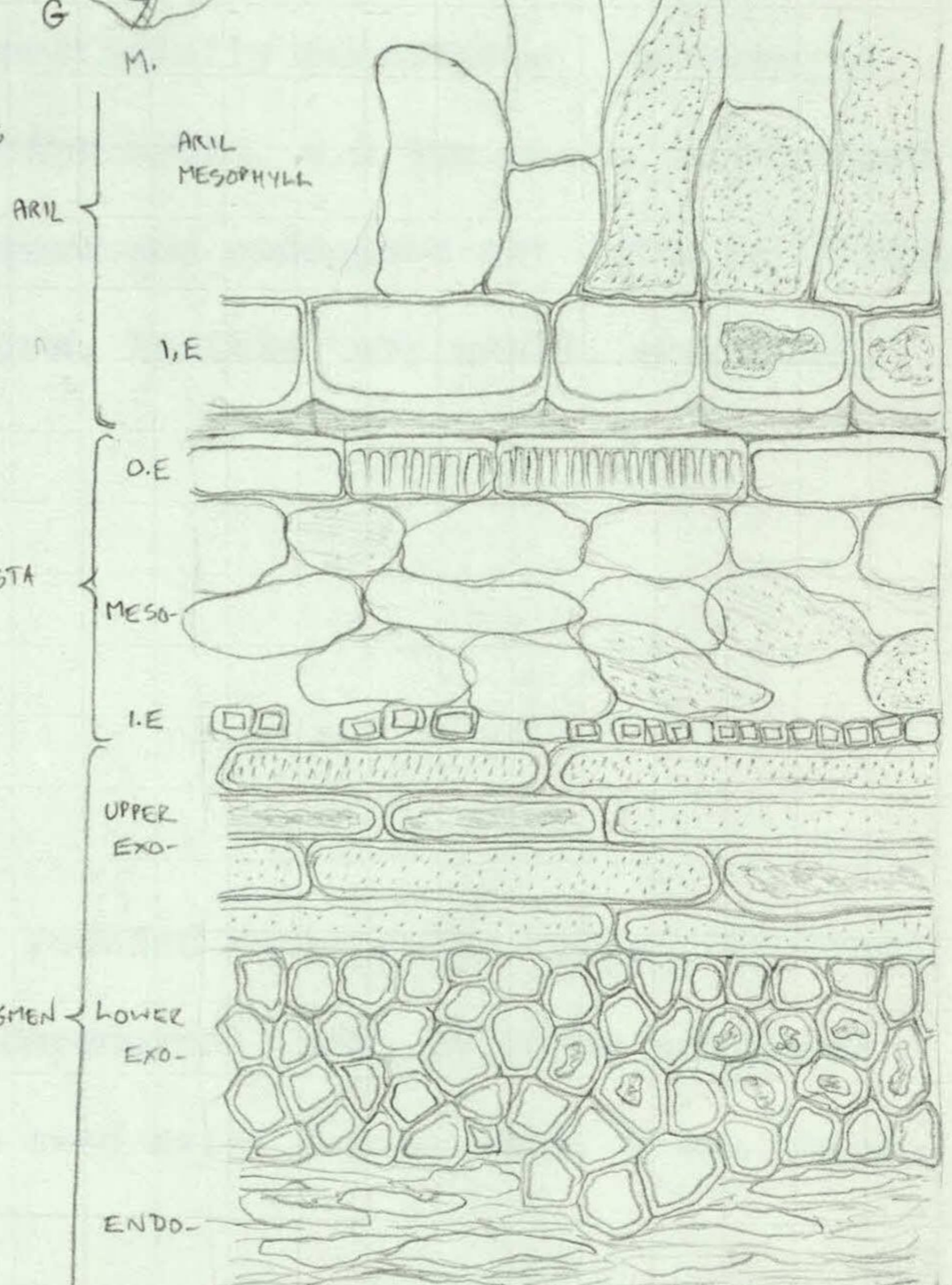

DORSAL VIEW SEED, 'PRE-RAPHE' EXPOSED

10 mm

L.S. SEED




L.S. INTEGUMENTS



seed (pendulous) of the fertile locule. Fruit vascular bundle axile, indurate, impressing a furrow in the ventral seed surface.

Seed obovoid to ellipsoid, to 22mm long, 15mm broad. Completely enveloped in succulent white raphe-aril, c. 0.5mm thick, edges only overlapping (near the chalaza) slightly.

Raphe extends ventrally from chalaza (basal pole of seed) to micropyle (apical pole of seed), the narrow hilum tapering from 2mm wide at main vascular port near micropyle to 0.3mm near chalaza, extending from chalaza to micropyle (to 28mm long), largely sunk in lower half into the furrow impressed in seed by columella vascular bundle. Pre-raphe extends from main vascular port of hilum to micropyle and apparently beyond for 7-10mm into dorsal area of seed, its vascular bundle continuing in the 'aril' (where it adheres to the testa) for about the same distance towards the chalaza. Chalaza cup-shaped to shortly cylindrical, constricting the basal end of the seed, c.4.5mm long, 5.5mm wide, wall c.0.75mm thick. Micropyle not superficially detectable, obscured by pre-raphe. Seed-coat glossy chestnut brown, c.0.3mm thick, not ridged or furrowed apart from raphe. Perisperm and endosperm not detected. Embryo of two collateral, equal cotyledons. Radicle very small, obconical, exserted, 1mm long, 2mm wide.

ANATOMY

TESTA

Cuticle: very thin.

O.E. single layer of prostrate, rounded rectangular cells, 18(-27um) high and 42-70um wide in LS. In paradermal view, extended polygonal (c.4:1), usually longitudinal to seed axis. O.p.w. thin, 3-4um thick,

medium brown. Anticlinal walls with prominent radial thickenings c.2.5um wide in LS, lumina with colourless, sparse cytoplasmic contents.

Mesophyll 2 to 7 layers of ± aerenchymatous, prostrate ellipsoid cells, 21-28um high and 35-41um wide. Walls deep brown, rather thick (to 2um). Lumina with deep brown finely granular contents, sometimes absent. Often damaged by crushing.

I.E. single layer of small, sub-cuboidal, colourless cells, each c.8(-14um) in diam. and usually containing a single prismatic crystal of slightly smaller dimensions.

TEGMEN

Exotegmen of 8-10 layers of fibrous cells in two distinct zones. The upper orientated longitudinally, the lower transversely. Each zone of 4-5 layers of fibres of similar proportions. Cells of ± uniform dimensions, averaging 196um long, 10-17um width and height in TS. Walls straw brown, irregular, 2-4um thick, with simple, sometimes slightly slitted pits. Lumina large colourless or with thin brown contents.

Endotegmen largely crushed to an amorphous dull brown layer 28-49um thick; remains of large prostrate, long rectangular cells (TS and LS) detectable.

Heynea trijuga Roxb. ex Sims

This description based on Pennington 7877 and 7927.

Collector's notes: 'Fruit in drooping axillary panicles to 2' long, bright and shiny pink pericarp' (7877); Capsule bright, pinkish-red and shiny. Green seed surrounded by a white aril'(7927).

PLATE 39

HEYNEA TRIJUGA

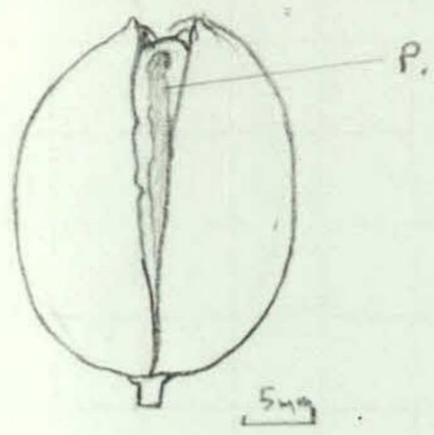
A-C FRUITS. NOTE SINGLE-SEEDED AND DEHISCENT.

D-H SEEDS. NOTE ELONGATED HILUM AND ALL-ENVELOPING, FUNICULAR PRE-RAPHE ARIL (cf. WALSURA PINNATA- PLATE 38).

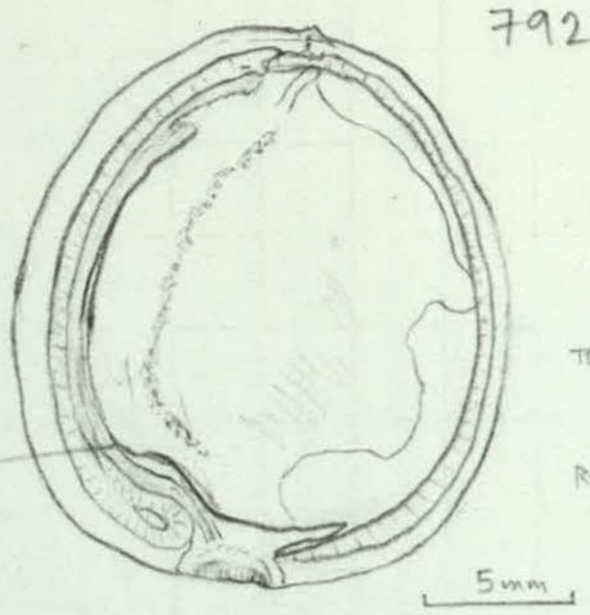
NOTE VARIATION IN EMBRYO ORIENTATION.

# HEYNEA TRIJUGA

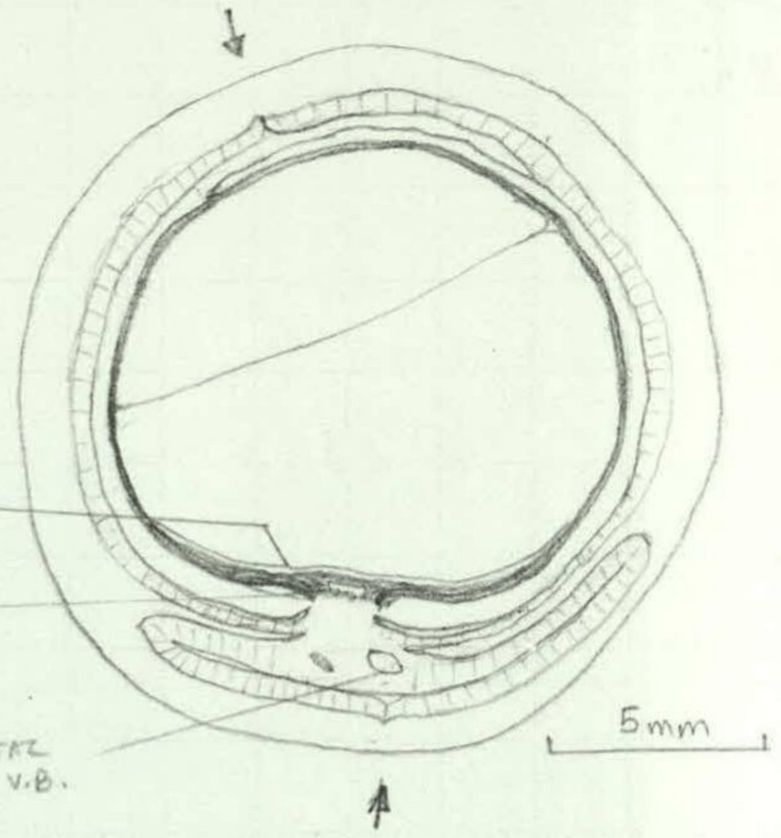
A. 7877
Fruit. Lateral view.



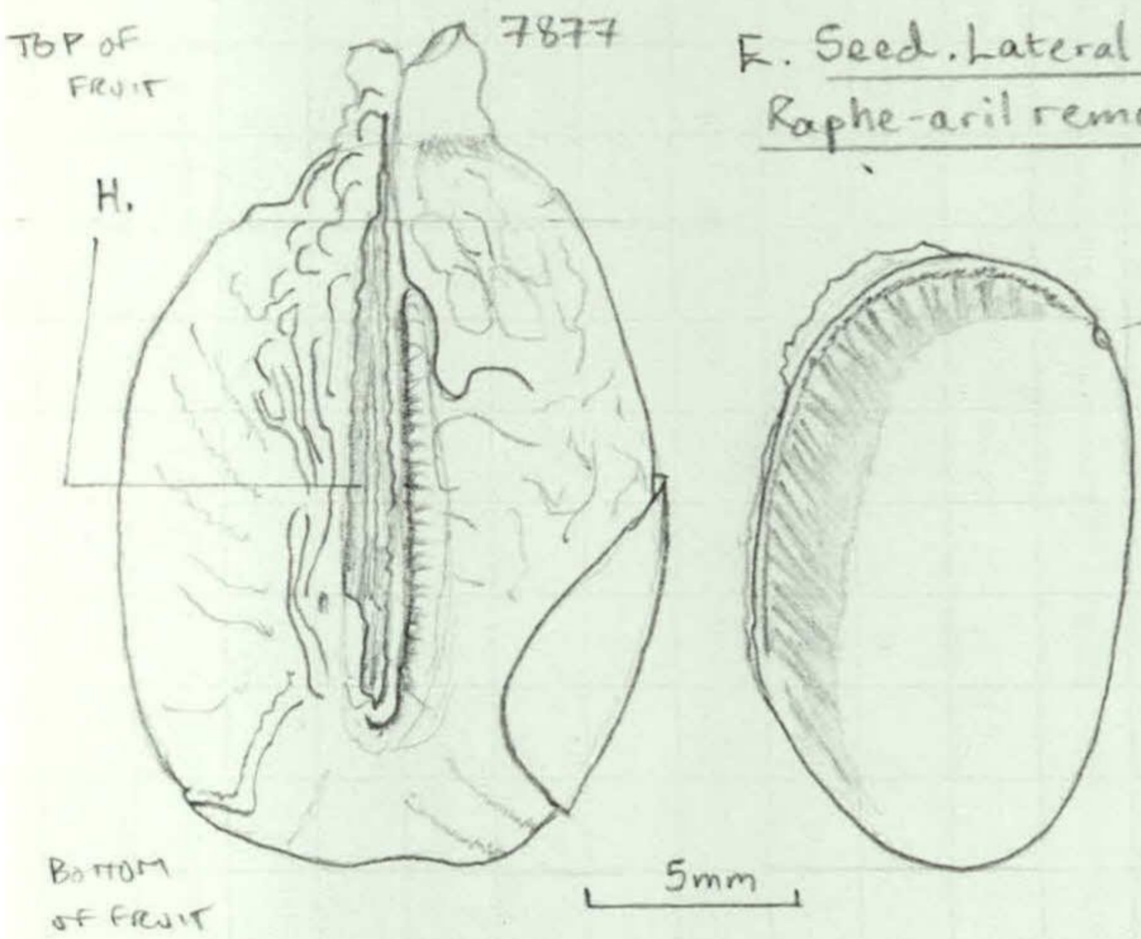

B. Fruit. Median Section through placenta
7927




C.
Fruit. T.S. (c. equatorial)
Sutures arrowed 7927



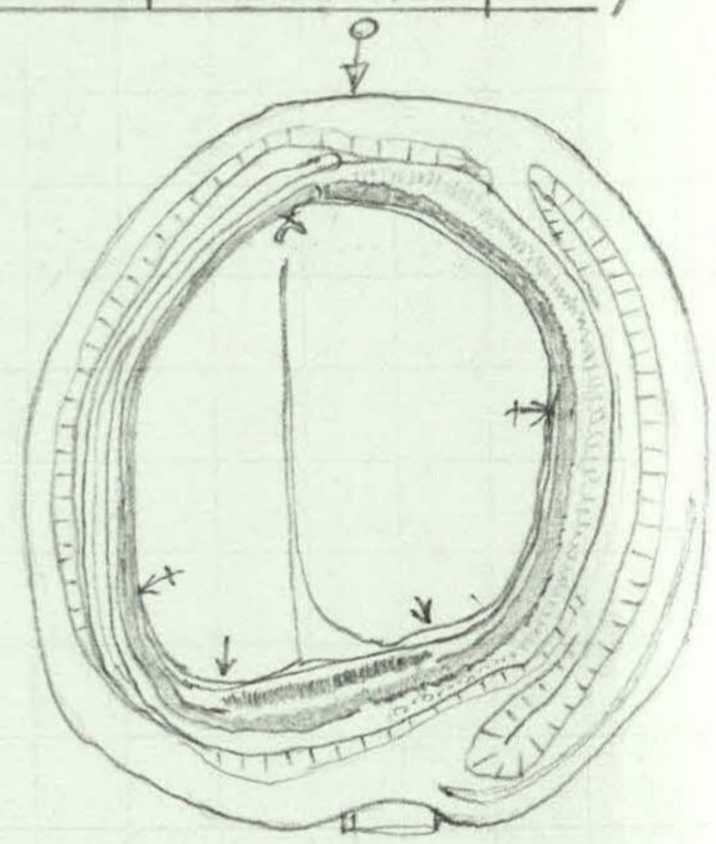

D. Seed. Ventral View
7877



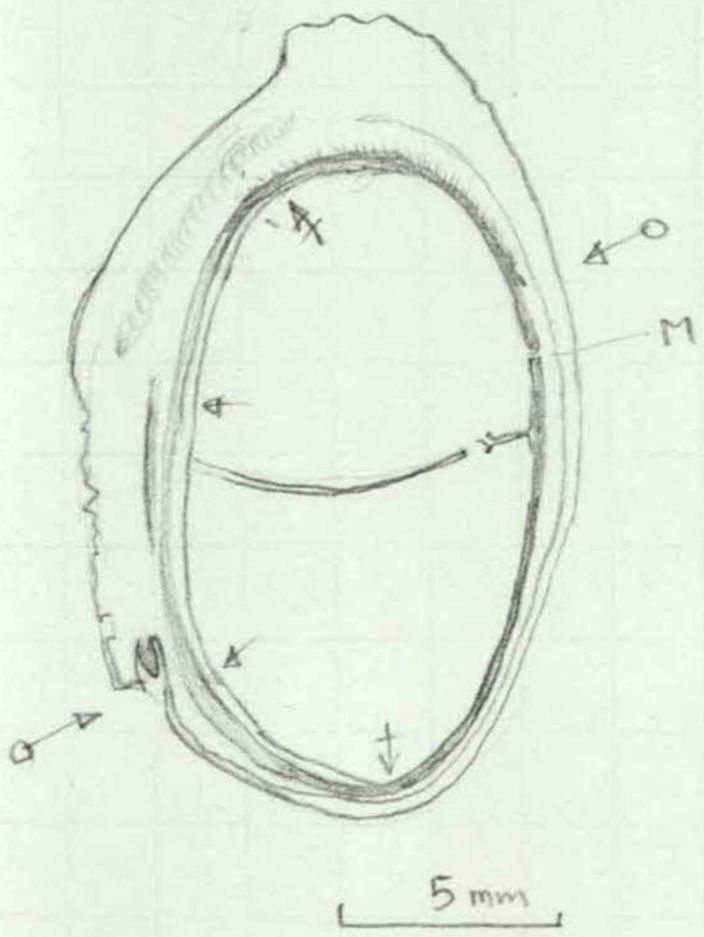

E. Seed. Lateral View
Raphe-aril removed.
7877




F. (reverse of B.) 7927
Fruit & Seed. Sub-Median L.S.
(arrows explained in caption)




G. L.S. SEED. 7877
SHOWING A VARIATION (cf. F.)
IN EMBRYO & CH.: M. ORIENTATION




H. ABERRANT GEMINATE SEEDS (7877)

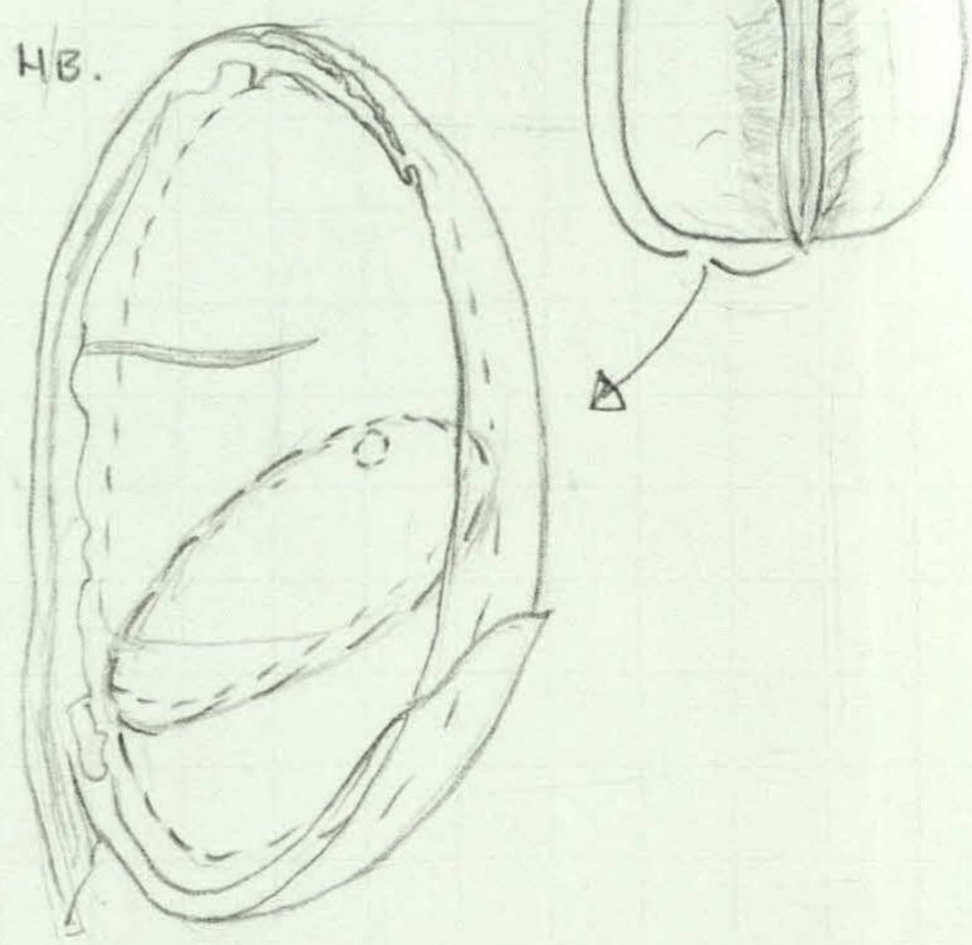


PLATE 40

HEYNEA TRIJUGA

A & B VARIATION IN THE COLUMNAR TESTAL O.E. NOTE LINEA LUCIDA.

C SEED-COAT AND ARIL ANATOMY.

NOTE AERENCHYMATOUS TESTAL MESOPHYLL &
LACK OF TESTAL C.E. CRYSTALS.

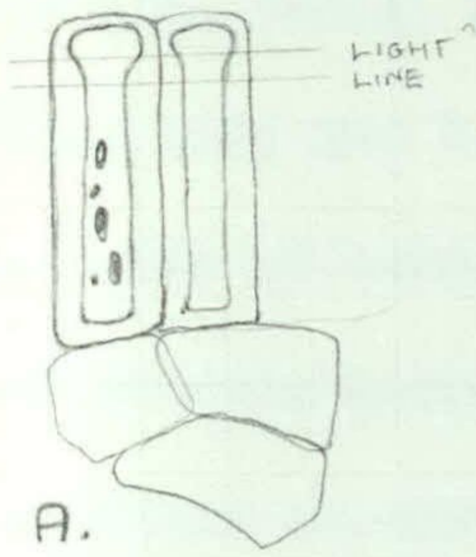
TEGMEN WITH VERY WEAKLY DEVELOPED FIBRES,
WHICH ARE ONLY INTERMITTENTLY PRESENT.

NOTE VASCULARIZED TEGMEN.

HEYNEA TRIJUGA

L.S. SEEDCOAT - near chalaza

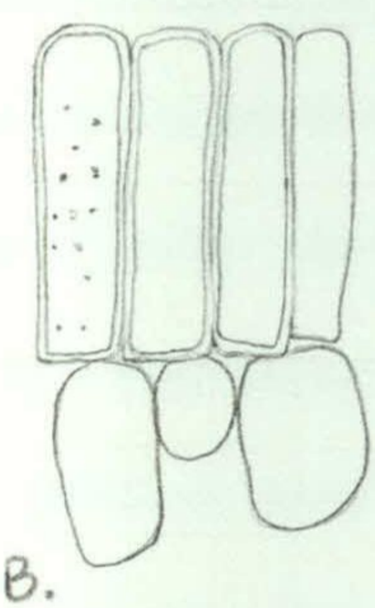
L.S. 7927



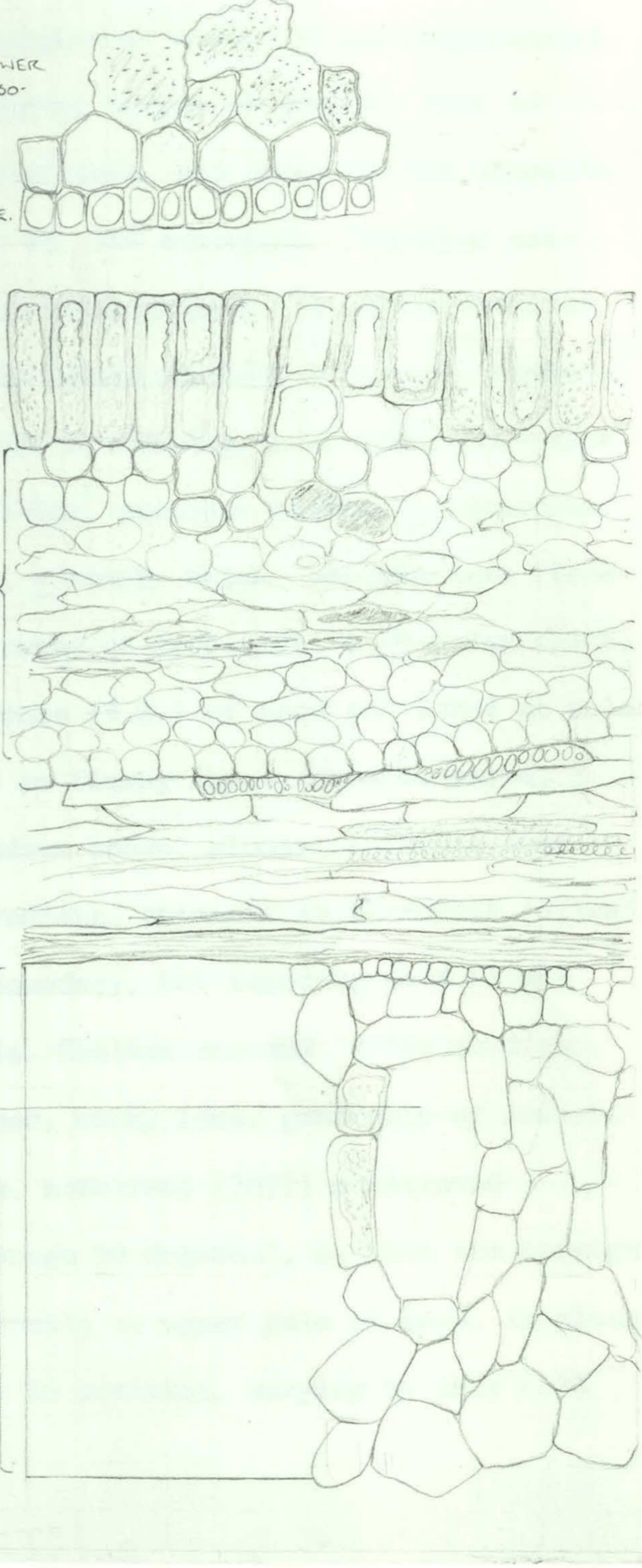

A.

VARIATION IN TESTAL O.E.

L.S. nr. micropyle



B.




LACUNAE
- OLEORESIN CAVITY?

50 um

C.

GROSS MORPHOLOGY

Fruits prolate, glabrous, 15-19mm diam., 17-20mm long, 2 opposite, low longitudinal ridges to 1.5mm, calyx persistent. Pericarp c.1.2mm thick, leathery, the endocarp woody c.0.4mm thick. Dehiscing from apex by two valves (at ridges), one suture to fertile locule, one to infertile locule pressed to one side but with own endocarp.

Seed single (rarely two), axile and pendulous in placentation, c.20mm long, 9-12mm radial width, 10-13mm tangential width. Hilum longitudinal, c.18-21mm long and 1-1.5mm broad, running length of adaxial face to within c.3mm of lower (chalazal) end of seed, and above to the opposite pole or shortly beyond, to or almost to, the micropyle. Vascular port from placenta in uppermost 7mm (where hilum raised), no major vascular connection across lower part of hilum (where surface furrowed). Raphe extends under hilum from vascular port to chalaza, c.11-12mm, pre-raphe from vascular port to micropyle, c.4-9mm, vascular bundles + discrete, not quite exserted from testa. Thin, ± evenly thick, vascularized (from raphe) fleshy layer extending from raphe on each side. 0.25-0.7mm thick, each encompassing 1/2-3/4 circumference (T.S.) of seed and lobed at polar ends. Entire seed tightly enveloped in fleshy layer, in some parts, 3 layers thick. Testa very pale to medium brown, glossy, thickest near hilum (0.2mm) where raised ridges radiate, thinnest at micropyle (0.1mm). Tegmen about as thick at chalazal boundary, but tapering to a flimsy pellicle, not reaching the micropyle. Chalaza rounded, 6-8mm in diam., plainly detectable by dark, thickened, corky lens; generally at lowest pole of seed, but position variable, sometimes (7877) positioned ventrally near equator (rotated through 90 degrees), so that the straight embryo, normally directed longitudinally to upper pole of seed, is almost transverse. Micropyle more constant in position, varying by only c.45

degrees. Embryo of two subequal collateral or slightly superposed cotyledons, without endosperm, green when fresh, with small (0.8mm long, 1.2mm wide) glabrous radicle just included (covered by c.0.5mm cotyledon) at micropylar end. Surface minutely pitted (presumably due to lacunae: see below).

ANATOMY

TESTA

Cuticle thin, yellow, uneven, 0.25-3mm thick at transition with chalaza.

O.E. 1 layer of strongly columnar cells with thick yellow brown walls. Anticlinal walls 1.5-2um, o.p.w. 6-7um thick. Lumina constricted slightly at apex (slightly dumb-bell shaped). Weak linea lucida. Filled usually with grey cytoplasmic, occasionally with orange globules. Cells 50-58um high, 9-13(-18)um wide. Frequently, individual columnar cells have undergone 2 periclinal divisions giving 3 stacked, shortly columnar cells.

Sub-dermal layer 0-2 layers thick: upper layers of mesophyll sometimes develop wall thickness and colouration of O.E.

Mesophyll 10-15 layers thick. Near chalaza, cells isodiametric, almost spherical or shortly radially extended, width c.27um, walls colourless, 0.9mm thick but becoming shortly prostrate elliptic (c.35um wide, 17um high) near micropyle, where aerenchymatous, cells commonly with pronounced intercellular arms; airspaces. Lumina with thin, grey-brown contents. Lower part of testa (especially near chalaza, not at micropyle) with abundant vascular elements, bundles not or hardly intermixing with mesophyll above or below. Associated fibrous cells remarkably similar to exotegmic pattern.

I.E. single layer of isodiametric (especially near chalaza) sub-cuboidal to prostrate elliptic or rectangular cells 10-15um high, 12-35um wide. Without endocrystals, lumina colourless, some protoplasm. Walls 1.75um thick.

TEGMEN

Essentially redundant. At transition zone 10-12 layers thick, but 350um towards micropyle, reduced by crushing to 4 layers. Within 3-5mm of transition zone, crushed completely to a layer 15um thick. Cells not differentiated into exo- and endotegmen; thickened fibrous cells in uppermost layer absent or only sporadically expressed as idioblasts. Cells prostrate, extended polygonal, 20um high, 42-64um wide, walls c.1.25um thick, lumina with sparse finely granular, pale grey contents.

PERISPERM/ENDOSPERM

Remnants detected as single layer beneath tegmen at transition zone.

EMBRYO

O.E. single layer of very small cuboidal cells 8um across, dense grey protoplasm.

Mesophyll of larger, isodiametric (to shortly randomly extended), 5-6-sided, rounded polygonal cells, 30-50um wide with thin yellow walls (0.5um thick) and thin grey-granular protoplasm. Non-collenchymatous corners. Numerous radially elongate lacunae in uppermost part, commonly 40um wide, 80um high: latex canals?

FLESHY LAYER (TS)

Cuticle 0.75um thick, even.

O.E. single layer of (sub-cuboidal to) very shortly columnar cells with thick, straw-coloured walls, o.p.w. 2um thick, remaining walls slightly thinner, to c. 1.75um thick. Cells 8.5-12um wide, 13.5-28um high. In paradermal view, cells longitudinally (w.r.t. raphe; transversely w.r.t.

Seed) extended (5:1), less frequently isodiametric, polygonal cells. Length (50-) 84um, width 25(-70um).

Sub-dermal layer barely discrete from mesophyll: large rounded polygonal cells, to 35um wide, 35um high, but sub-isodiametric and thick-walled to 1.25um.

Mesophyll of large, thin-walled, prostrate elliptic cells, c.70um wide, 40um high, walls c.0.5um thick, very fragile and usually badly crushed on sectioning.

Lepidotrichilia volkensii (Harms)J.F.Leroy

This description based on Cheek et al. 1675

Collector's notes: 'Fruits indehiscent, yellow under rusty stellate hairs, thin skinned, juicy, sweet. Eaten by birds (according to S. Mathingi)'.

GROSS MORPHOLOGY

Mature fruits bi-lobed and biloculate (probably by abortion from 3 locules), each with a single seed. Fruits broader than long, 7.5-8.5mm long, 9-11.5mm x 6.5-8mm broad, pedicel with persistent calyx, stellately hairy, c.3.5mm long.

Outer surface without rostrum or stipe, densely stellately hairy.

Pericarp 0.6-1.5mm thick, lightly vascularized, fleshy; endocarp hardly differentiated.

Seeds bun-shaped (rounded hemispherical) by mutual compression, 6.5-7mm long, c.4.5mm radial width, c.6mm tangential width, placentation pendulous and axile, hilum irregular, transverse, c.2mm wide, c.1mm long. Seed-coat dark, grey brown, sub-glossy. Micropyle at distal end (w.r.t.

PLATE 41

LEPIDOTRICHILIA VOLKENSII

(CHEEK B1508)

FLOWER AND FRUIT: FRUIT INDEHISCENT, ORANGE, COVERED WITH STELLATE HAIRS X 2.5.


41

PLATE 42

LEPIDOTRICHILIA VOLKENSII

(CHEEK 1657)

A-C FRUITS.

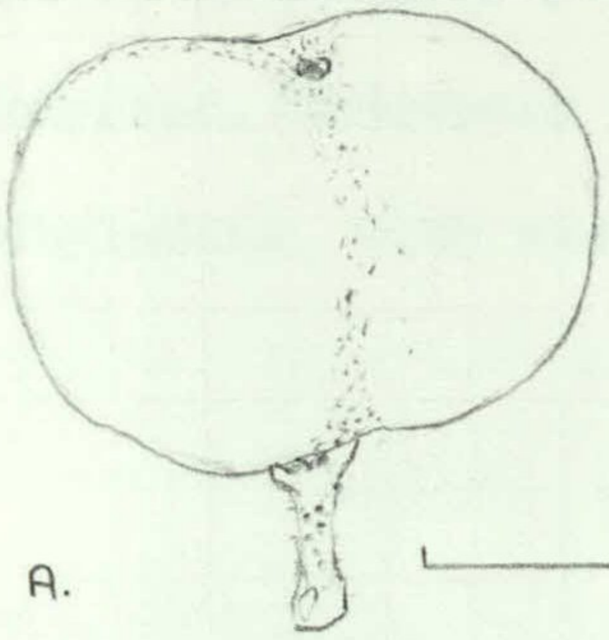
D-F SEEDS.

G-H SEED-COAT ANATOMY: NOTE UNITEGMIC, VASCULARIZED SEED-COAT:

RELATIVELY POOR IN CHARACTERS.

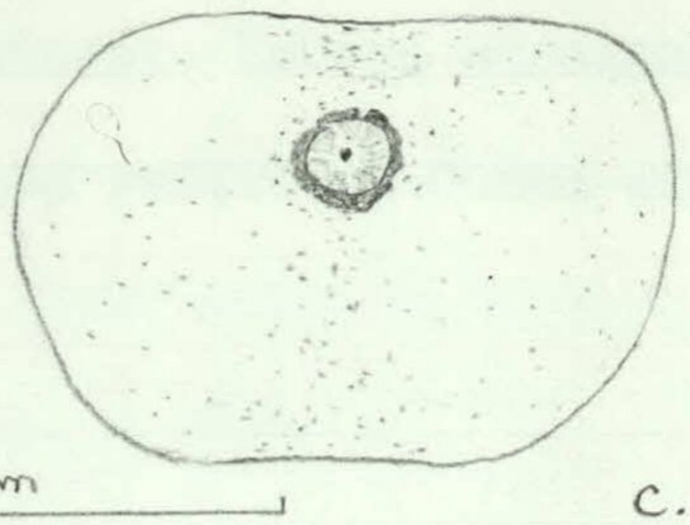
# Lepidotrichilia volkensii

FRUIT: OBLIQUE LATERAL VIEW



A.

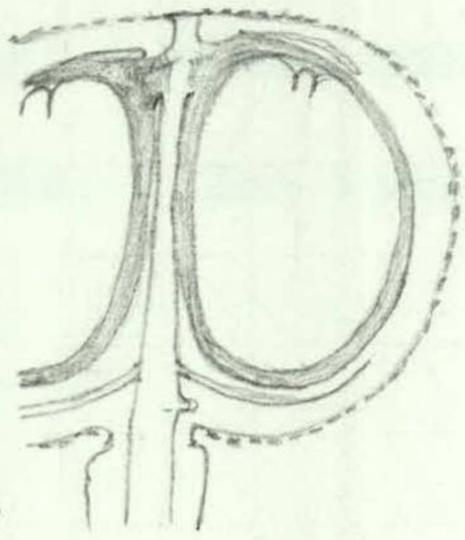
PLAN VIEW



B.

1cm

MEDIAN SECTION



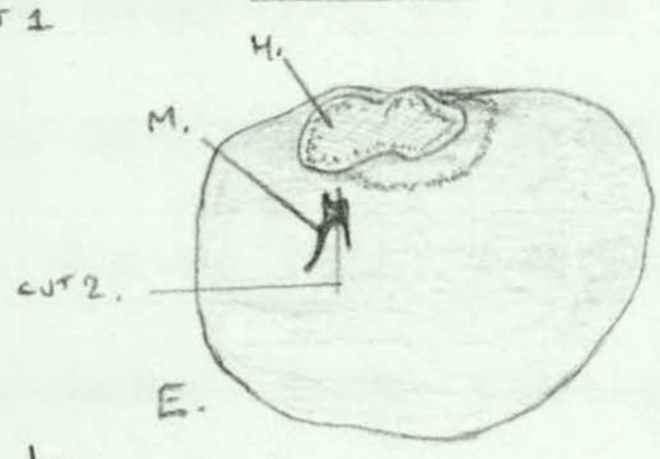
C.

SEED: LATERAL VIEW




D.

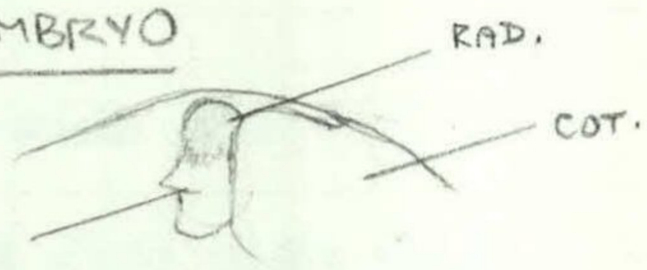
PLAN VIEW




E.

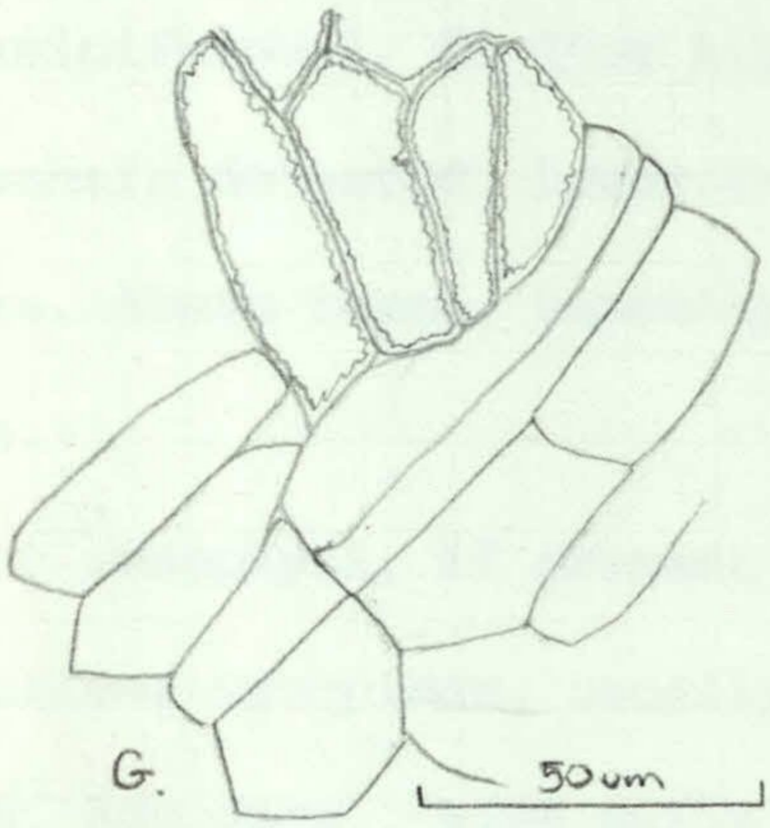
1cm

EMBRYO




F.

PARADERMAL VIEW:
O.E. SEEDCOAT

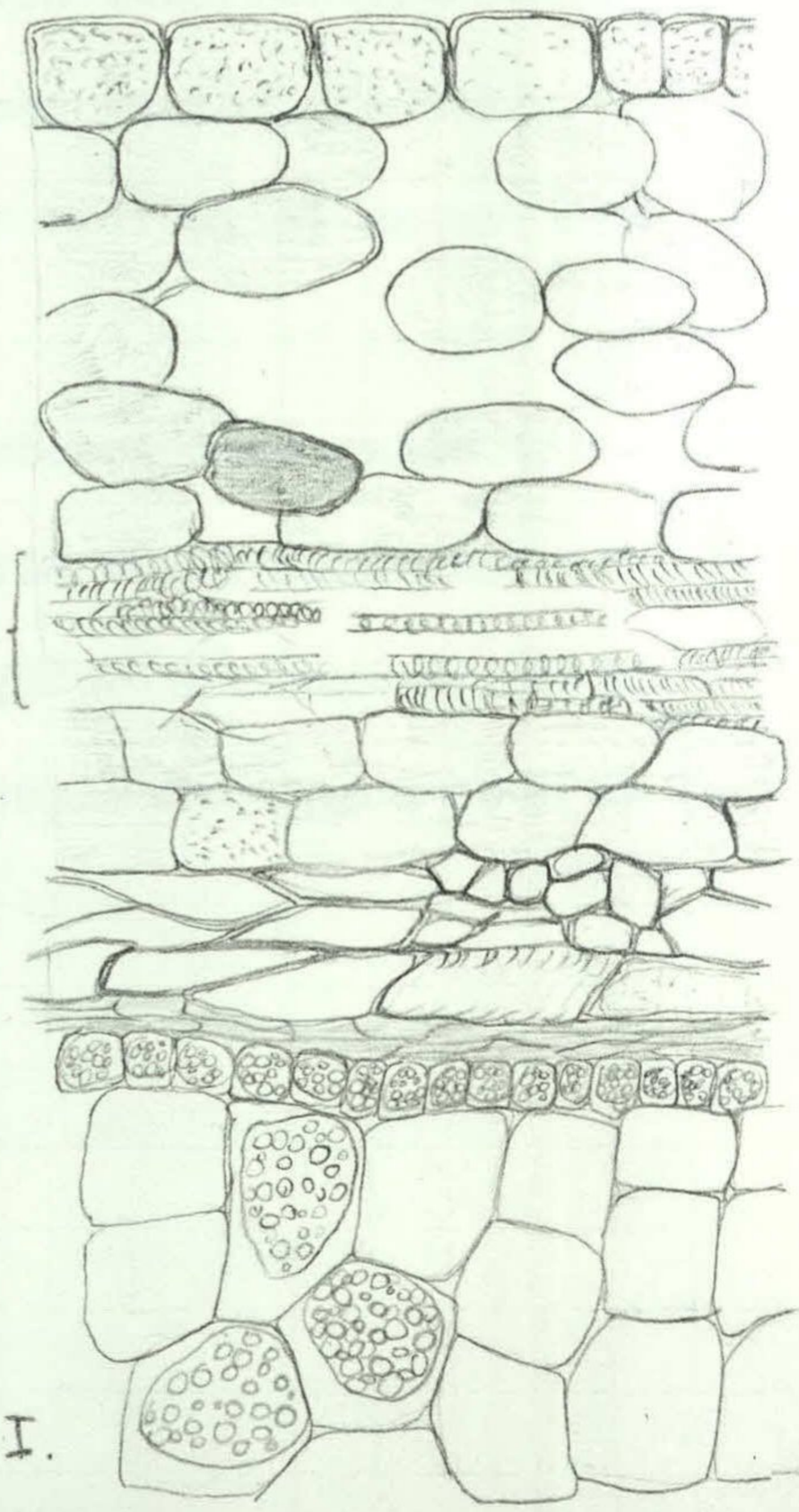


G.

50um

T.S. SEEDCOAT (COT 1)

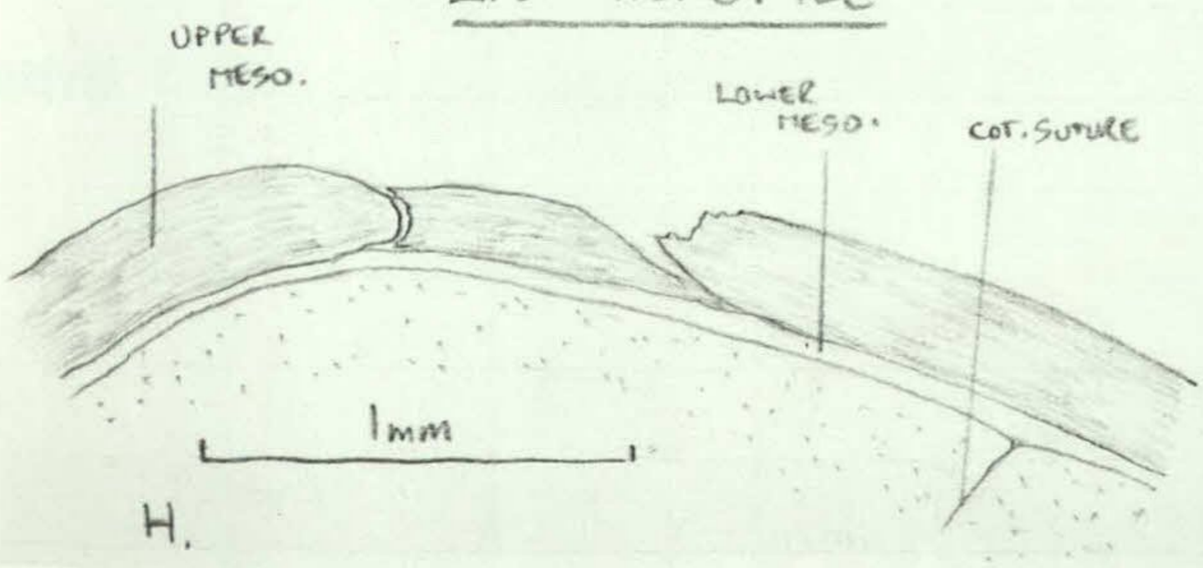
50um




I.

TISSUE PLAN:

L.S. MICROPYLE




H.

fruit), usually immediately adj. to hilum, irregular, up to 0.9mm diam.. Seed-coat apparently largely pachychalazal, c. 0.3mm (-0.75mm) thick, thinly vascularized. Endosperm ± absent. Embryo straight; 2 plano-convex, collateral cotyledons, with exserted radicle c.0.6mm wide, 1.2mm long.

ANATOMY

Seed-coat

Apparently pachychalazal all way through to micropyle.

O.E. prostrate, rounded rectangular cells 35-77(-105)um wide and 14(-23)um high, near micropyle extending to 31um wide and 25um high (L.S. and T.S.). In paradermal view, isodiametric to highly extended (to 5:1, direction random), 6-7-sided. O.p.w. thin, 1-1.5um thick, slightly convex, lumina with sparse or dense, dark, finely granular cytoplasm.

Upper mesophyll of 7-11 layers (thickest near micropyle), of spherical to prostrate shortly ellipsoid, aerenchymatous (numerous airspaces) cells with fairly thick, 0.75-1um walls and pale orange brown lumina (?tanniniferous), 21-35um high, 25-36um wide, with intercellular arms frequently detected. Lower 2-3 layers most densely packed, few air spaces. Above these, vascular layer (except near micropyle) up to 50um thick.

Lower mesophyll, if present of 1-5 layers of heterogenous cells all with colourless cytoplasm, usually densely packed, from small isodiametric cells, 6um diam., with walls 1um thick, to irregular rectangular cells 50um long, 17um high. Below, layers of crushed cells forming a zone up to 45um thick.

ENDOSPERM AND PERISPERM not detected.

EMBRYO

O.E. single layer of ± cuboidal cells, 10-14um diam., contents as below.

Mesophyll, rounded cuboidal (21-52 um diam.), to slightly (usually radially) extended (to 63um long), thin-walled (0.5um thick cells. Cytoplasm usually contracted away from walls (this prep.), with dull yellow, equilateral plastids, 3-5um in diam..

?Latex canals. Cavities, c.60um wide, c.90um high, fairly frequent in outer cotyledons.

Malleastrum gracile Leroy

This description based on Cheek et al. 2-21-3.

Collector's notes: 'Fruits pendulous, glossy pink overlaying cream. Outer pulp succulent. Seeds brown, ellipsoid'.

GROSS MORPHOLOGY

Fruits obliquely ovoid with apical nipple, 12-14mm long, 7-9mm broad; Pedicels 1-1.5mm long, singly, by abortion, on peduncles 14-20mm long. Fleshy mesocarp 0.5-1mm thick, endocarp thin, sub-parchment like. Uniloculate. Seeds glossy, medium brown, single by abortion of one ovule (persistent), ellipsoid, usually slightly transversely flattened or with 1-2 longitudinal ridges. Hilum lanceolate or narrowly elliptic, inserted equatorially or towards distal pole of fruit longitudinally above pedicel insertion, 1.25-3mm wide, 4-9mm long. Micropyle conspicuous, raised aperture, c.10mm diam., at distal end of fruit under apical nipple. Radicle sometimes exserted. Seed-coat thin (0.1-0.25mm) and leathery, largely chalazal, integuments forming only 15-20% seed-coat as an irregular ± circular area ± centred on micropyle, superficially

PLATE 43

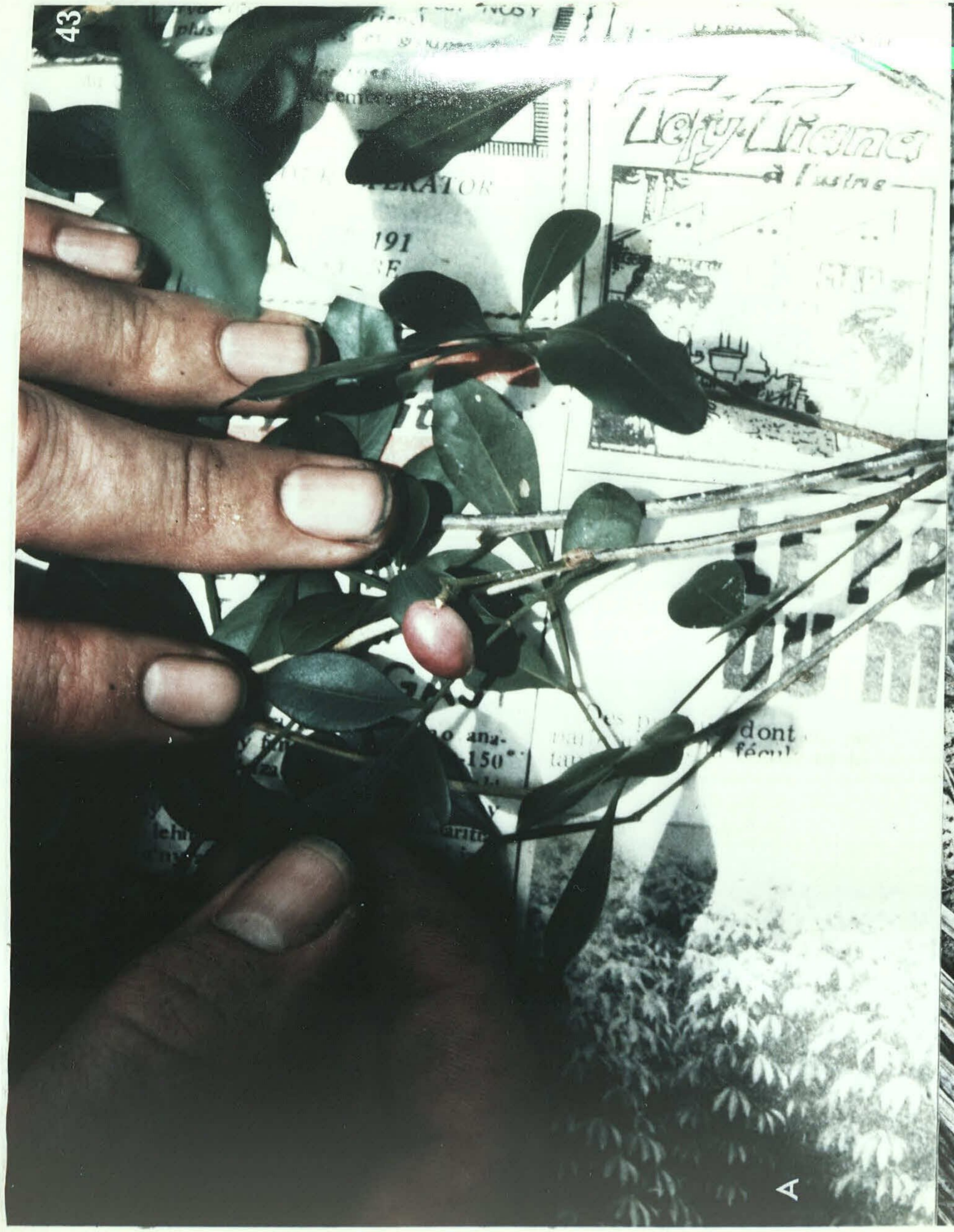
VARIATION IN MALLEASTRUM FRUITS

(ALL FLESHY AND INDEHISCENT)

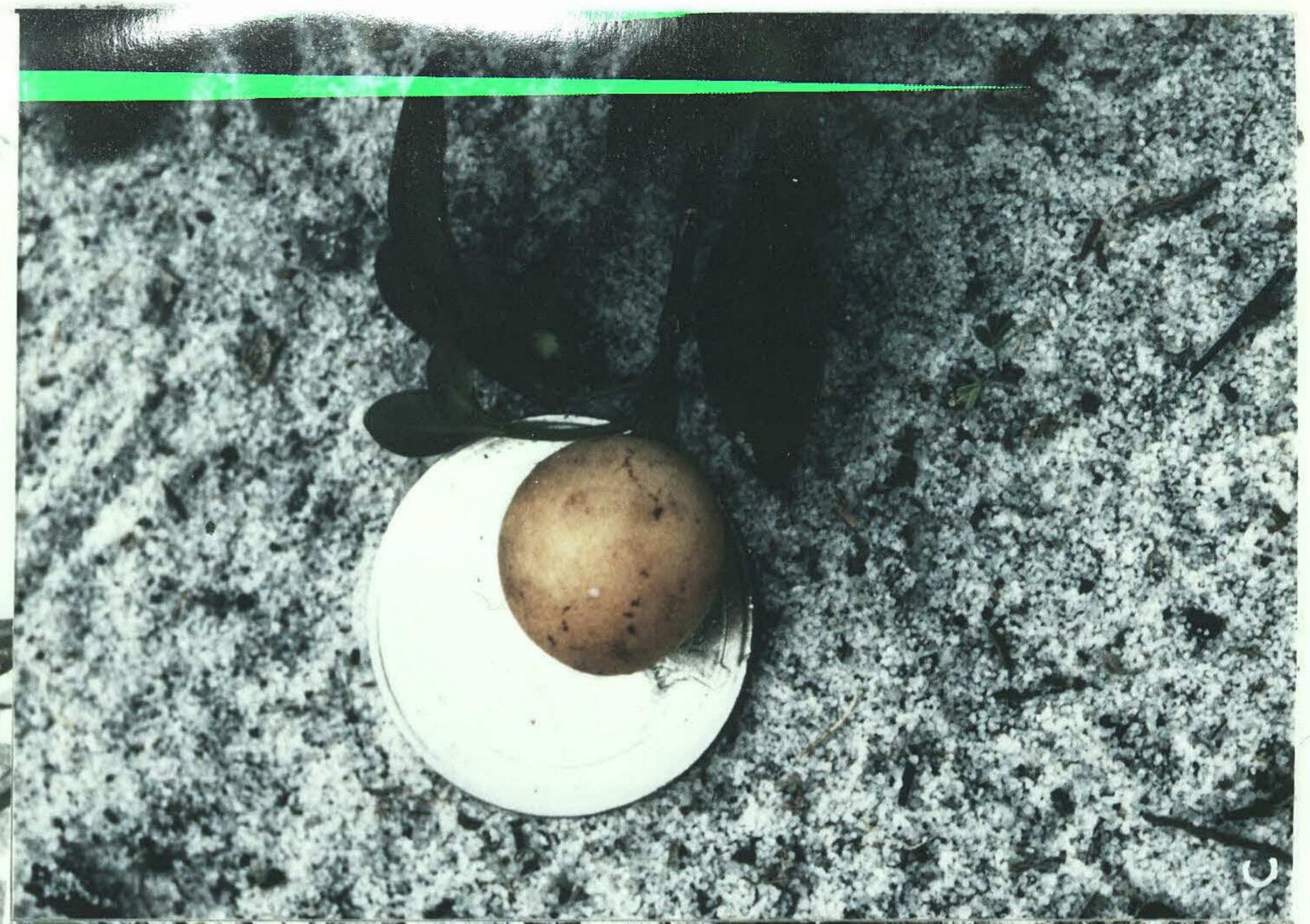
A-M. GRACILE- NOTE OBLIQUE PEDICEL INSERTION X 1.

B-M. PSAMMOPHILUM X 0.5.

C-M. MANDENENSE X 1.




A



C



B

PLATE 44

MALLEASTRUM GRACILE

A-B FRUITS.

C-E SEEDS: NOTE LARGELY PACHYCHALAZAL SEED-COAT &
ABSENCE OF FLESHY APPENDAGE.

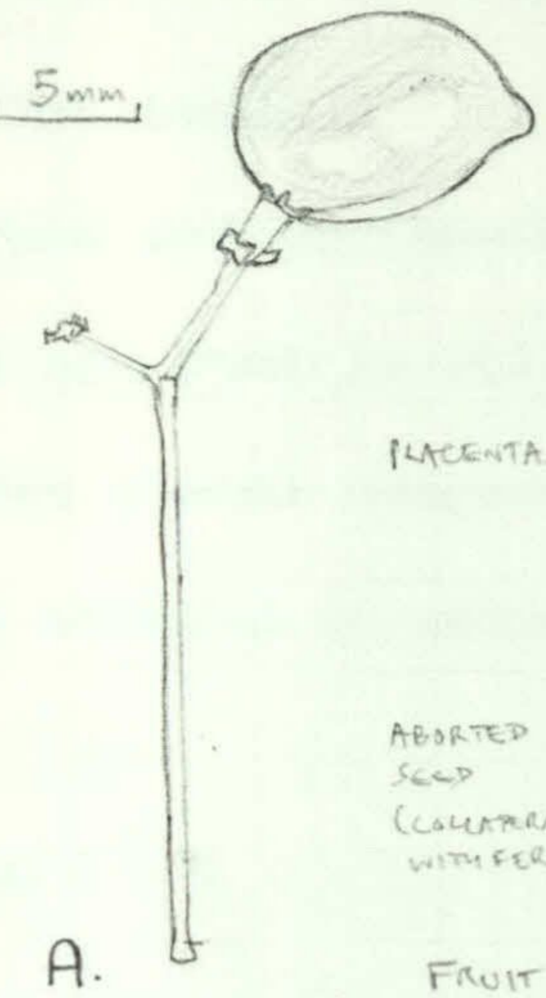
F EPICOTYLAR HAIR.

G SEED-COAT (BITEGMIC PART). NOTE AERENCHYMATOUS, SLIGHTLY
? TANNINIFEROUS TESTAL MESOPHYLL.
NOTE WEAKLY DEVELOPED TEGMEN.

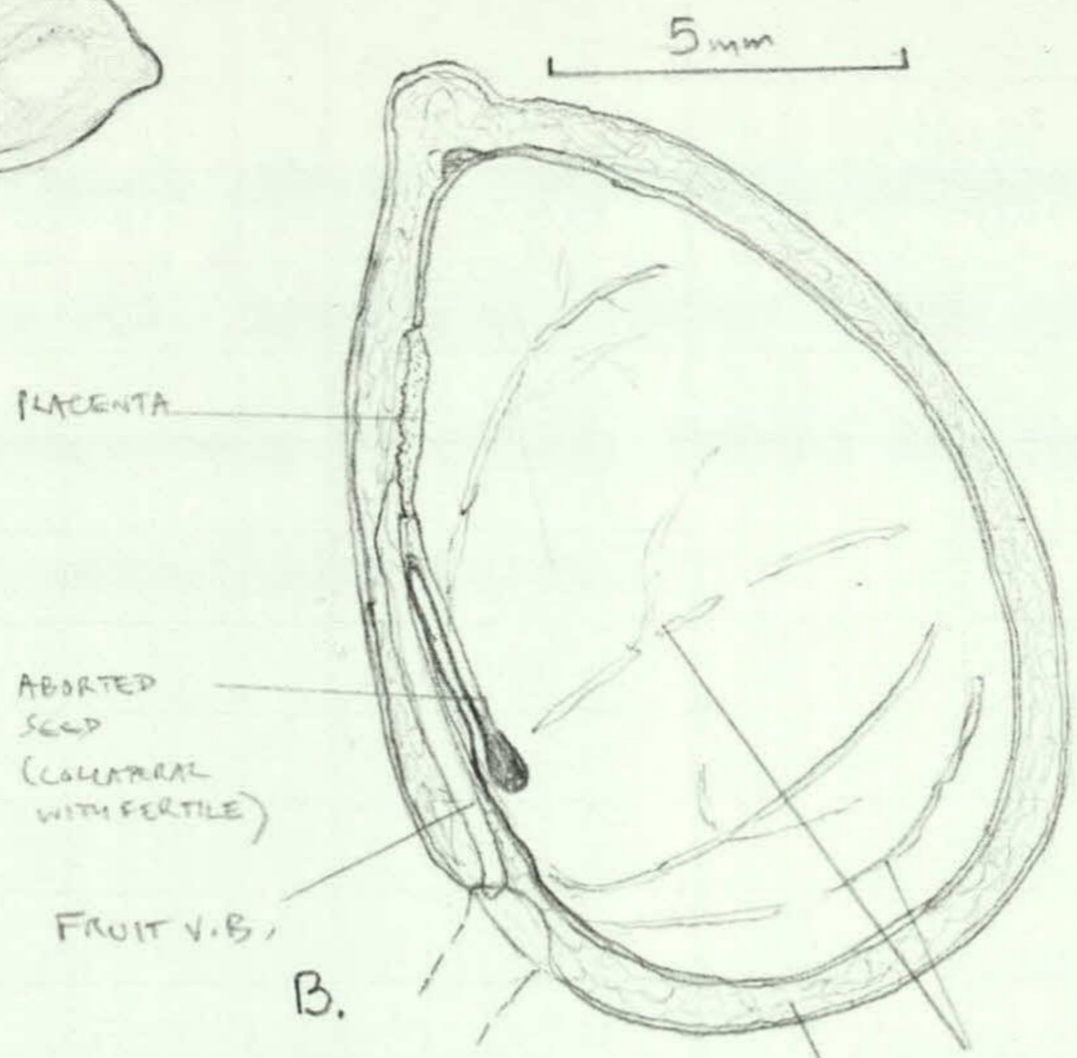
# Malleastrum gracile



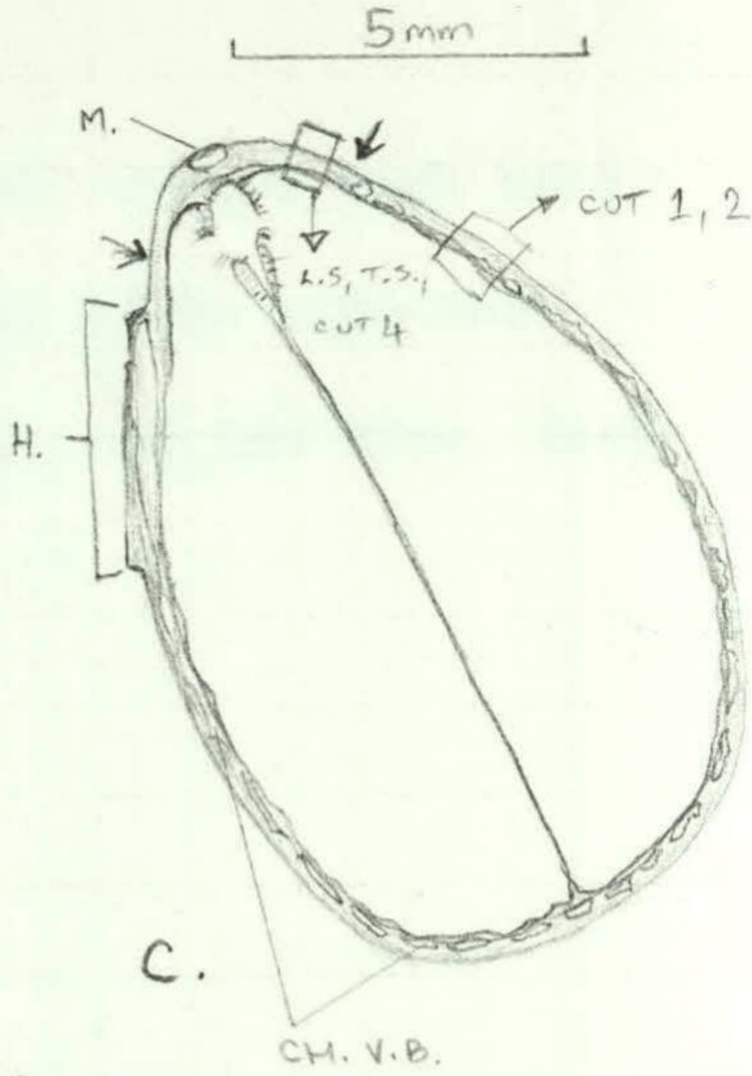
FRUITING PEDUNCLE



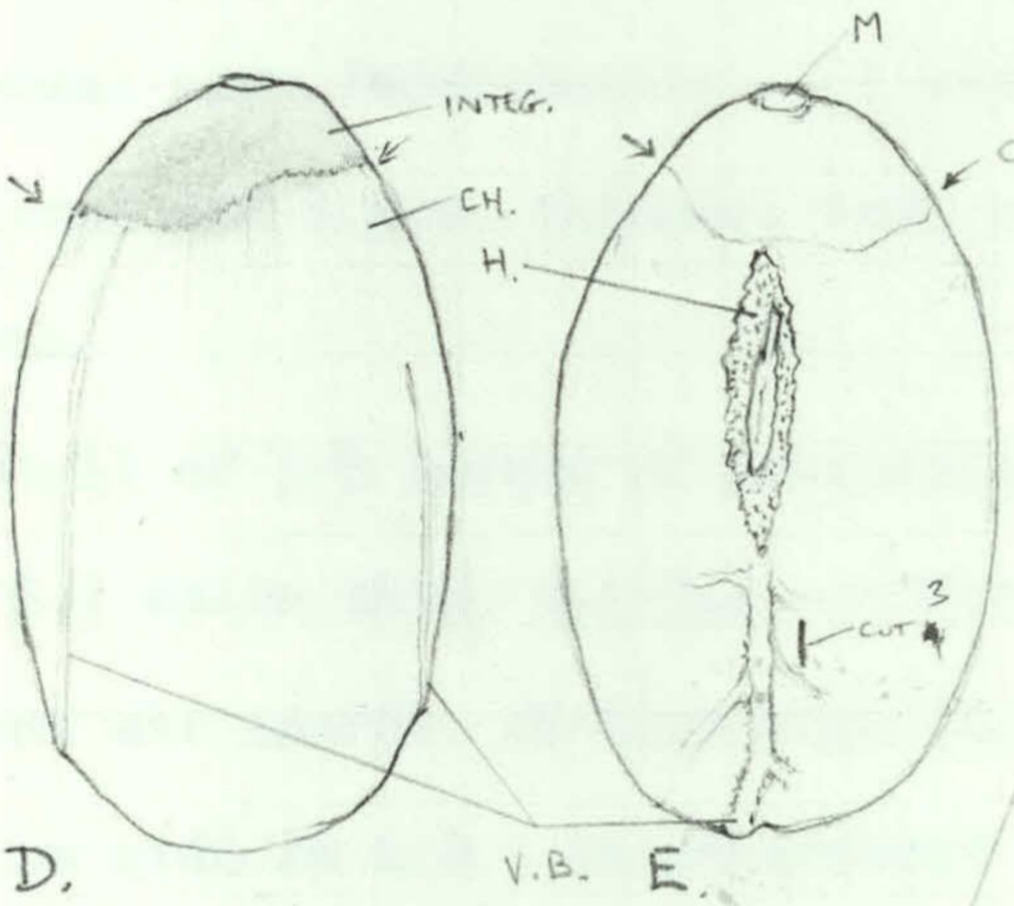

MEDIAN L.S. FRUIT
(SEED REMOVED)



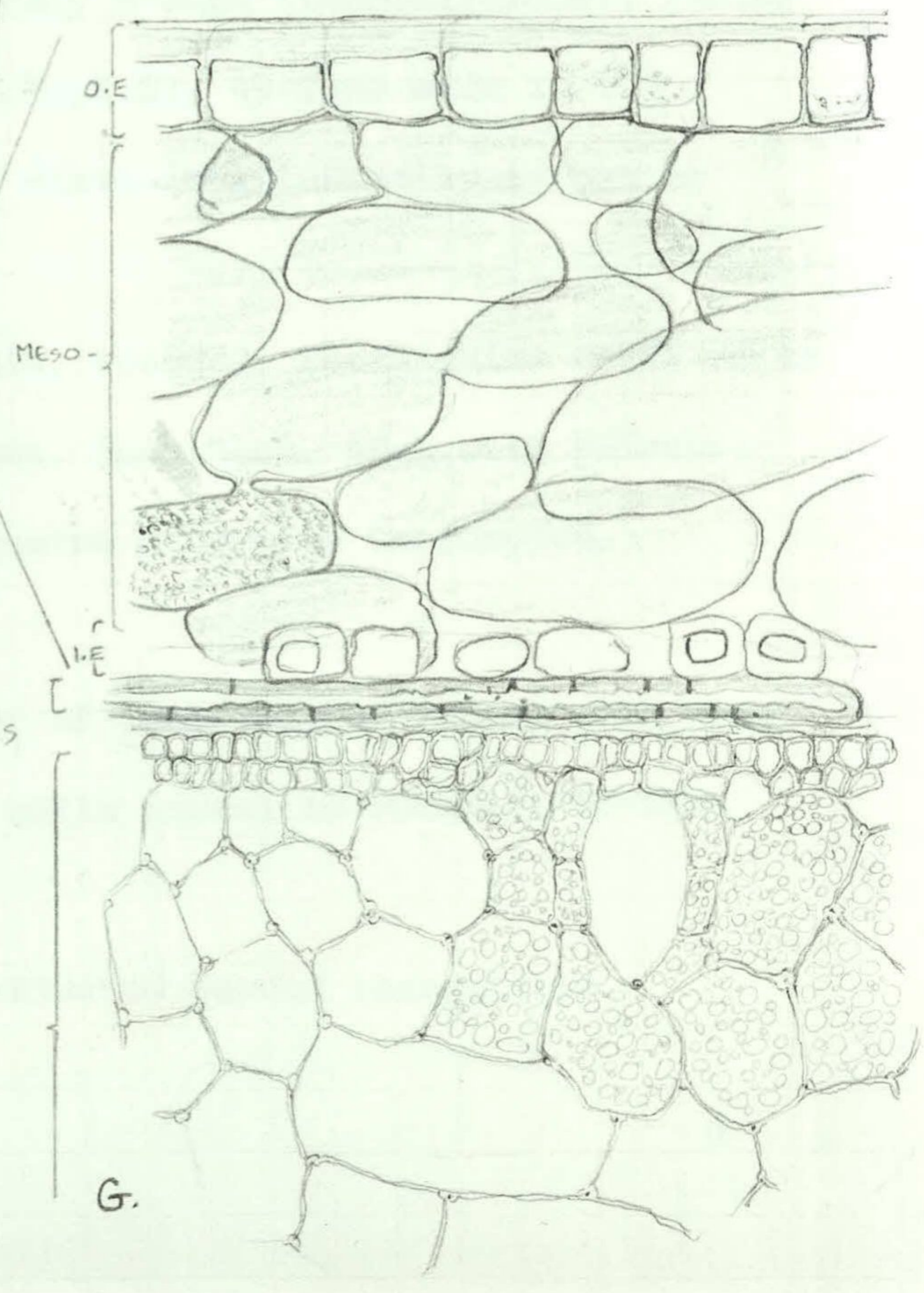

MEDIAN L.S. SEED.



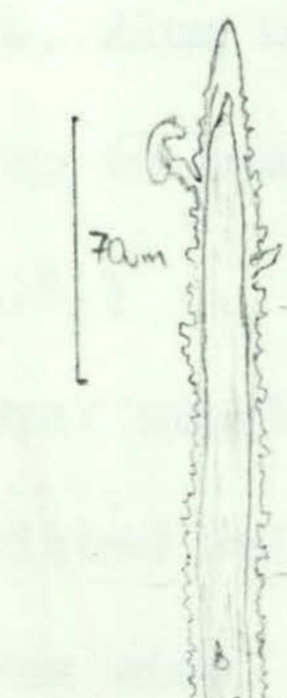

SEEDS: DORSAL & VENTRAL VIEWS




L.S. INTEGUMENTS




EPICOTYLAR HAIRS



detectable by slightly greyish colour and absence of vascular bundles, largest of which in chalaza may form longitudinal angles or ridges, up to 1 or 2 per seed.

Endosperm and perisperm absent. Cotyledons collateral, embryo with both plumule and radicle well developed, latter 1-2mm long, c.1mm wide and sometimes almost completely exserted; former 2mm long, c.0.5mm wide. Both densely covered in unicellular hairs.

ANATOMY

TESTA

Cuticle thick and even, dull cream, to 3um thick.

O.E. ± cuboidal (T.S. and L.S.), 22-35um wide, to 44um high, in paradermal view isodiametric, 5-7 sided. O.p.w. thick, 4um, pale orange. Anticlinal and i.p.w. thinner, 1um, pale brown. Lumina with living contents.

Mesophyll of 3-5 layers of prostrate irregularly ellipsoid cells (T.S. and L.S.) walls thin, c.1-2um, uniformly orange (tanniniferous?) lumina, frequent air spaces. 20-62um high (L.S.,T.S), 49-77um wide in T.S., 56-140um wide in L.S., in paradermal view, longitudinally irregular ellipsoid with short arms.

I.E. single sparse layer of prostrate, rounded, rectangular cells up to 14um high, 22um wide, walls colourless, 2um thick, each with prismatic crystal up to 6um high, 10um wide, lumina otherwise unoccupied.

TEGMEN(L.S.)

Exotegmen: single intermittent layer of longitudinal fibres with pale brown, pitted walls, 5um thick, end walls normal to rounded, 40-65um long, 14um wide.

Endotegmen: if formed, crushed or absorbed beyond recognition.

CHALAZA

O.E. as testa.

Mesophyll (upper) as testal mesophyll, to 3 layers thick.

Mesophyll (lower) equal or greater than upper mesophyll. Largely composed of vascular bundles and associated tissue sometimes sandwiched above 2-3 layers of tanniniferous cells.

I.E. single, poorly distinguished layer of cells 28-50um wide, c.10um high, often crushed, lumina colourless.

PERISPERM AND ENDOSPERM

Not detected.

EMBRYO

Outer boundary irregular, with shallow depressions and projections.

O.E. 1-3 layers of cuboidal cells c.8um diam., walls thick, 1um.

Mesophyll: isodiametric to shortly, randomly extended polygonal cells, 42-100um long, 28-63um wide, walls dark brown with collenchymatous corners, thickness 1.5um, lumina densely packed with spherical, colourless plastids, 4-7um diam.

Latex(?) canals frequent in outer embryo, to 50um diam.

Plumule and radicle densely covered in sharply pointed unicellular hairs, 175-210um long, 18-21um wide, walls thick 5-7um including strongly verrucate cuticle.

Malleastrum isalense Leroy

Cheek et al. 3-26-5.

TESTA

O.E. as M.gracile.

Meso - 23-30 cells, 0.75mm thick.

I.E. remains of endocrystals.

Malleastrum psammophilum Leroy

Cheek et al 2-27-7.

TESTA

O.E. as M.gracile.

Meso - 7-9 cells. Inner, compact, flattened, no air spaces.

I.E. - ?

Exotegmen as M.gracile.

EMBRYO

As M.gracile, hairs with less verrucation.

Meso - as M.gracile, but tanninized cells also.

Malleastrum mandenense Leroy

Cheek et al. 3-17-1.

Fruits spherical.

Thick pericarp. Yellow.

2-locular, but fruits 1-seeded by abortion.

TESTA

O.E. prostrate, rectangular in L.S. with thick yellow o.p.w.

Mesophyll rather thick.

I.E. - ?

Exotegmen - ?

EMBRYO

Hairs twice as long as M.gracile.

Cuticle forming bosses.

Plastids with central speck.

PLATE 45

EKEBERGIA CAPENSIS

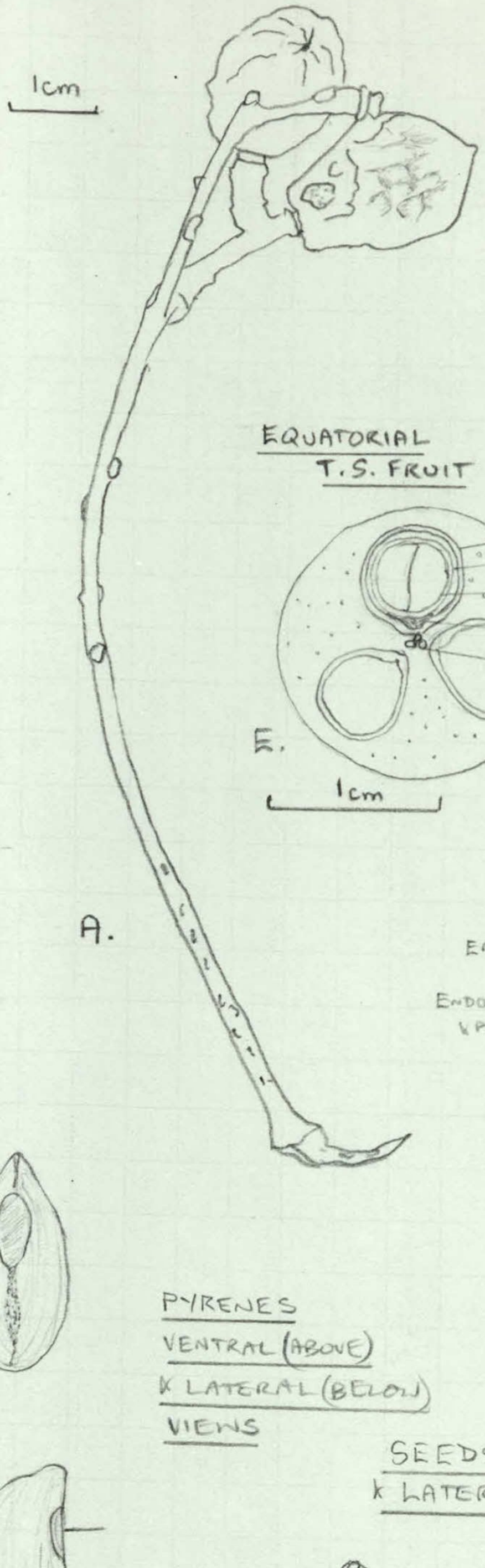
A-G FRUITS, VARIOUS VIEWS AND VARIATION.

F-K SEEDS & EMBRYO. NOTE VENTRAL CHALAZA.

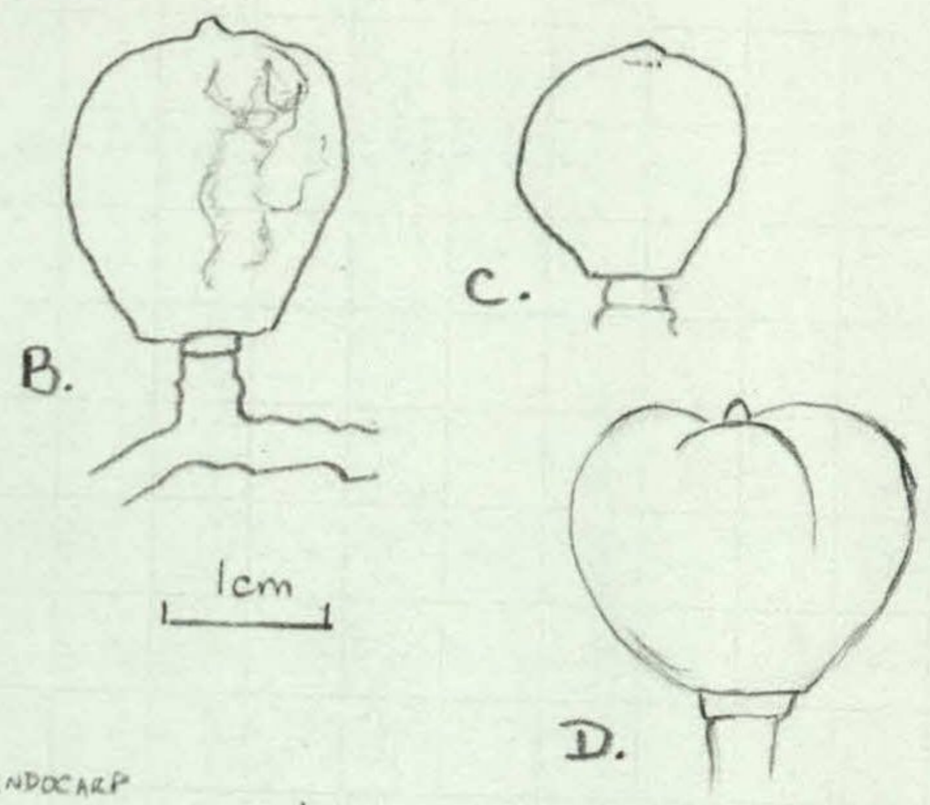
# Ekebergia capensis



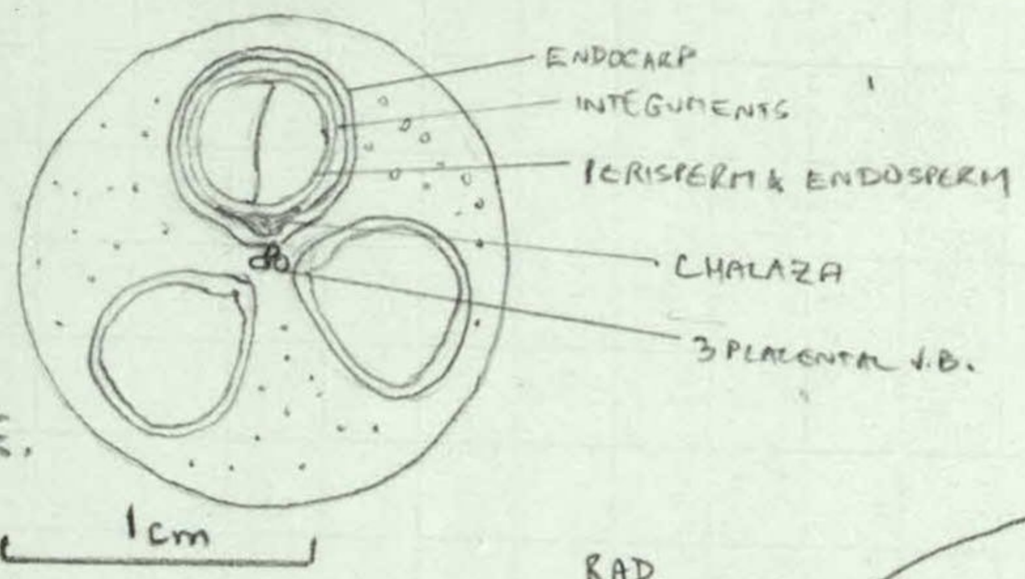
INFRUCTESCENCE (c. 10 FRUITS DETATCHED)



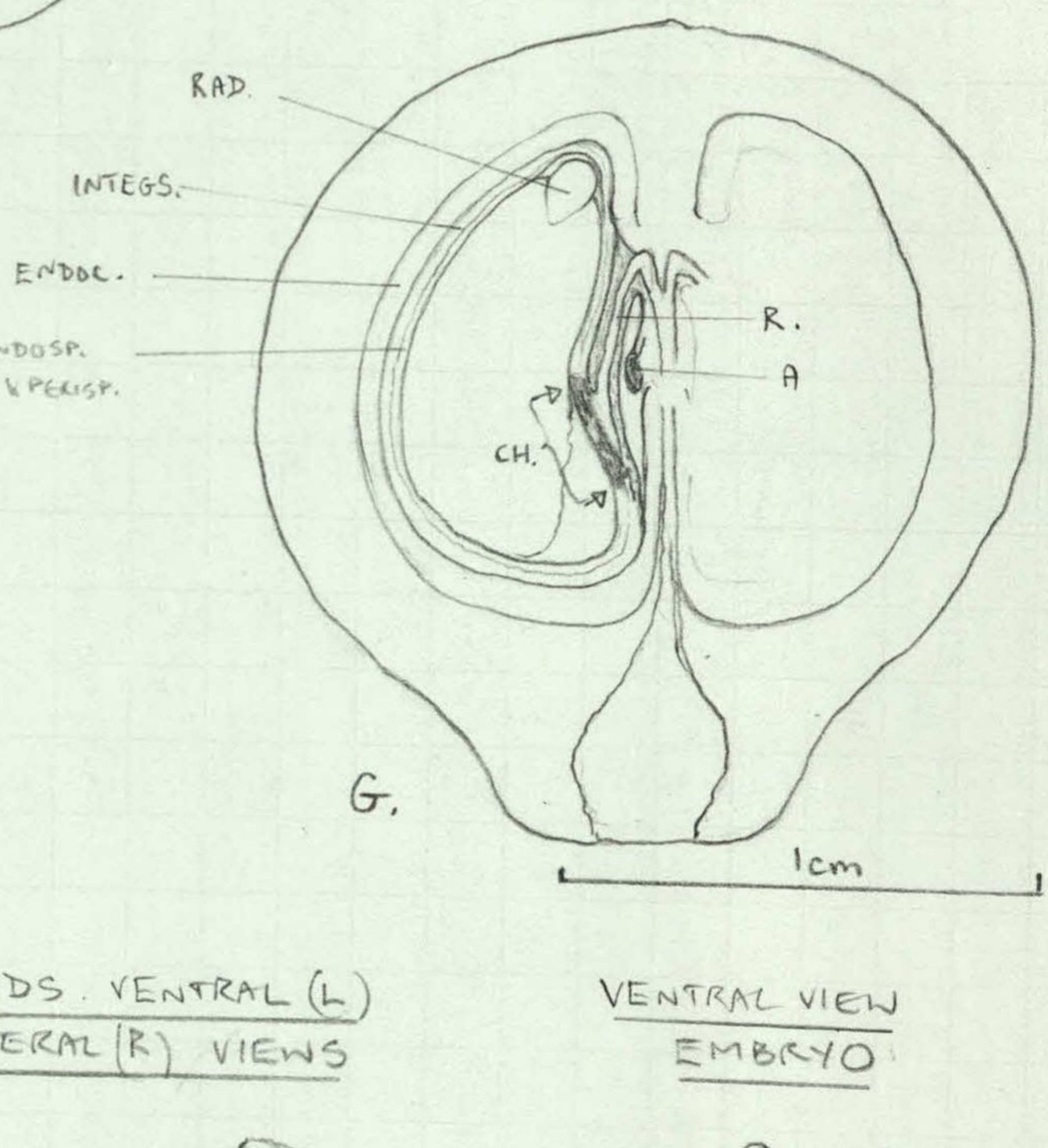

VARIATION IN FRUIT SHAPE & SIZE




EQUATORIAL T.S. FRUIT




MEDIAN L.S. FRUIT & SEED



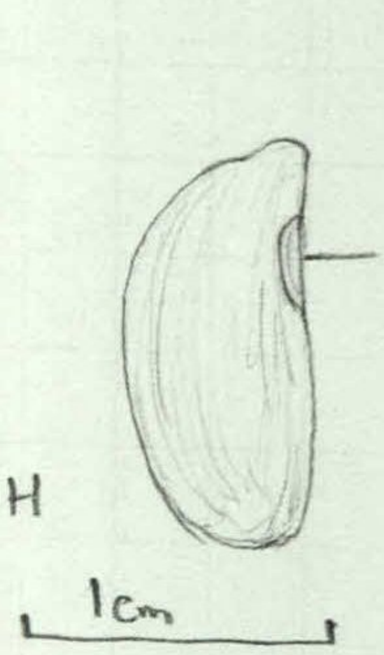


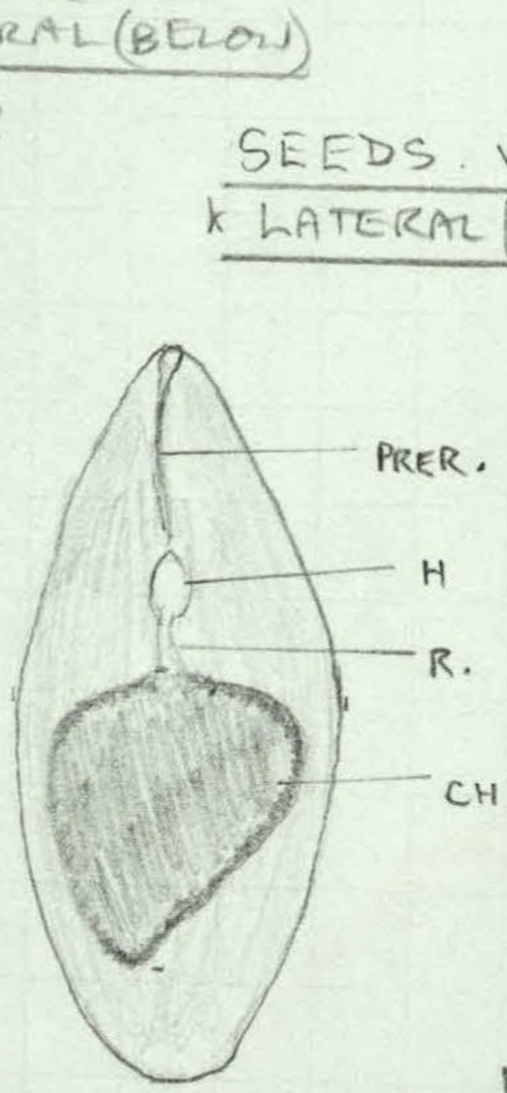


PYRENES VENTRAL (ABOVE) & LATERAL (BELOW) VIEWS

SEEDS. VENTRAL (L) & LATERAL (R) VIEWS

VENTRAL VIEW EMBRYO







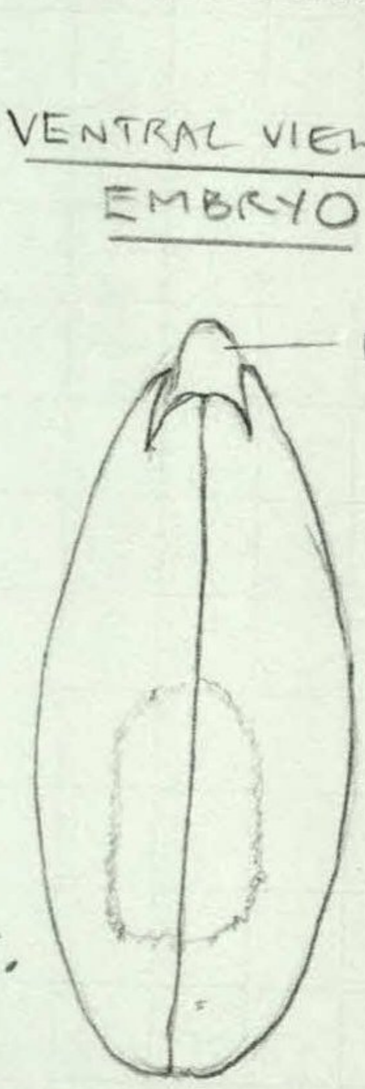


PLATE 46

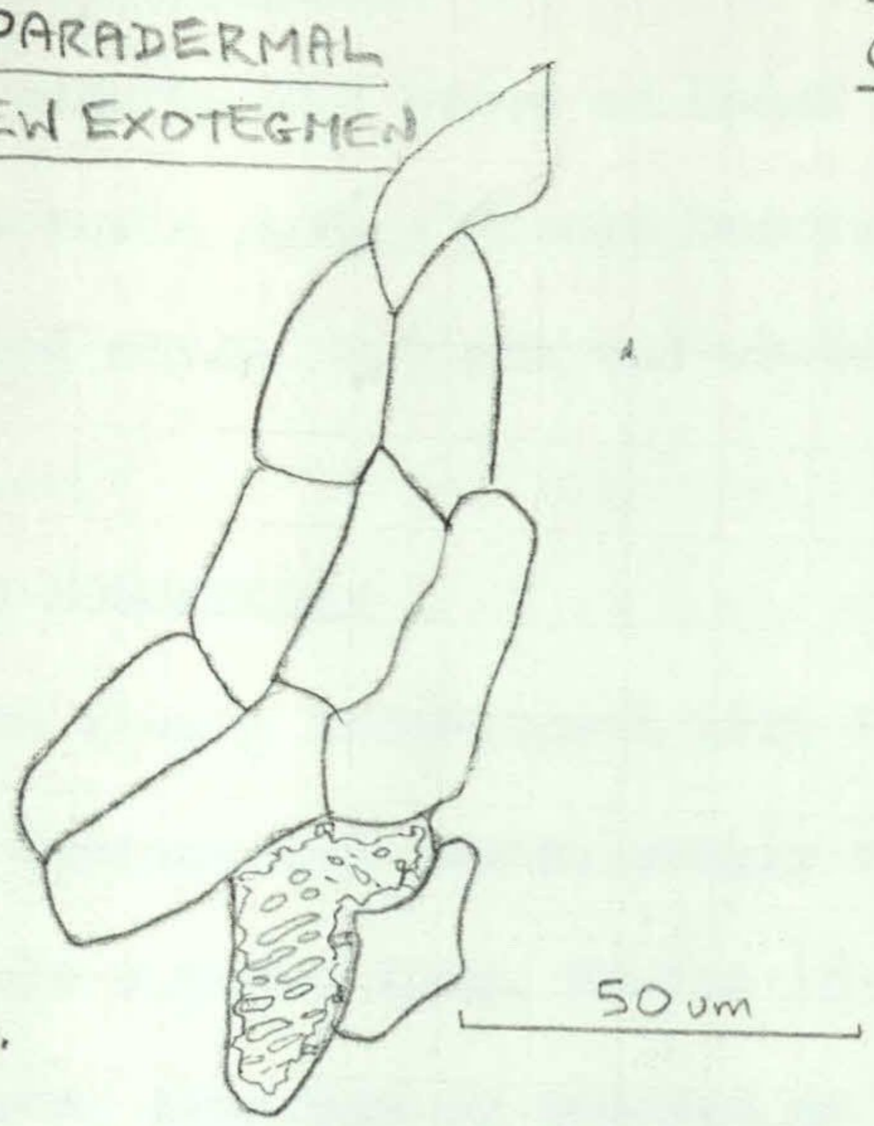
EKEBERGIA CAPENSIS

A-D SEED-COAT. NOTE BITEGMIC CONSTRUCTION, RELATIVELY WELL-DEVELOPED ENDOTEGMEN AND UNUSUAL SHORT EXOTEGMIC 'FIBRES'.

# Ekebergia Capensis

50 um

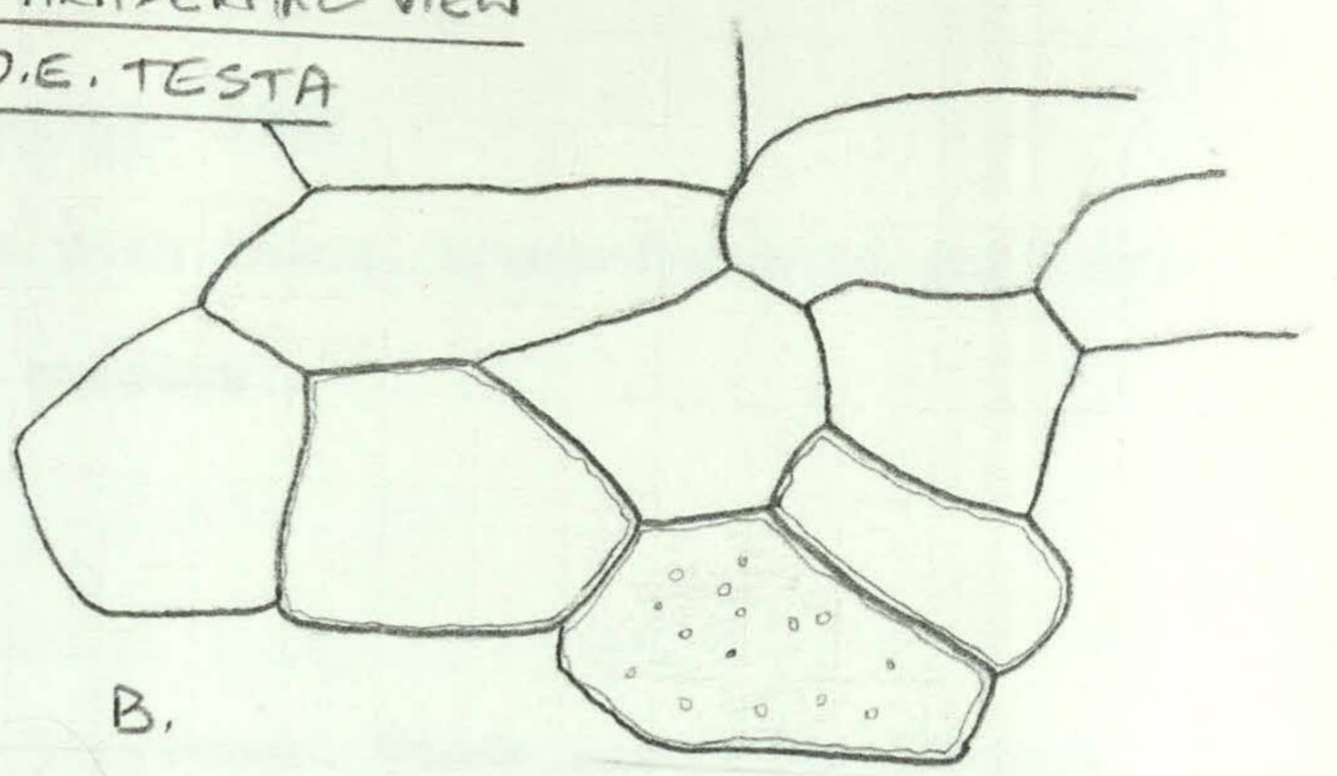
PARADERMAL VIEW EXOTEGMEN



A.

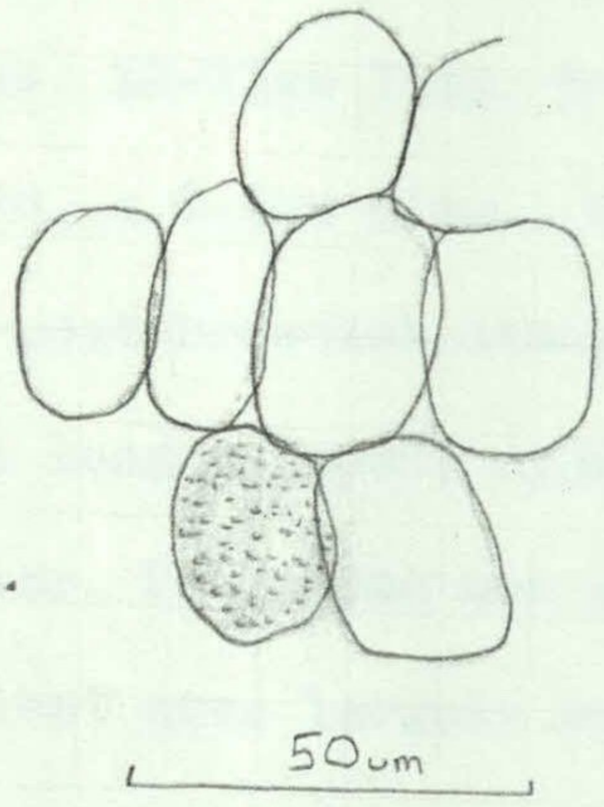
50 um

PARADERMAL VIEW O.E. TESTA



B.

PARDERMAL VIEW I.E. TEGMEN

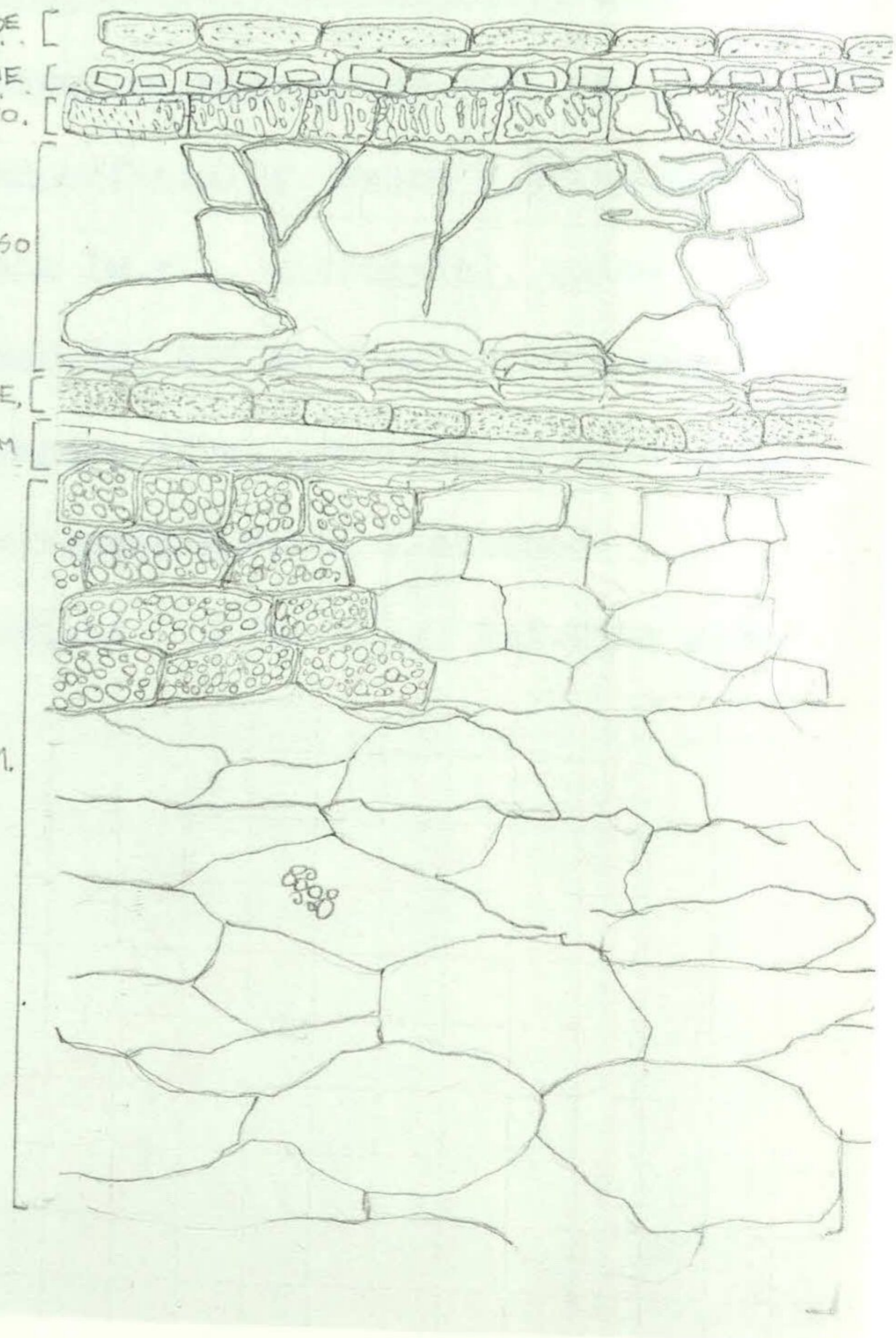


C.

50 um

L.S. INTEGUMENTS

50 um




D.

Ekebergia capensis Sparrm.

This description based on Cheek et al. 1055.

Collector's notes:'Orange berries with thick, brown-freckled pericarp. Reported eaten by black and white colobus'.

GROSS MORPHOLOGY

Fruits fleshy indehiscent with 1-3 pyrenes. Woody peduncles 10-16cm long, bearing 1-5 fruits singly on partial peduncles 7-14mm long. Pedicels 1.5-2mm long. Fruits 18-25mm long, 15-18mm diam. Spherical to pyriform, truncate or rounded at tips, but usually with distal nipple 1mm long. Mesocarp 1.5-4mm thick. Pyrenes to 14mm long, 8mm radially, 7mm tangentially, endocarp c.0.3mm thick, rigid and bony (sclereids), united by a central column of vascular strands, detached by moderate pressure.

Seed slightly bean-shaped with hilum and chalaza in shallow adaxial recess. 12-13mm long, 5-6mm broad tangentially and radially. Micropyle raised, c.0.3mm diam., at most acute end of seed, distal in fruit. Seed-coat brownish orange, glossy, sub-coriaceous, mechanically weak. Hilum longitudinal, c.3mm long, c.2mm wide, on micropylar side of equator. Pre-raphe not always visible superficially. Raphe 0.5-2mm long. Chalazal area largely on far side equator (w.r.t. micropyle), quite distinct superficially, roughly isodiametric, 4-5 mm diam., chocolate brown. Seed-coat 0.15-0.4mm thick. Endosperm firm, adhering to seed-coat, c.0.3mm thick. Cotyledons collateral, slightly curved, flattened plano-convex and thin, 1.25mm thick. Radicle 1.5-2mm long, 1-1.25mm wide, exserted.

ANATOMY

TESTA

The testa is extremely thin and difficult to section, often appearing crushed to only 24um thick.

Cuticle: <1mm, rather thin, straw-coloured, even.

O.E. single layer of prostrate rounded rectangular cells 35-55um wide, c.25um high, o.p.w. 2-2.5um thick: T.S.. In paradermal view isodiametric to slightly extended polygonal, 5-6 sided with sparse pale orange cytoplasmic contents.

Mesophyll absent or single layer of thin-walled vertically-compressed, often crushed, parenchyma.

I.E. well developed. Single layer of sub-isodiametric cells 13-25um diam. usually containing a single ± prismatic crystal 7.5-12.5um long.

TEGMEN

Exotegmen single layer of short, prostrate fibres, apparently not always orientated longitudinally, 27-40um long, 11.5-13um wide and 12-25um high (T.S. and L.S.). In T.S. square or slightly columnar. In paradermal view sometimes slightly sinuous. End walls truncate and normal, not oblique or rounded. Walls 2.5-4um thick, almost colourless, with pits slit-like to scalariform.

Mesophyll many layers of isodiametric (63-75um diam.) to transversely extended ellipsoid cells with thick (1-2um) yellowish walls. Most of lowest layers crushed to c.20um thick. Nevertheless, this thickest part of seed-coat.

I.E. single layer of square to prostrate rectangular cells with densely finely brown granular contents 10-12.5um high, 14-38um wide (T.S. and L.S.). In paradermal view, rounded broadly rectangular cells.

?PERISPERM(L.S.)

Sometimes crushed to an amorphous layer but often with at least two layers remaining ± intact. These fibrous in L.S., 4-5um high and up to 94um long with truncate or slightly oblique end walls. Walls very thin, >1um, contents colourless.

ENDOSPERM(L.S.) of 2 portions:

Upper of 4-5 layers (80-100um thick) smaller prostrate transversely extended polygonal (4-7 sided) cells with walls c.1um thick, 15-20um high, 30-45(-60)um wide. Contents densely packed with densely with translucent, colourless spherical inclusions 5-7.5um diam.. Upper epidermal layer tending to isodiametric, slightly smaller.

Lower portion 4-6 layers (c,150um) thick, cells less tightly packed, more ellipsoid, larger, 60-90um wide, 25-35(-52)um high, without or with few scattered plastids.

Astrotrichilia asterotricha (Radlk.)Cheek ined.

This description based on Cheek et al. 2-25-2.

Collector's notes: ' Fruits green, turning yellowish; apparently indehiscent'.

Pennington and Styles (1975): 'Fruit a 1-3 locular drupe; loculi 1-seeded; mesocarp thin and fleshy; endocarp thick, woody with a cartilaginous inner face, sometimes with loculicidal dehiscence. Seed radially compressed, exarillodiate, with an indistinct sarcotesta'.

GROSS MORPHOLOGY

Fruits oblate to sub-spherical, 16-20mm diam., 18-21mm long, including a terminal nipple to 2mm long (upper surface umbonate). Thin, ± succulent

PLATE 47

ASTROTRICHILIA ASTEROTRICHA

FRUITS- INDEHISCENT, WITH VERY HARD FRUIT-WALLS.


47

PLATE 48

ASTROTRICHILIA ASTEROTRICHA

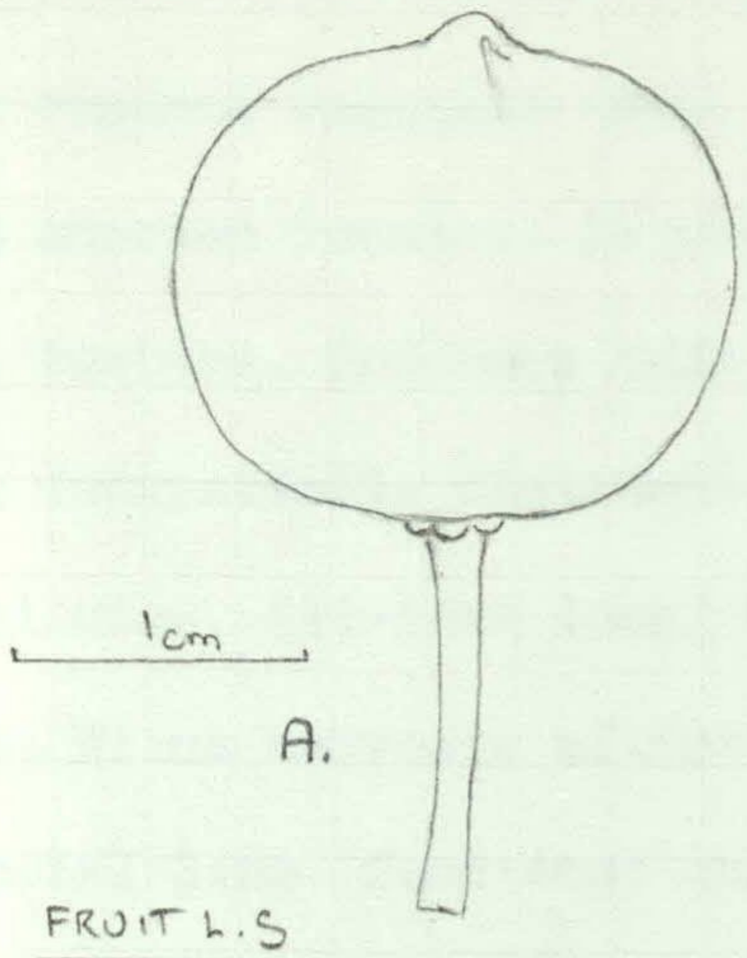
A-C FRUITS WITH SEEDS EXPOSED. NOTE LATERAL COMPRESSION OF SEEDS AND VERY THICK PERICARP (B).

D-E SEEDS. NOTE APPARENT ORTHOTROPY, FOLIAR COTYLEDONS, EXSERTED RADICLE & COPIOUS ENDOSPERM.

F SEED-COAT ANATOMY. NOTE BITEGMIC CONSTRUCTION.

# Astrotrichilia asterotricha

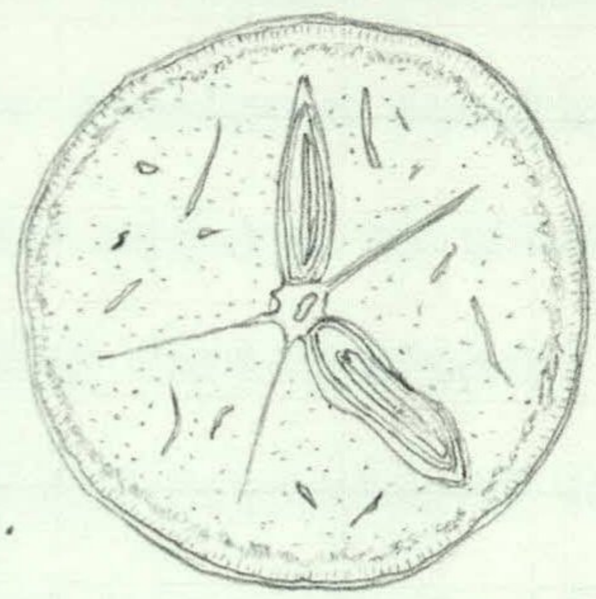
FRUIT LATERAL VIEW



1cm

A.

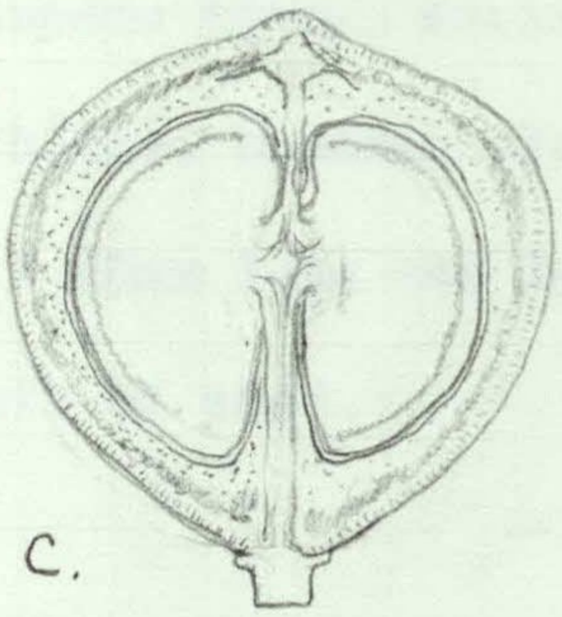
FRUIT
EQUATORIAL T.S.



B.

1cm

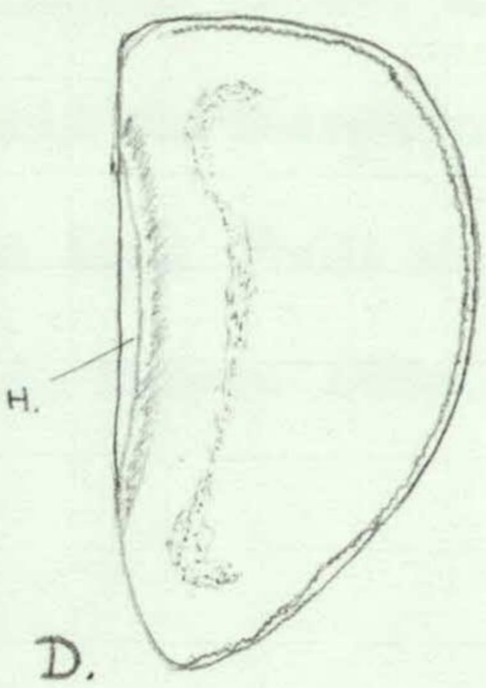
FRUIT L.S



C.

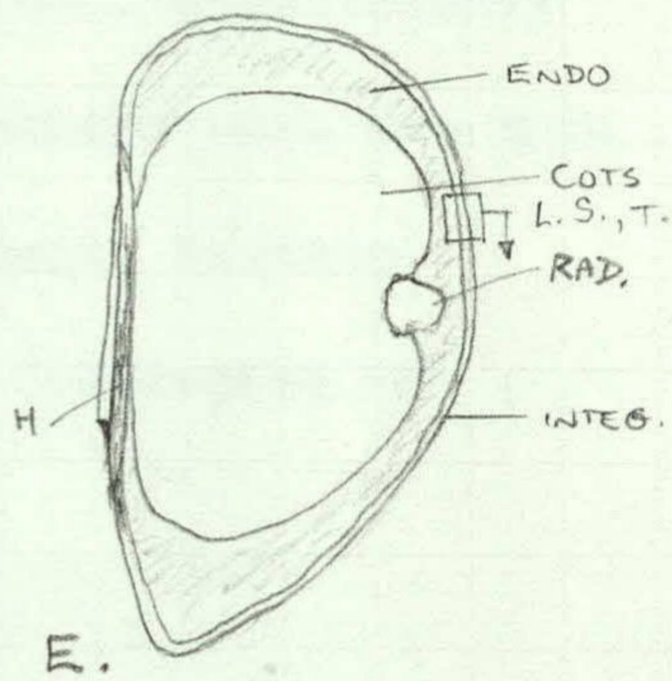
1cm

LATERAL VIEW
SEED




D.

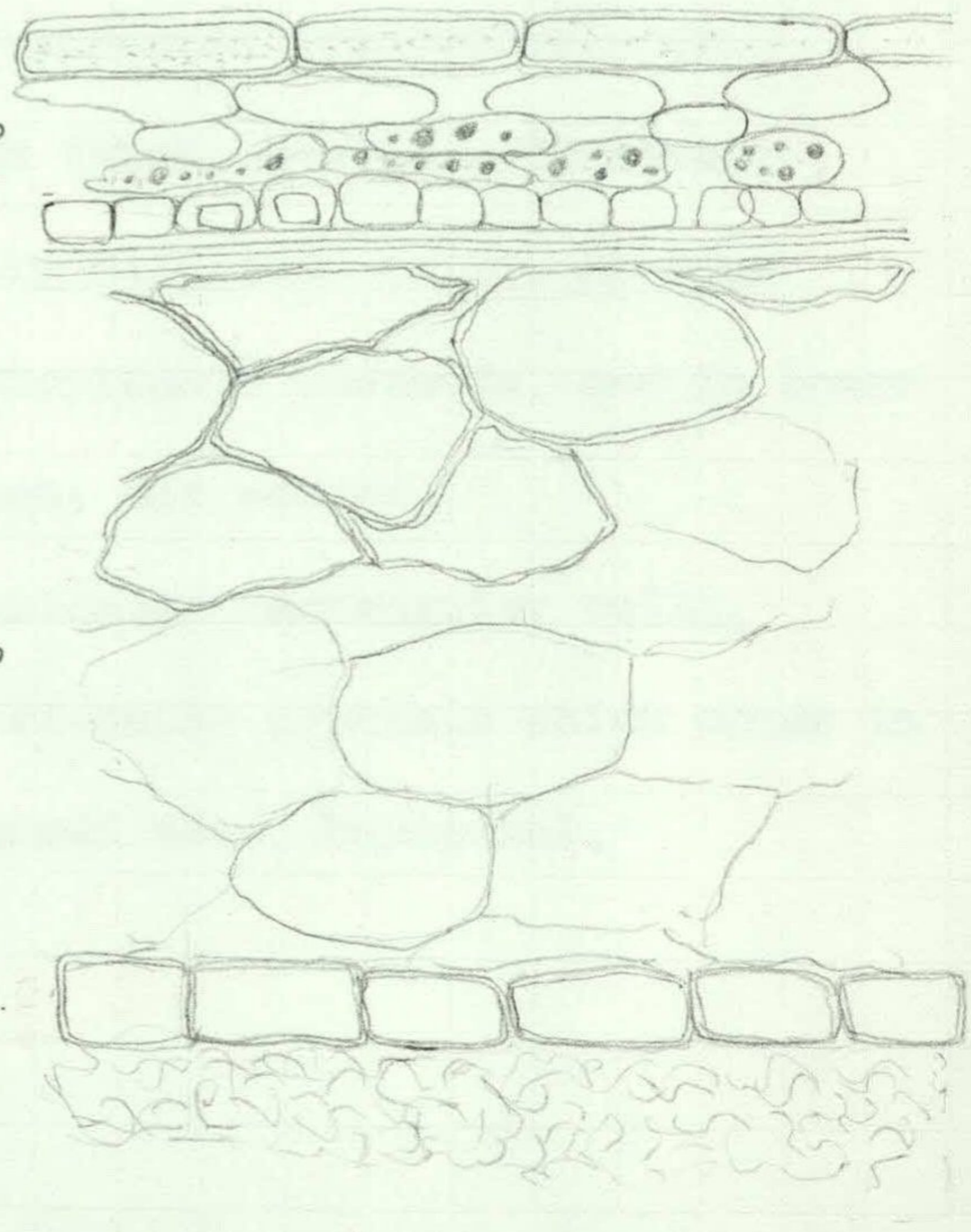
L.S. SEED




E.

1cm

L.S INTEGUMENTS




F.

50um

layer c.3mm thick over sclerified main mass (apparently mesocarp) of fruit which 1-2 (abortion from 5)-loculate. Locules arranged radially around central vascular core, woody mesocarp often developed equally around aborted locules. In older fruits woody layer softens to thick, gritty texture. Endocarp thin (c.0.5mm) and leathery cartilaginous.

Seeds tangentially flattened in fruit (c.2mm broad), bean-shaped in lateral view, (11-12mm long, 6-8.5mm wide), chalaza and hilum in adaxial recess. Hilum narrowly elliptic, c.3mm long, c.1mm wide, largely above equatorial line. Seed-coat thin (c.0.2mm thick, mid-brown, structurally weak. Endosperm thick, enclosing well differentiated embryo with two thin (c.0.5mm thick), broader (7mm) than long (4mm) cotyledons. Radicle exserted, 1.25mm long and 1mm broad. Embryo straight, transverse to longest axis of seed.

ANATOMY(L.S. AND PARADERMAL SECTIONS)

TESTA

Cuticle: not detected.

O.E. single layer of square to prostrate rectangular cells 15um high, 40-70um wide in L.S.. In paradermal view, highly extended polygonal cells c.25-40um wide, to 75-250um long, largely directed transversely or obliquely to axis of seed. O.p.w. only 2um thick. Lumina colourless.

Mesophyll: 3-4 layers of prostrate shortly ellipsoid cells, 25-40um wide, 10-15um high, lumina with sparse cytoplasmic contents, and in lower layers, few brown (tanniniferous?) globules; air spaces.

I.E. single layer of prostrate shortly extended rectangular cells, 15-20um wide, 10-13um high, rarely with prismatic crystals which occur in isolated clusters of 1-7 cells. In paradermal view, hexagonal, isodiametric.

TEGMEN

Exotegmen single layer of yellow brown, long (to 1250um) thin-walled (3-5um) fibres 7.5-10um high, 18-25um wide (paradermal view), finely tapered, pits infrequent, simple, very large, 4-5um diam., poorly defined.

Mesophyll 3-4(-6) layers of large parenchymatous prostrate elliptic cells c.60um wide, c.35um high often partly compressed. Without contents.

I.E.single layer of prostrate, shortly extended, rectangular cells, c.20um high, c.40um wide, cytoplasmic contents dark, restricted to periphery of lumina. Walls c.1.5um thick.

ENDOSPERM

Thin-walled, small (21-28um), sub-isodiametric parenchymatous cells with small (c.5um), ?lipid globules.

ENDOCARP

Cylindrical fibres, 8um diam., to 480um long with frequent simple pits and lumina negligible.

MESOCARP

Parenchyma interspersed with frequent clusters of short, polygonal sclereids, c.35um wide, c.54um long, walls 14um thick with simple pitting.

Owenia venosa F.Muell.

This description based on J.H.McWhirter 7.

Collector's notes: 'Fruits red, spherical (diam.3/4'-1') borne individually or in pairs of 3 or 4 (sic), on stalks arising from leaf

PLATE 49

OWENIA VENOSA

A-D FRUIT: INDEHISCENT, MESOCARP, THIN, FLESHY.

NOTE VERY THICK ENDOCARP.

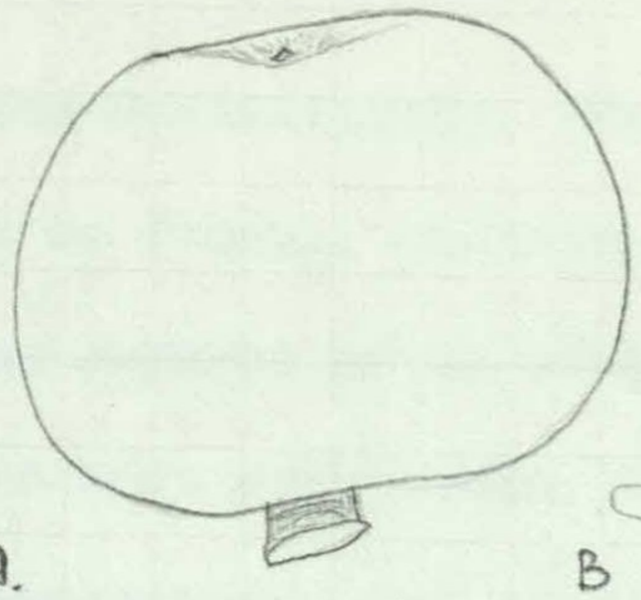
E-F SEEDS. NOTE ABSENCE OF FLESHINESS.

G-H SEED-COAT ANATOMY. NOTE THAT UNITEGMIC (PACHYCHALAZAL?)

AND HIGHLY VASCLARIZED.

# Owenia venosa

FRUIT. LATERAL VIEW



A.

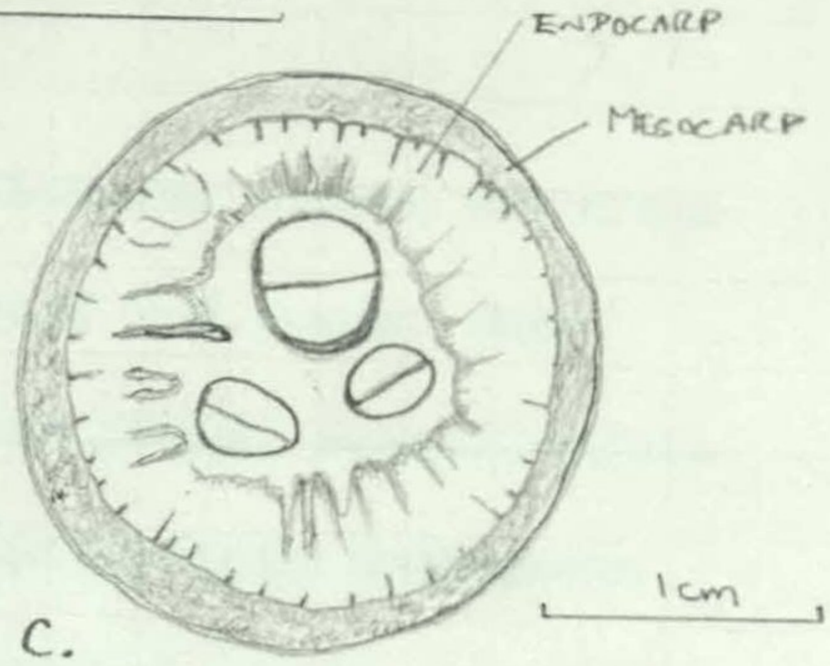
CALYX
PLAN VIEW




B

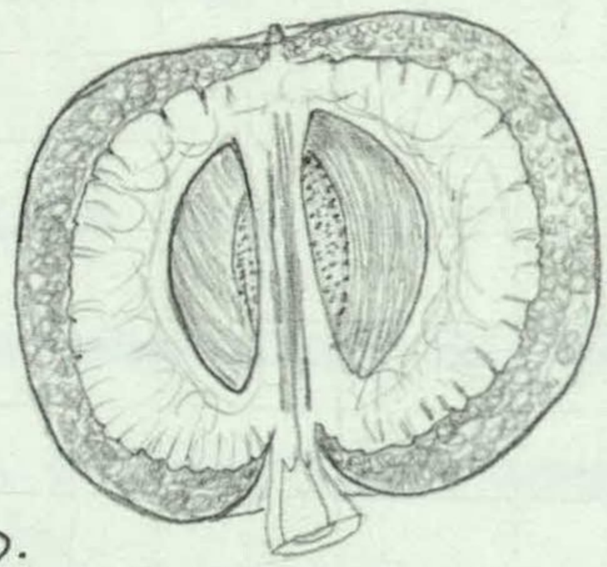
1cm

FRUIT T.S.




C.

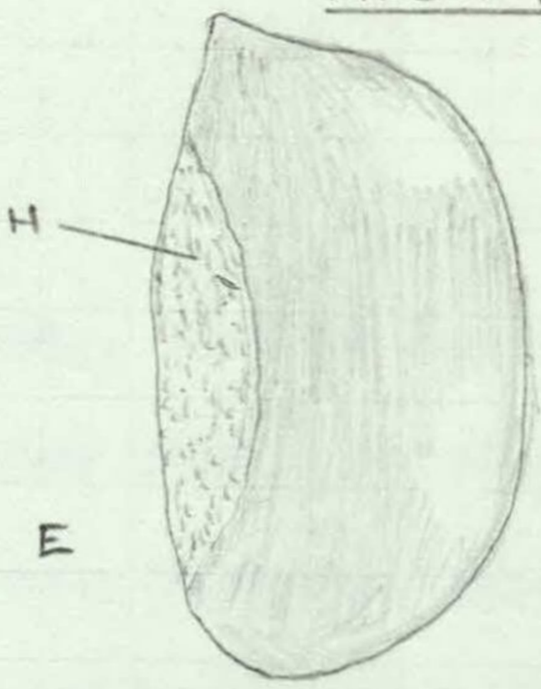
FRUIT: L.S.



D.

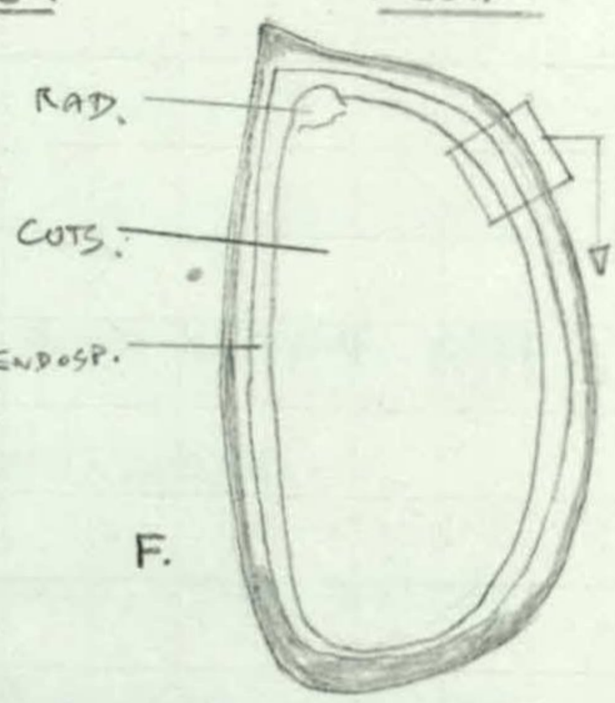
1cm

SEED
LATERAL VIEW



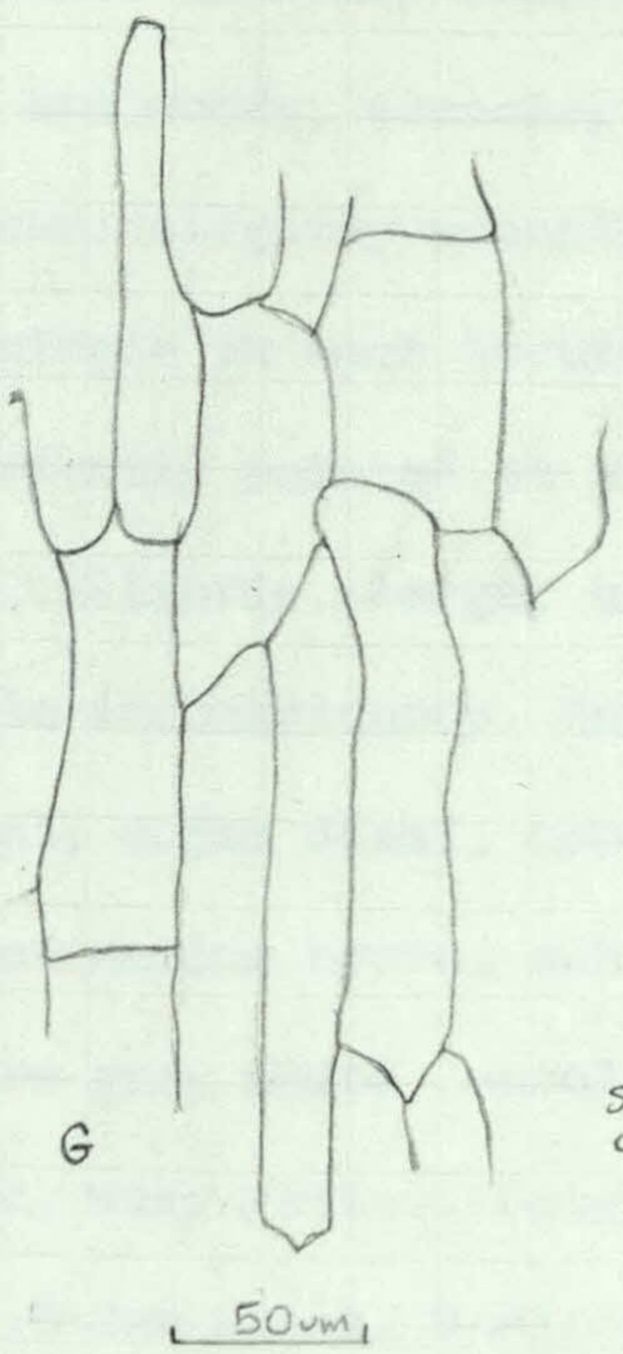

E

SEED L.S.
MEDIAN




F.

1cm

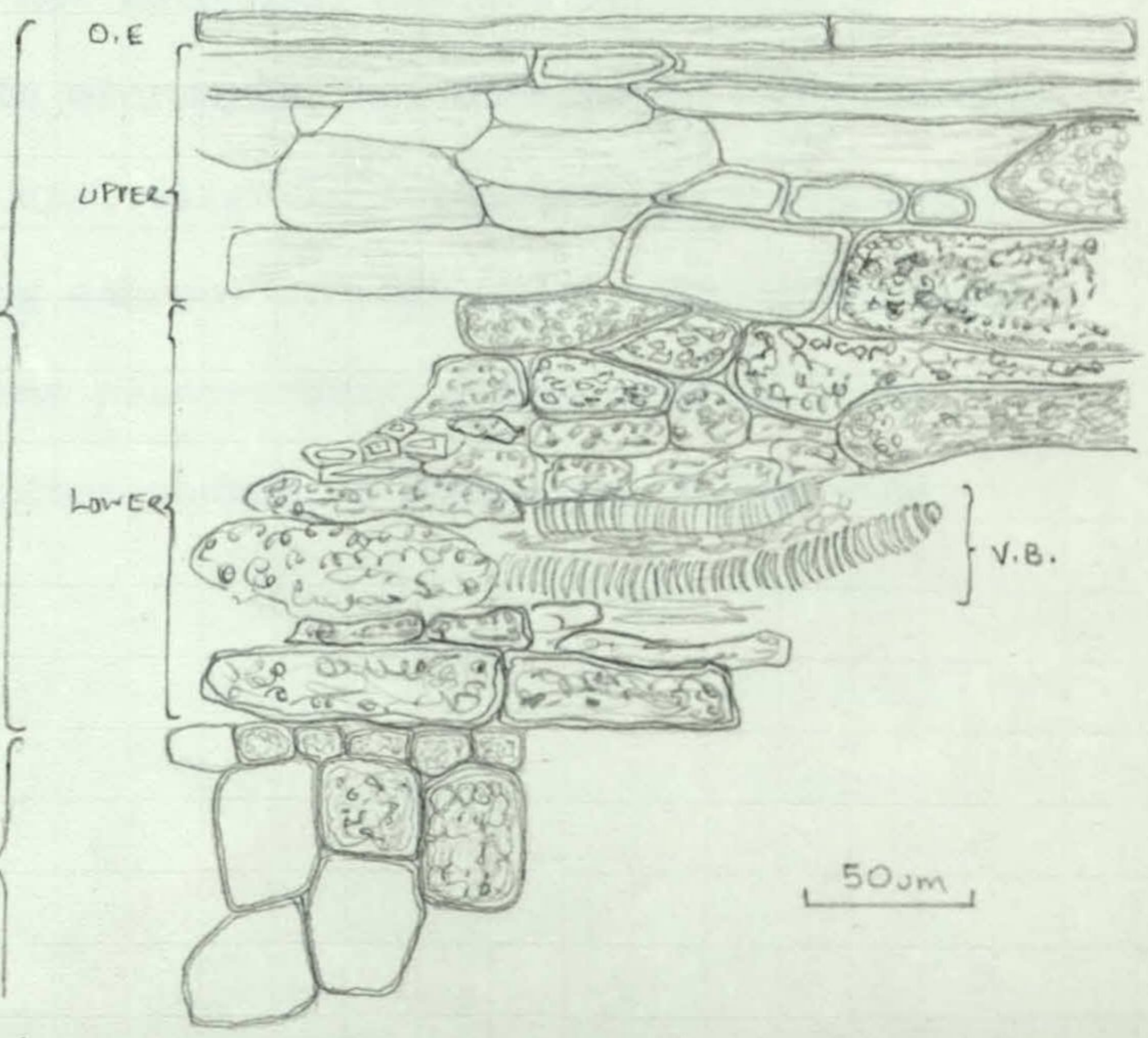


G

SEEDCOAT O.E.
PARADERMAL VIEW

50um

L.S. SEEDCOAT (THINNER PART)




H

50um

axils varying from 2'6' in length. Fleshy exterior (firm) around hard, woody stone'.

Pennington and Styles(1975): 'Fruit a 2- or 3-locular drupe; mesocarp thin, leathery or fleshy, endocarp very thick, hard and woody. Seed shaped like the segment of an orange, depressed or ovoid, exarillodiate, with a complete thin sarcotesta. Embryo surrounded by thin endosperm; cotyledons plano-convex, collateral; radicle superior, short, slightly exserted or extending to the surface'.

GROSS MORPHOLOGY

Fruits oblate-spheroidal, 20-26mm diam., 18-22mm long. Apex sunken, with style remnant. Pedicel 1.5mm long, 2.5mm diam., persistent calyx. Pericarp glabrous, slightly rough, finely flaking. Mesocarp thin, pulpy, c.2mm thick. Endocarp comprising bulk of fruit, up to 18mm diam., white, fibrous and woody, mesocarp detaching ± cleanly. Locules 1-3, inner face dark brown, slightly wrinkled, glossy, tightly fitting seed-coat.

Seeds single in each locule, roughly ellipsoid, 8-9mm long, 5mm in diam.. Bluntly pointed at micropylar end (distal in fruit). Hilum adaxial, elliptic, large, apparently covering c.25% of seed-coat. Micropyle inconspicuous. Raphe not detected. Chalaza apparently ± spherical, c.3mm diam., opposite micropyle, not detectable superficially. Seed-coat medium brown, sub-glossy, slightly irregular, to 0.6mm thick. Endosperm grey white, enveloping embryo, c.0.2mm thick. Embryo straight, elliptic, waxy yellow. Cotyledons plano-convex, c.6mm long, 2.5-3mm wide, 1.8-2mm thick. Radicle button-shaped, 1.25mm long, 0.5mm wide, exserted.

ANATOMY

Seed-coat apparently pachychalazal, but only poor sections obtained, possibly owing to incomplete penetration (when field collected) by fixative of exceptionally thick, woody endocarp.

O.E. single layer of cells 9-14um high and 10-70um wide (T.S. and L.S.).In paradermal view, highly extended (obliquely transverse to seed axis), polygonal, 8-10um wide and 49-92um long. O.p.w. thin, c.1um thick, lumina translucent orange-brown (tanniniferous?).

Upper seed-coat of 1-4-layers (to160um) of ?tanninized cells, of variable size and shape. In T.S. up to 28um high (when c.60um wide), with walls to 5um thick, or 140um wide and 10um high. In paradermal view, cells ± isodiametric to extended and lobed, rounded.

Lower seed-coat 150-400um thick of heterogeneous composition, the basal matrix of prostrate ellipsoid cells, c.60um wide, c.25um high with dense grey-black granular contents, these cells very brittle in sectioning. Interspersed are vascular bundles and short fibrous sclereids as idioblasts or small clusters.

ENDOSPERM

100-200um thick.

Cipadessa sp.

This description based on material cult. Hort. Bot. Munich.

No collection notes available.

Corner(1976), using living material of C.baccifera(Roth.)Miq. from Java: 'Ovule; 2 cells thick; i.i. 4-5 cells thick.

Testa 3 cells thick, the outer two layers thin-walled and crushed; I.E. composed of small cells, each with a crystal. Tegmen 6-7 cells thick, the inner layers becoming large-celled, then crushed; O.E. as a compact layer

# PLATE 50

## CIPADESSA SP.

A-B FRUITS: INDEHISCENT, FLESHY.

C-G PYRENES AND SEEDS. NOTE HEMI-ANATROPY, CURVED EMBRYO, LONG EXSERTED RADICLE AND THICK ENDOSPERM (cf.TURRAEA)

H-J SEED-COAT ANATOMY. NOTE HIGHLY REDUCED, BUT BITEGMIC CONSTRUCTION: OFTEN ONLY TWO CELLS THICK.

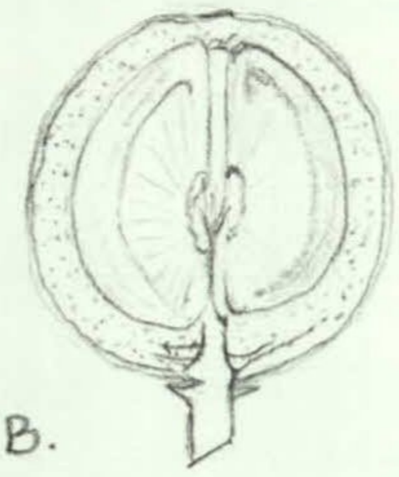
# Cipadessa sp.

Fruit. Lateral view



A.

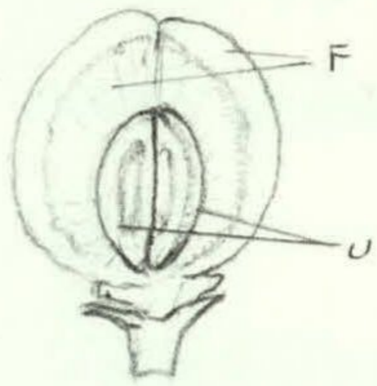
Median Section



B.

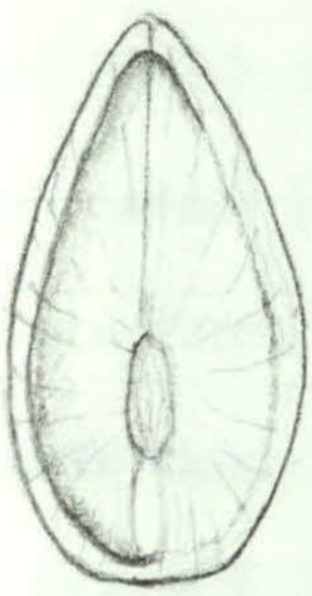
5mm

Lateral view
Mesocarp removed




C.

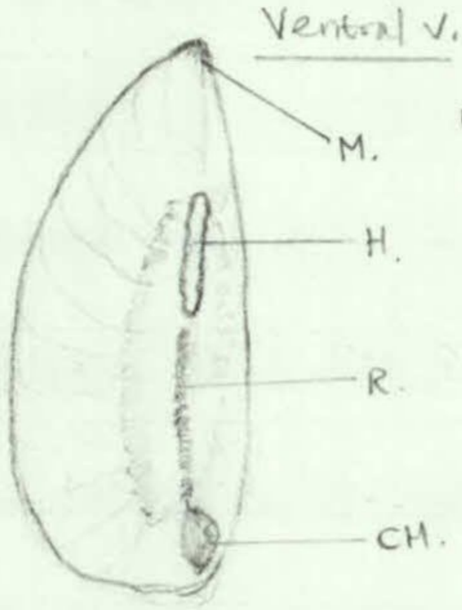
Pyrene. Ventral view



1mm

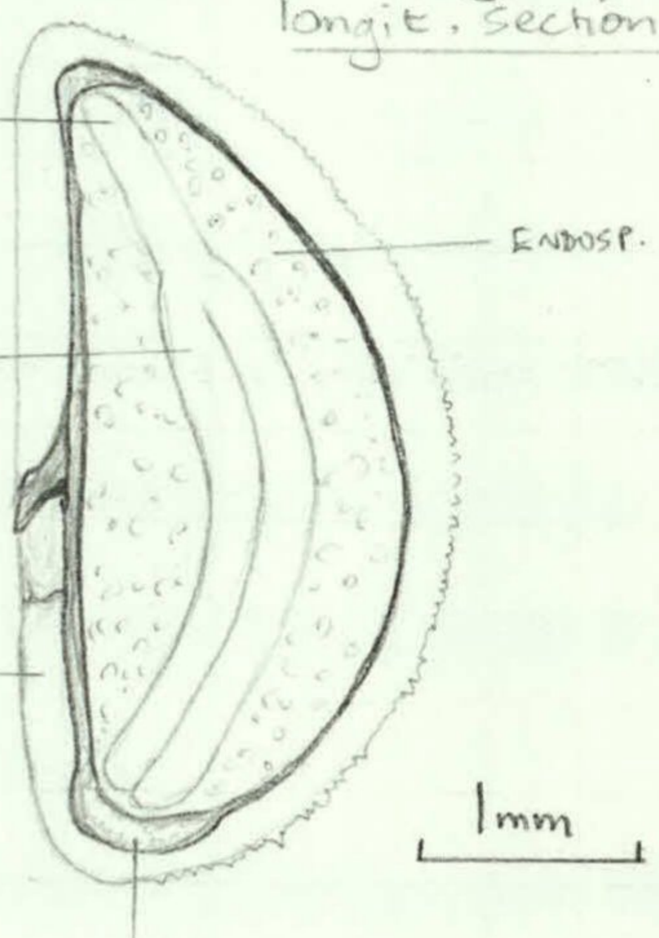
D.

Seed 3/4
Ventral V.




E.

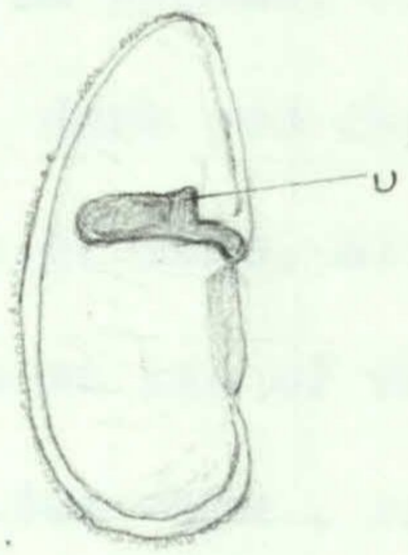
Seed x Pyrene
longit. Section




1mm

F.

Pyrene, l.s. fertile
seed removed




G.

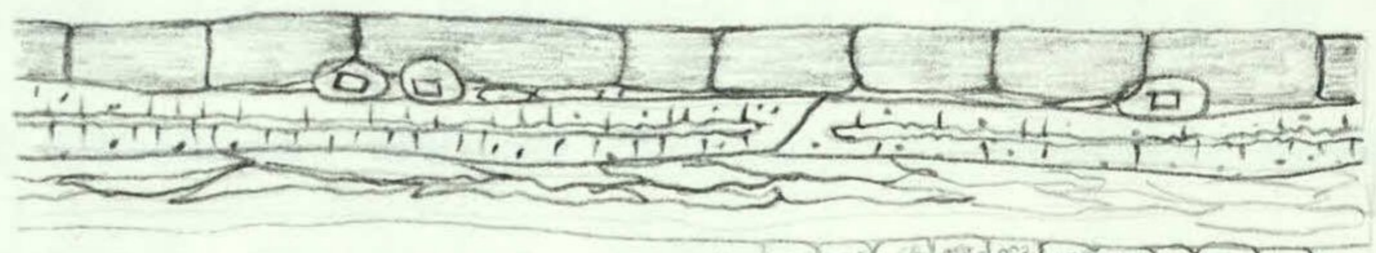
Testa. i.e
Plan View



H.

Integuments L.S.

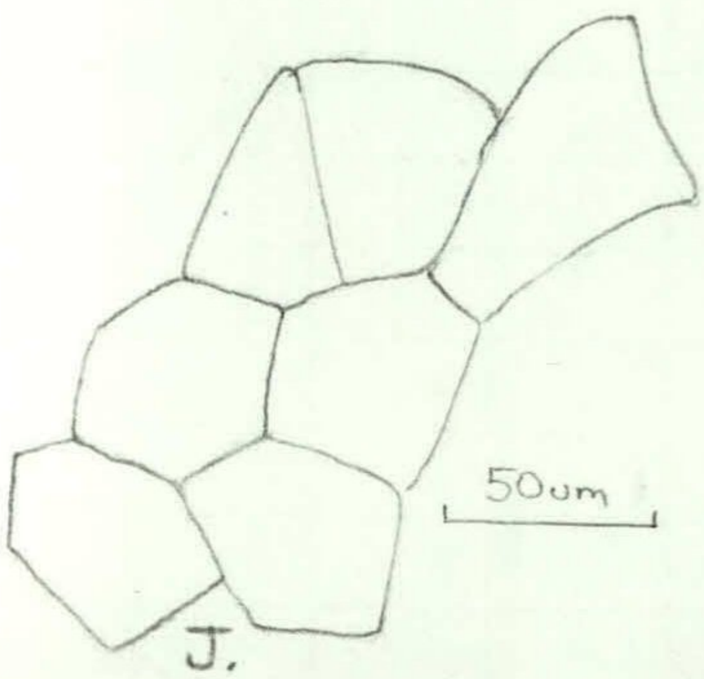
50um




I

ENDOSPERM

Testa o.e.
Plan view



50um

J.

of narrow, sub-cylindric, thick-walled, pitted, longitudinal fibres, not or slightly lignified, forming a pellicle around the endosperm'.

GROSS MORPHOLOGY

Fruits oblate-spheroidal, c.4.5mm long, c.6mm wide; persistent style base 0.2mm diam.; persistent calyx 1.8mm diam.. Pericarp pale, glossy with brown flecks. Mesocarp c.0.5-1.5mm thick, soft and fleshy, surrounding 5 free pyrenes of which 1-5-fertile. Fertile pyrenes one seeded by abortion from two, aborted persisting conspicuously; orange-segment-shaped in T.S./planar view, narrowly ovate in radial view. c.4mm long, 1.7-2.1mm radially, 2.1-2.2mm tangentially. Pyrene coat translucent amber yellow, seed visible within; separating cleanly from mesocarp in mature fruit, bony, c.0.15mm thick. Adaxial cavity (vascular port) towards base, c.0.9mm long, c.0.3mm wide. Infertile pyrenes flattened 1/2-3/4 length of fertile. Vascular column projecting c.0.9mm from receptacle before branching to each pyrene.

Seed shaped as pyrene, c.3mm long, c.1.25mm wide radially, c.1.5mm wide tangentially, dark red chestnut brown. Hilum adaxial, midway or just above, length of seed, slit like, sides raised, c.0.3mm long, c.0.1mm wide. Chalaza at tip of widest end of seed, a prominently raised black hemisphere 0.4mm diam., raphe raised, black, c.0.9mm long. Micropyle at tip of pointed seed end, black, raised. Endosperm very thick (up to 0.6mm) forming bulk of seed contents. Embryo curved c.80 degrees from straight line, cotyledons foliar, flattened, c.2mm long, 0.3mm thick. Radicle thick, long, exserted, 0.9mm.

ANATOMY

TESTA

O.E. single layer of prostrate, rectangular cells 28-35um wide, 9-14um high (T.S., L.S.), lumina uniform dark chestnut brown (?tanniniferous); in paradermal view, isodiametric or very shortly extended 5-6-sided cells.

Mesophyll absent.

I.E. single layer of prostrate, elliptic cells, 7-14um wide, c.7um high, lumina buff, with single, long rectangular (paradermal), to 10um x 4um endocrystal. Largely crushed, but extensive lenses remain.

TEGMEN

Exotegmen single layer of strongly developed, long (140-630um), longitudinal fibres. Sub-isodiametric to shortly columnar in T.S., 7-14um wide, 14-16um high with walls irregularly thickened to 7um thick, all but occluding lumina; prominent but relatively sparse simple pits. end walls slightly oblique.

Endotegmen at least three layers of large, crushed parenchymic cells up to 60um wide, above a translucent yellow layer of completely crushed cells 7um thick.

ENDOSPERM

Outer epidermis of cuboidal to shortly radially columnar cells 9-14um high, with fine granular cell contents.

Cortex of larger, isodiametric cells 30-60um diam., wall thickness c.0.75um, protoplast with apparently glutinous yellow bodies 2-5um diam..

EMBRYO

## DISCUSSION

### Anatomical characters: assessment of taxonomic value

#### Fleshy-seeded genera.

##### Testa.

O.E. and cuticle. Whilst the latter is unvaryingly even and provides little variation of taxonomic value, the O.E. exhibits a variety of shapes and wall thickenings. Isodiametric cells occur in American Trichilia, whereas longitudinally elongated cells occur in Pseudobersama and some African Trichilia species; Heynea trijuga Roxb. ex Sims has markedly columnar cells. The outer periclinal wall (o.p.w.) is usually rather thick and convex on its inner surface. The thickness seems to be of some use at the species level: in T.capitata Klotzch (Africa) the lumen is almost entirely occluded by the o.p.w., whereas the o.p.w. form only 1/3 the radial length of the cell in others. The anticlinal walls in Walsura species have radially directed thickenings, whereas those of Heynea species are thickest just below the o.p.w., giving an hour-glass shape to the lumen. No sub-epidermis or hypodermis was detected in any of the material investigated.

Mesophyll. This tissue is usually 3-6 layers thick, relatively thick-walled and uncrushed. That of Corner's American Trichilia is unusual in being only 1-2 layers thick and crushed. In Pseudobersama, the cells are notably robust and thick-walled, whilst in Trichilia capitata they are, in addition, pitted. Multi-layered, thin-walled mesophyll occurs in Heynea (c.12 layers with lacunae) and in the sarcotestal seeds of T. grandifolia Oliv.(c. 36 layers).

I.E. Generally a single layer of small undifferentiated cells

with single crystals. Not detected in Pseudobersama (possibly present but obscured by pigment), only dubiously present in Trichilia grandifolia, and absent in Heynea trijuga. Cell shape shows little variation, but crystal shape and size are variable and may prove to be of use at the species level.

Tegmen. The exotegmen is usually a single layer of long fibrous cells, columnar in T.S. (i.e. 'ribbon'-like). Length, wall thickness, breadth, height, end walls and pitting appear useful at the species level. In Heynea trijuga, the fibres are only sporadically expressed and small and short, with very large pits, a similar situation occurring in Trichilia grandifolia but in the middle layers of the tegmen. Sub-palisade fibres (little wider than high in L.S.) occur in Pterorhachis and Pseudobersama. The longest fibres occur in American and Malagasy Trichilia species. Multiple layers of sclerotic cells, probably formed by the inner layers of the tegmen being lignified occur in Walsura species, two East African Trichilia species and in Pseudobersama. In all but the first, these cells, in T.S., become wider and less high as one progresses deeper into the seed-coat. The lowest layers are wider than high. In Walsura pinnata Hassk., the lowest layers are ± equal to the upper in dimensions, but transverse in orientation.

As in Turraeeae, this portion of the seed-coat clearly produces the characters of most taxonomic value, though less overwhelmingly so than in that tribe.

The endotegmen is usually completely crushed. In Pterorhachis, it is parenchymatous and only very slightly crushed and a distinct I.E. is formed. In Heynea trijuga, it is uncrushed but largely vascularized and no I.E. is detectable.

Vascularization. Apart from the tegmen of Heynea trijuga, vascular integuments have otherwise only been noted in Trichilia grandifolia (testa) and the unitegmic species.

The unitegmic seeds of Trichilia monadelpha (Thonn.) J.J.de Wilde, T. emetica and of Walsura chrysogyne (Miq.)Bakh.f. all lack completely the stratification testa: O.E./mesophyll/I.E. and tegmen: exotegmen/endotegmen and their seed-coats appear instead as a chaotic assortment of vascular bundles, tanninized cells and sclereids which structure is impossible to relate to other members in the genus except in the matter of the uppermost epidermis. A pre-raphe occurs in Heynea, Walsura and Pterorhachis, the latter peculiar in having two distinct bundles and an accompanying superficial groove. A pre-raphe is not recorded from Trichilia or Pseudobersama, but the raphe-funicular bundle in the latter is doubled back on itself exhibiting a hairpin bend within the aril. The aril in Walsura is partially vascularized.

Arils and Sarcotesta. Arils are found in all genera in this group of the Trichilieae (i.e. those with fleshy seeds). The aril of Pterorhachis is chalazal, those in Walsura and Heynea species predominantly funicular/pre-raphe, in Pseudobersama funicular-raphe as are those of the East African Trichilia species. Those of most American and Malagasy Trichilia species are raphe-arillate to partly sarcotestal, but verge on the sarcotestal. The unitegmic African species are sarcotestal, many appearing pseudo-arillate and superficially similar to the raphe-arillate species.

In both Heynea trijuga and Walsura pinnata, the testa is enshrouded in the overlapping aril. In the former it is free, but in the latter it is united to the testal O.E. and shows a very well-thickened o.p.w., far

thicker in fact than the testal O.E. which it seems to protect. This species seems pseudo-sarcotestal.

Anatropy seems to be the basic condition in the tribe. But Cipadessa shows hemi-anatropy and Pterorhachis is sub-orthotropous.

## THE GENERA: VARIATION, DELIMITATION & AFFINITIES

### Trichilia & Pseudobersama

Trichilia (plates 29-32), the core genus of the tribe shows, the greatest variation in seed structure, which is hardly surprising in view of the fact that it has most species and is the most intensively investigated here where nine species are considered in detail. Seven species are dissected here for the first time and published data used on a further two. The first two species investigated in this work, Trichilia monadelpha (T. heudelotii Planch. ex Oliv.) and T. emetica (T. roka Chiov.), were closely similar, lacking completely the characteristic Meliaceae seed-coat stratification and appearing unitegmic. Although no ontogenetical study was made, these seeds are believed to be pachychalazal in the sense of Corner (1976); indeed he suggests there that this may be the case for T. emetica. Were these seed-coats the product of the loss of one integument, then it is highly likely that remains of the other integument would persist in a recognizable state. Instead, the seed-coat is composed of a seemingly random mixture of vascular bundles, sclerotic and tannin-filled cells interspersed with parenchyma. This is not seen in any part of the seed-coats of other species except the chalaza. The variation, even in adjacent parts of the same seed-coat is bewildering, since pockets of sclerotic cells crop up in one place and another, here the cells are tannin-filled and there they are not. There seems no order in this construction, and no way of

describing it nearly as predictably as in species of the bitegmic construction. Thus it is very difficult to convey how one might distinguish these two species on seed anatomy. The upper 3-4 layers of cells comprising the O.E and parenchyma, comparable with the testal O.E. and its mesophyll, are less variable and more amenable to taxonomic work. There are slight differences in the cell dimensions and periclinal wall thickenings between the O.E. of the two cells and these might provide a useful if slender source of characters at the species level. The parenchyma cells vary less and although it is possible that careful quantitative analysis might prove them of use, the fact that they are easily distorted by crushing does not raise expectations. It is chiefly these parenchyma layers that account for the difference in appearance between the thick, red , soft, 'arillate' part of the seed and the black, hard 'testal' part. In the latter, the cells are smaller, thick-walled, and more densely packed, whilst in the former, they proliferate, are thinner-walled with more airspaces. But, at the boundary between 'aril' and 'testa', the two are confluent and intergrade, whilst, below, the contiguous sclereids, fibres and vascular bundles that constitute the bulk and mechanical part of the seed-coat remain unchanged, except that tannin-filled cells seem less numerous under the 'aril'.

The other unidentified American species that was considered by Corner has the standard bitegmic pattern and is quite different from the previous two species. Here the same type of O.E. exists: cuboidal to rectangular in T.S. and L.S., with a thick o.p.w. (concave inner face) and the cells isodiametric or very slightly longitudinally extended in paradermal section, however in contrast to the foregoing species, the parenchyma beneath is only c. two layers thick and delimited below by a layer of smaller sub-rectangular crystalliferous cells: quite

unmistakably the testal I.E.. The exotegmen is a single layer thick, the cells columnar in T.S., and very long, at least six times and probably nine times as wide as high in L.S. (it is difficult to be sure from Corner's data) with tapered ends and thick pitted walls. Pockets of sub-palisade cells occur intermittently in this layer. The endotegmen is depicted as parenchymatous and c. five layers thick with the central ones crushed. To confirm Corner's observations, material of a named american species, T. pallida Sw. was investigated. This was closely similar to the foregoing in the very small testal I.E., very thin testal mesophyll and single layer of long exotegmic fibres. It is difficult to make a good comparison based solely upon Corner's drawings, but T. pallida appears to have longer fibres with much thinner thickenings. The chalaza in this species occupies only 5-10% of the entire coat. The fleshy structure appears to be a raphe-funicular aril as Corner describes for his species.

Before continuing the survey of Trichilia, De Wilde's (1968) monograph of the African Trichilia was consulted. Here he highlights the distinctiveness in this context of T. capitata and draws attention to its morphological links with the American species. Although no spirit material was available, a fruit taken from a fine herbarium collection revived extremely well. Here the normal Meliaceous seed-coat obtains, quite unlike T. monadelpha & T. emetica, but resembling the American species and having in addition a raphe-funicular aril. Apart from these similarities, the structure is very different in many characters from the American species, and much more elaborate. The testal O.E. is strongly longitudinally elongated on the dorsal surface in paradermal section, the thickened, distinctively bi-coloured periclinal walls almost occluding the lumen. The mesophyll, though similarly of 2-3 layers, is uncrushed,

the cells much larger, the walls thick and pitted. The exotegmen is multi-layered, some of the lower tegmic layers becoming lignified, so that there are 3-5 layers of lignified cells rather than the single layer seen in the American species. The upper layer is columnar in T.S., as in the American species, but the fibres are proportionally shorter, 3-6 times as wide as high in L.S. and very much more heavily thickened, a distinct inner thickening, seemingly free of pits, being detectable. The lowest layers are much shorter in length and, in T.S., are all twice as wide as high, in marked contrast to the columnar upper layer. The endotegmen is parenchymatous but largely crushed.

Pseudobersama & the 'East African Group'

At this point was noticed the strong resemblance in seed-coat structure between T. capitata and Pseudobersama (which has already been investigated, monotypic in East Africa with 5-locular warty fruits, Plates 33-35). Here too, the testal O.E. is longitudinally extended, with a thick, bi-coloured o.p.w.; here too, the mesophyll is uncrushed, of rigid thick-walled cells; here too, the exotegmen is multi-layered and the distinct double thickening obtains, and the lowest layers are about twice as broad as wide. None of these characters is shared with any of the other Trichilia species surveyed. There are differences. The testal mesophyll of Pseudobersama has 3-4 layers and is more deeply pigmented, the cells are smaller and no pitting is detectable; the testal I.E. has no detectable crystals (the absence of the latter two characters perhaps due to the pigment obscuring them); the upper layer of the exotegmen has very short, sub-palisade cells scarcely wider than high and the second layer in T.S. is intermediate (isodiametric) between the upper columnar layer and the lowest, broad, layer. The seed has a funicular-raphe aril, as does T. capitata, but this one possesses a remarkable hair-pin

vascular bundle while the seeds are superposed. Despite these differences, the similarities between Pseudobersama and T. capitata in anatomy of testa, tegmen and aril are too strong to be entirely coincidental. A year later was examined material of what transpired to be a new species allied to T. capitata, Trichilia lovettii Cheek ined., which has the same suite of seed anatomical characters linking Pseudobersama and T. capitata (see above) but are otherwise unknown in the nine species of Trichilia surveyed. In addition, the fruits are slightly warty, intermediate between the other two species. These three species are referred to here as the 'East African Group'. In some of the seeds of T. lovettii , the raphe-aril scar is extremely broad, covering a wide area of the adaxial seed surface; the seed flesh is thin there, not forming a flap and so verging on the sarcotestal state, perhaps indicating a link with the partly sarcotestal seeds of the Malagasy Trichilia species.

Malagasy Trichilia species

Two species, Trichilia sp. 1 (Cheek, B1315) and Trichilia sp. 2 (Cheek, s.n.) were examined. They are closely similar to one another and resemble the American species in their easily crushed, thin-walled testal mesophyll, and single layer of long, relatively thin-walled exotegmic fibres. They differ from the American species in that the aril, although appearing similar, is not raphe-arillate, but locally sarcotestal over the micropyle and adaxial surface.

Trichilia grandifolia

This is the most distinctive of the Trichilia species considered here. It seems closest to T. emetica and T. monadelpha in Africa in that its seed-coat is 2/3 unitegmic (pachychalazal). The anatomy of the bitegmic portion is not matched elsewhere. The extremely thick (30 cells),

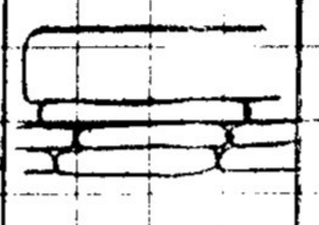


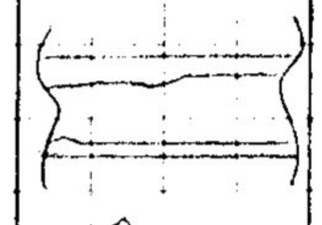


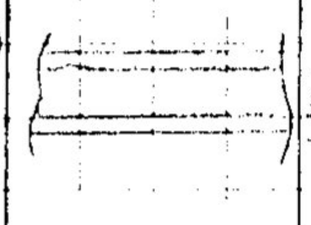
| TAXA | PTERO-RHACHIS | PSEUDO-BERSAMA | CAPITATA & LOVETTII | TRICHILIA | GRANDIFOLIA | MONADELPHA & EMETICA | MALAGASY SPECIES (2) | HEYNEA TRIJUGA | WALSURA PINNATA |
|---|---|---|---|---|---|---|---|---|---|
| TESTA: O.E. SHAPE UNUSUAL THICKENING | ISODIAMETRIC | LONGITUDINALLY EXTENDED | PERICLINAL WALL OCCLUDES HALF OR MORE OF LUMINA | | UNKNOWN | ± ISODIAMETRIC | | HIGHLY COLUMNAR ANTICLINAL CONS. LINEAR LUCIDO | LONGITUDINALLY EXTENDED RADIAL BARRIER ANTICLINAL WALLS |
| TESTA: MESO. NATURE NO LAYERS | UNCRUSHED 4 | UNCRUSHED THICK-WALLED 3-6 | UNCRUSHED WALLS THICK & PITTED 2-3 | | ? UNCRUSHED c.36 | NONE | CRUSHED 2-3 | UNCRUSHED 3 | UNCRUSHED SPONGY-BARRIER TAPPING? |
| TESTA: I.E. CRYSTALS? | ✓ | OBSCURED? | ✓ | | ? | ✓ | ✓ | ✓ | — |
| TEGMEN: EXOTEGMEN: NO LAYERS | 1 | 7 | 3-5 | | 0-1 | — | 1 | 8 | 0-1 |
| TEGMEN: EXOTEGMEN: SHAPE | SUB-PALISADE | | | | SHORT FIBRES | NONE | LONG & FIBROUS | | SHORT FIBRES |
| TEGMEN: EXOTEGMEN: I.S. | | | | | NOT KNOWN | NONE | | | |
| TEGMEN: EXOTEGMEN: T.S. | | | | | | NONE | | | |
| TEGMEN: EXOTEGMEN: DOUBLE THICKENED | ✓ | ✓ | ✓ | | ? | NOT APPLIC. | — | — | — |
| TEGMEN: ENDO. | V. SL. CRUSHED | CRUSHED | CRUSHED | | SL. CRUSHED | NONE | CRUSHED | SL. CRUSHED | UNCRUSHED THICK-WALLED |
| TEGMEN: I.E. | DISTINCT | NOT-DISTINCT | NOT DISTINCT | | NOT DISTINCT? | NONE | ± DISTINCT | DISTINCT | NOT DISTINCT |
| FLESHY APPENDAGE TYPE | CHALAZAL ARIL | RAPHE-FUNICULAR ARIL | RAPHE-FUNICULAR ARIL | | SARCOTESTA! | SARCOTESTA (PSEUDO-ARILLATE) | RAPHE ARILLATE BUT SARCOTESTA | RAPHE ARILLATE | PRE-RAPHE-FUNICULAR ARIL |
| VASCULAR SUPPLY: PRE-RAPHE IN ARIL? | PRE-RAPHE | — | — | | — | — | — | — | PRE-RAPHE |
| VASCULAR SUPPLY: INTEGUMENTS | VASC. ARIL | — | — | | — | — | — | — | VASC. ARIL |
| VASCULAR SUPPLY: OTHER | NO RAPHE | RAPHE-FUNICUL HAIRPIN | — | | IN TESTA | IN SEEDCOAT (PACHYCHALAZAL) | — | — | — |
| HILUM SHAPE | <2:1 | <2:1 | <2:1 | | <2:1 | <2:1 | <2:1 | >9:1 | >9:1 |
| RADICLE | JUST INCL. | EXSERTED | EXSERTED | | DEEPLY INCLUDED | INCLUDED | ± INCLUDED | JUST INCLUDED | JUST INCLUDED |
| ENDOSPERM? | — | ✓ | ✓ | | — | — | — | — | — |
| SEEDS SUPERPOSED? | — | ✓ | — | | — | — | ✓ | — | — |
| TROPY | ± ORTHOTROPOUS | | | | ± ANATROPOUS | | | | |
| INTEGUMENTS | BITEGMIC | | | | TWO-THIRDS PACHYCHALAZAL | COMPLETELY PACHYCHALAZAL? | | | BITEGMIC |



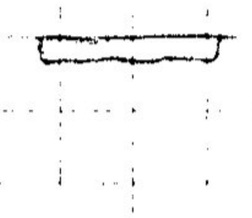














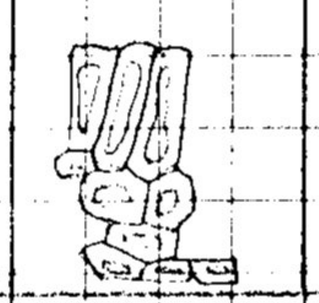




TABLE 5

GENERIC DISTRIBUTION OF SELECTED SEED CHARACTERS IN THE FLESHY-SEEDED GENERA OF TRICHILIEAE

vascularized, sarcotestal testal mesophyll and tegmen with weakly expressed exotegmic fibres, are unknown elsewhere in the species of Trichilia examined.

In describing T. lovettii as a new species, it was pointed out that it has close links morphologically with T. capitata and Pseudobersama, and that these, the 'East African Group' are quite distinct from the Guineo-Congolian species (e.g. T. monadelpha and T. emetica ) and seem more closely related to the American and Malagasy species on these characters (Cheek, 1989c). Seed anatomical characters, as outlined above are completely concordant with this analysis. They seem strongly correlated with the morphological characters. There is no doubt that the variation in seed structure illustrated here (summarized in table 5 ) can be of great use in determining species affinities in this genus.

Pterorhachis (plates 36 and 37) is distinguishable from all Trichilia species morphologically by having more than two appendages from each locule, and from most by its stellate hairs and winged rhachides (Pennington and Styles 1975). In seed structure it is much more distinct from Trichilia than is Pseudobersama, the other African satellite genus, having sub-orthotropous seeds with a vascularized chalazal aril and pre-raphe unusually with 2 vascular bundles and an associated furrow and slight fleshiness above, none of which is known in Trichilia. The evolutionary significance of these is discussed under 'Phylogenetic Speculation'.

The seed anatomy has few outstanding characters excepting the tannin-filled cells of the crystalline testal I.E. An affinity with the East African Group of Trichilia is suggested by the exotegmen which is sub-palisade and with a double thickening. Unlike that group, there is

only one layer of lignified cells and the testal mesophyll, although similarly uncrushed, is not so thick-walled; moreover the testal mesophyll, although similarly uncrushed, is not longitudinally extended. An affinity with Walsura and Heynea is suggested by the well-developed pre-raphe with an indication of fleshiness. Heynea also has an uncrushed tegmen, but this character also occurs sporadically in Trichilia with an accompanying, if undifferentiated I.E.

Walsura (plate 38) seems to be distinguished morphologically from Trichilia by its pulvinate petiolules and indehiscent fruit. Material of 3 species was studied ( Terry Clark now suggests c.14 species in the genus) but only one in detail, W. pinnata Hassk. The anatomy of this species is quite different from anything seen in Trichilia. This species has radial anticlinal wall thickenings in its testal O.E., not seen in any other member of the tribe. The mesophyll is aerenchymatous, the cells with intercellular arms (not seen in Trichilia.) Its remarkably thick exotegmen (eight layers thick, even thicker than that of Pseudobersama: seven layers) has the upper four layers longitudinal, the lower 4 transversely orientated. Cross-ply exotegmen has otherwise only been noted in Munronia (Turraeeae). In addition, this is the only species, with the possible exception of Heynea, noted as having the upper layer of fibres isodiametric in T.S. (all others columnar). The fibres are also unusual in the small size of their pits and rounded endwalls. The anatomy is further unusual in that the I.E. of the aril that completely ensheathes the testa is firmly united by adhesion with the testal O.E. and has a thicker o.p.w.. No other genus has been noted with the aril supplied by an extension of the pre-raphe. This species shares with Heynea the presence of a long (length:breadth ratio >9:1) encircling

hilum, a pre-raphe and an all-enclosing pre-raphe-funicular aril and the many layered aerenchymatous testal mesophyll.

Through the kindness of Terry Clark, two further species were examined, both considered by him to be outliers of W. pinnata and its associated species which form the bulk of the genus. 'W. rhomboidea', which has weakly dehiscent fruit (teste Terry Clark), also has strongly arillate seeds apparently with pre-raphe-funicular aril as in W.pinnata, but the material available was highly immature and no other comparison could be made. A third species investigated, W.chrysogyne, had seeds lacking any fleshy aril and are apparently unitegmic, possibly pachychalazal, certainly lacking the normal Meliaceous seed-coat stratification.

Heynea (plates 39 and 40) has lately been sunk into Trichilia (Bentvelzen, 1962), largely on the grounds that it has dehiscent fruits and that the differences Harms (1940) gave for discriminating Trichilia and Heynea cannot be applied through overlapping of their characters. Some earlier authors such as Kurz (1875), Baillon (1875), Harms (1896, but recanting in 1940), have united it with Walsura. However, as Bentvelzen (1962) points out, 'Up to the present day Heynea has almost unanimously been distinguished as a separate genus in the alliance of Walsura and Trichilia'. Pennington and Styles stated that 'Although we have some strong reservations, we agree with Bentvelzen (1962) that, on the basis of evidence presently available, Heynea should be reduced to Trichilia'.

The seed anatomical evidence shows that Heynea trijuga Roxb. ex Sims is much more closely related to Walsura than to Trichilia (see Walsura above for shared characters.) yet quite distinct from the species of Walsura studied. It is distinct from all the tribe in that the testal O.E. is strongly columnar, the lumina often hour-glass shaped, the tegmen heavily

vascularized. Like Trichilia grandifolia, the testal mesophyll is also multi-layered, sub-aerenchymatous and the integuments are vascularized, the exotegmic fibres poorly expressed. However, that species does not have an aril of any sort and much more importantly it is the testa that is vascularized. Such a difference normally separates families and is surely sufficient for the delimitation of genera. Heynea trijuga is also unusual in the lack of testal I.E. crystals (otherwise only absent in Pseudobersama and perhaps present there but masked by pigment). This makes delimitation between testa and tegmen less sure, but is convincingly demonstrated near the chalaza where the testal I.E. is present as a distinct and unbroken layer of isodiametric cells above the similarly distinct longitudinally extended cells of the upper exotegmen layer in which exotegmic fibres are occasionally present (see plate 40 ).

Heynea trijuga seems to be quite constant in its anatomical characters (see description: variation). In order to be completely sure of the re-instatement of the genus, it would be useful to look at the seed structure of the second species ( H. velutina How and Chen ) recognized as distinct by Bentvelzen, to see if it also possesses the remarkable characters of H. trijuga. It would also be useful to look at more 'typical' Walsura to see whether any of these show additional Heynea characters, unlikely though this is. Although the data are far from complete, on a wealth of seed anatomical characters, Heynea is very distinct from Trichilia and if it is to be united with any genus, it must be Walsura. However, the evidence presented here suggests that it be maintained as a genus in its own right. This is in accordance with the cytology recorded by Khosla and Styles (1975).

Non-fleshy-seeded genera.

Malleastrum (plates 43 & 44) differs from Trichilia in its valvate petal aestivation and fleshy indehiscent fruit with a non-fleshy seed. In the principal species investigated, M. gracile Leroy, 80-85% of the seed-coat is composed of a pachychalaza. The remaining bitegmic portion , despite being only six cell-layers thick, has both key characters of a Meliaceous seed-coat, that is, a fibrous exotegmen and a testal I.E. with prismatic crystals, but the fibres of the former are scattered and not detectable in every section. The aerenchymatous, slightly tanninized testal mesophyll also occurs below the epidermis of the vascularized pachychalaza and the whole of the latter is reminiscent of the state in Lepidotrichilia volkensii: perhaps an affinity is indicated here. The fibres are isodiametric in T.S., rather than columnar (the normal condition in Trichilieae) which may well indicate a derived state. The paucity of fibres and their small diameter suggests that they are on the verge of being lost and that the species is becoming unitegmic by total loss ( by absorption ) of the tegmen - again a derived condition. Alternatively, the pachychalaza may expand and the two integuments be reduced to one this way.

It may be possible to delimit this genus on seed anatomical characters, perhaps by a combination of fibre shape and the presence of large epicotylar hairs, but since the former may not always be expressed and the latter were not rigorously sought in other genera of this tribe, this seems unlikely.

Infra-generic variation. Other species of this genus, for example M. mandenense Leroy, do show total loss of the tegmen. By the line of reason used above, this species thus appears more advanced, even though by other indicators, such as ovary locule number, it appears less advanced. In

other instances, seed anatomy appears to tie in more closely and predictably with morphological characters. For example M. psammophilum Leroy, which in my view is almost conspecific with M. gracile, is virtually indistinguishable anatomically except in a thicker and more compressed testal mesophyll ( 7-9 layers versus 3-5 ) and less verrucation of the epicotylar hairs, the former having been regarded (e.g. Turraeeae) as one of the least reliable seed characters. In M. isalense Leroy, undoubtedly distinct from M. gracile, the testal mesophyll is of 20-30 cell layers and much more significantly different from M. gracile than that of M. psammophilum.

Lepidotrichilia (plates 41 & 42) is distinguished morphologically by its stellate hairs, valvate aestivation and indehiscent fleshy fruits with 1-5 seeds contained in a thinly membranous to cartilaginous endocarp. The former two characters occur very rarely (and are not correlated) in Trichilia (Pennington and Styles, 1975). The seed-coat lacks either a testal crystalline I.E. or a lignified exotegmen and if there are two integuments, there is no detectable delimitation between them. The heavy vascularization, in combination with these deficiencies is suggestive of pachychalazal construction, but this will not be confirmed until earlier seed stages are examined. It is possible (though less likely) that this seed is unitegmic by crushing of the tegmen. This type of seed construction, being depauperate in characters, is very difficult to compare with any but other such genera, since bitegmic seed-coats, the usual condition, are not directly homologous with that state.

The aerenchymatous upper parenchyma and elongated O.E. may indicate a link with Walsura, but such an affinity must be regarded as extremely

tenuous if based solely on these characters. The species examined here, L. volkensii (Harms) Leroy, can be regarded as having the most reduced fruit in the genus (e.g. fewest locules, smallest seeds). Examination of the less specialized species in Madagascar might reveal a bitegmic seed-coat containing characters more useful in the matter of indicating generic affinities.

Astrotrichilia (plates 47 and 48) is well segregated from Trichilia on morphological characters in its stellate indumentum and indehiscent fruits with a thick and very hard pericarp. In seed structure, the seeds are very different indeed from those of Trichilia species. The mature seeds are laterally flattened, the radicle is strongly exserted, the cotyledons foliar, the endosperm copious and the orientation of the embryo on the same line as the hilum- suggesting orthotropy. The structure of the seed-coat is remarkable in that the testal O.E. has stomates and that the exotegmic fibres are, in T.S., about twice as wide as high, whereas typically, they are columnar in this tribe- and certainly no other genus in the tribe has been recorded with with these traits. The expression of the endotegmen and presence of a distinct and uncrushed tegmic I.E. is unusual and unspecialized, but is also seen in some Trichilia, Pterorhachis and Ekebergia species. Caution should be used in giving weight to this character since whether these cells are present or not in the mature seed-coat seems to depend solely on whether or not they are subject to crushing during development.

Infra-generic variation seems relatively small. Astrotrichilia sp. 1 is extremely similar in structure, but has much shorter exotegmic fibres with larger pits.

Ekebergia (plates 45 & 46) is distinguished from Trichilia by its indehiscent fruits with a separate bony endocarp around each seed. The seeds, as represented by those of E. capensis Sparrm. have a slightly curved seed embryo, exserted radicle, endosperm and sub-hemi-anatropy which is reminiscent of Turraeeae. But the unspecialized anatomy of the seed-coat is similar to that of Astrotrichilia asterotricha, especially in the presence of an endotegmen and tegmic I.E. and to an extent in the shape of the testal O.E.. However, the exotegmic fibres here are much shorter, sub-palisade and in T.S. are isodiametric to shortly columnar with large pits, reminiscent of the 'East Africa Group' in Trichilia. The most striking affinity suggested is with Pterorhachis, which also has this exotegmen, together with the persistent endotegmen and tegmic I.E. (less reliable characters) and the presence of a pre-raphe. The large, crescent-shaped adaxial chalaza is not known in any other genus in the tribe.

Cipadessa (plate 50) is distinguished from Trichilia by the valvate aestivation of the corolla, and by the indehiscent fruit containing five pyrenes. As is the case with Ekebergia, the curved embryo, sub-hemi-anatropy, exserted radicle and copious endosperm suggest a link with Turraeeae and the genus was indeed placed there by Harms (1896). According to Pennington and Styles (1975) however, other morphological characters indicate its placement in Trichilieae, though in secondary xylem it is very distinctive and unlike that of any other member of the tribe, showing links with Vavaea.

Although the seed-coat is clearly of bitegmic origin, having both exotegmic fibres and a crystalline testal I.E., the latter is largely crushed and absorbed as are all other cell layers apart from exotegmen

and testal O.E.. This depauperate aspect, first reported by Corner (1976), makes it difficult to relate to other genera, or comment on tribal placement, simply for want of characters. Apart from the extent of the reduction, the only other unusual anatomical character is the completely tannin-filled testal O.E., which is not seen elsewhere in the tribe. The overall seed structure suggests a link with Ekebergia (in which genus it has been accommodated), or possibly Astrotrichilia. The sub-columnar (T.S.) exotegmic fibres are quite in keeping with the tribe and the reduced seed-coat together with long fibres might suggest an advanced placement within it.

Owenia (plate 49) is distinct from Trichilia in its indehiscent fruit and uni-ovulate loculi. It is unique in the family in its extremely thick, woody endocarp. Astrotrichilia also has a thick, tough pericarp, but that is derived from the high concentration of sclereids in the thick mesocarp, rather than multi-layered endocarp.

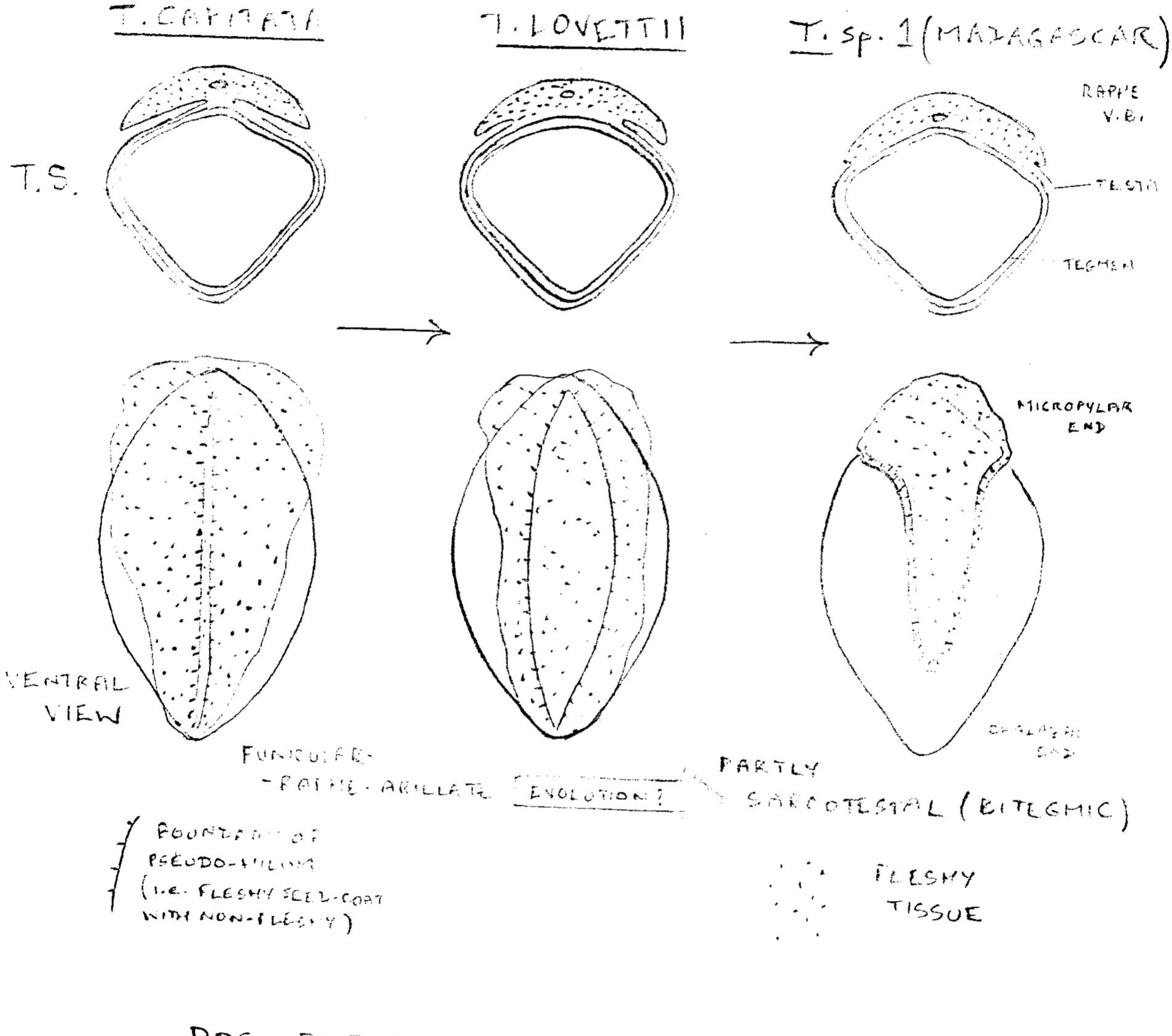
The gross surface morphology of the seed, plano-convex in lateral view with one end beaked and a large, long, central hilum, is remarkably similar to that in Astrotrichilia. But that genus has strongly flattened and orthotropous seeds. The similarity may be a convergence caused by the shared woody indehiscent fruit. The internal seed structure shows similarities with Ekebergia which also has persistent endosperm, hemi-anatropy and a slightly exserted radicle. The seed-coat anatomy appears unitegmic and is probably pachychalazal, being composed of a heterogeneous assemblage of thick- and thin-walled parenchyma, tannin-filled cells, sclereids and vascular bundles. A unitegmic seed-coat structure is recorded from Malleastrum and Lepidotrichilia, but it seems very likely that these seed-coats have arisen in parallel,

possibly within each genus (as has occurred in Trichilia and Walsura), rather than all being of a common origin (see phylogenetic speculation). In order to best find the affinities of Owenia using seed-coat anatomy, it will be necessary to find a representative with the primitive, bitegmic condition and compare that with other genera.

In brief, whilst the seed structure, particularly seed-coat anatomy, is extremely useful in resolving generic limits and determining their affinities and intra-generic alliances in the fleshy-seeded genera, this is much less so in the non-fleshy-seeded genera. There, the seed-coat provides far fewer characters, apparently owing to its being usually crushed or unitegmic. Unlike the fleshy-seeded genera, general organization of organs seems to provide as many useful characters as the seed-coat.

## TRIBAL DELIMITATION

The Trichilieae are far less easily defined on seed characters than are, for example, the Turraeeae. the only characters that seem to draw them together are those of anatropy and exotegmic fibres columnar in T.S. and, perhaps, the presence of a pre-raphe vascular bundle, but these features do occur in other tribes (though not the Turraeeae) and are far from always present in the Trichilieae, notably Astrotrichilia where the seeds appear both orthotropous and the exotegmic fibres are the reverse of columnar in T.S., that is, wider than high. This may indicate that the Trichilieae should be split further into additional segregate tribes or, perhaps re-united with its segregates to form a more coherent, if unwieldy, unit. But the evidence for doing so is far from convincing yet, and even were a greater body of seed anatomical evidence available, it is likely that sets of correlated morphological characters would have to be




POSSIBLE EVOLUTION OF SARCOTESTAL (BITEGMIC) FROM THE FUNICULAR-RAPHE-ARILLATE STATE

FIG. 4

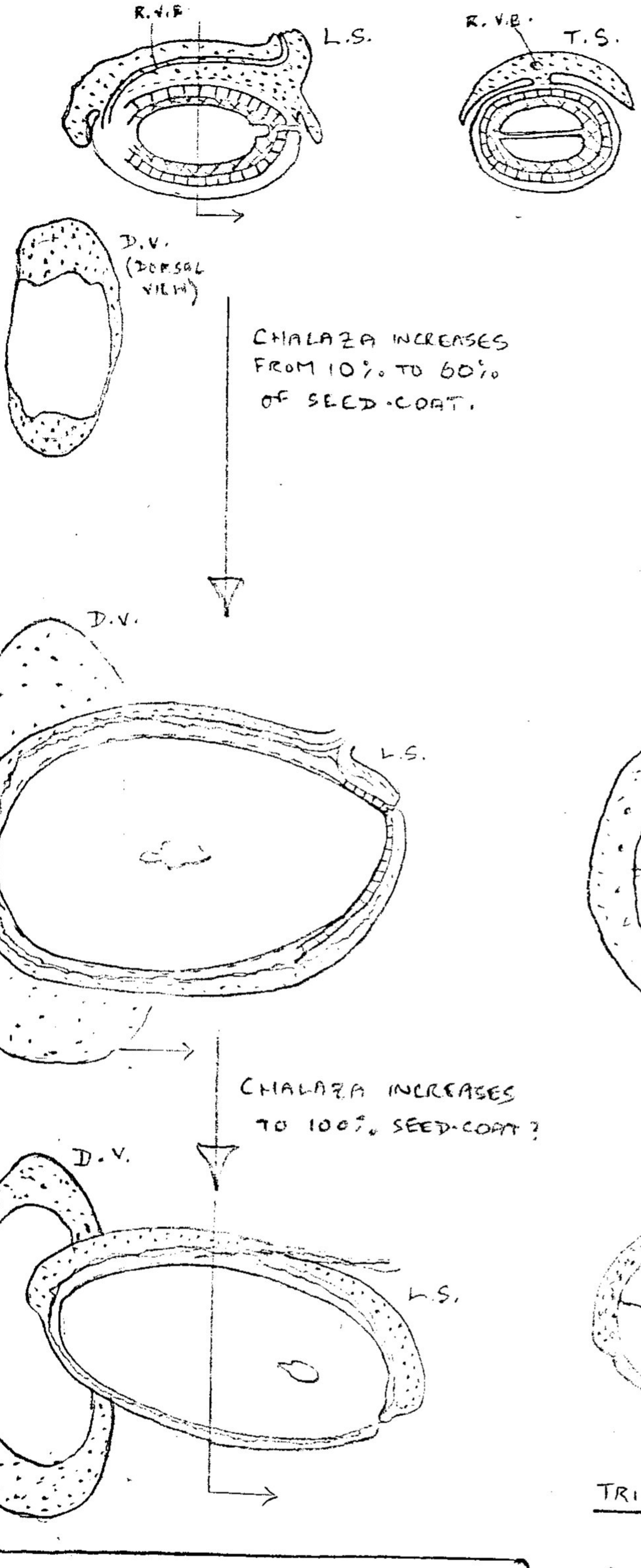
described before such a decision was accepted. For the moment, it seems best to accept the Pennington and Styles arrangement.

## PHYLOGENETIC SPECULATION

### Evolution in Trichilia.

The persistent endosperm, exserted radicle and funicular-raphe aril that characterize the East African Group are considered primitive characters by Sporne, (1948, 1974) as compared with no endosperm, included radicle and sarcotestal seeds prevalent in the other species of Trichilia. The accompanying short, sub-palisade exotegmen of this group (in Pseudobersama L.S., only just wider than high), earlier considered primitive in the Turraeeae can also be considered as primitive here. The multi-layered exotegmen may be an advanced character - it was so considered in Turraeeae. The nearest relatives to the East African Group, on the basis of the seed anatomical characters considered here, must be the bitegmic, funicular-raphe-arillate American species, advanced because of their long fibres and thin-walled, crushed mesophyll. They are closely followed by the bitegmic but partly sarcotestal Malagasy species, similarly advanced, perhaps from an ancestor such as T. lovettii with an incipient sarcotesta- see fig. 4.

The unitegmic seeds of the Guineo-Congolian species may as well belong to another family for all the similarity they show with the East African Group. However, T.grandifolia, the relict species from the island of Saõ Tomé, with partly (1/3) bitegmic seeds, may well represent a 'stepping stone' between the bitegmic condition manifest in the East African Group and the unitegmic state. The lack of other intermediates or bitegmic species in the Guineo-Congolian area may be explained by the mass extinction believed to occur there in the Pleistocene era when a period



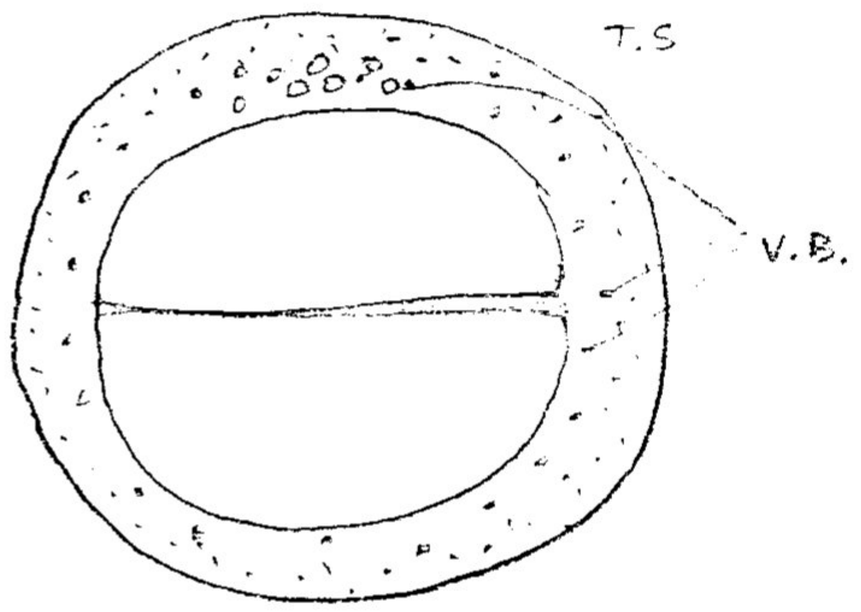

'EAST AFRICAN GROUP'

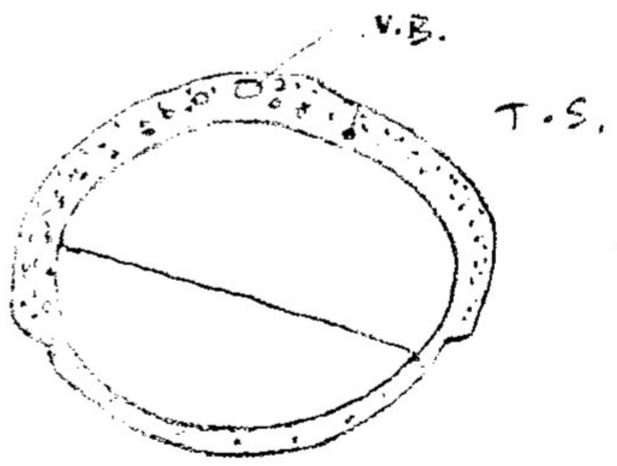
1. BITEGMIC
2. SEED LENGTH 7-9 mm
3. FUNICULAR-RAPHE-ARILLATE

NOTE. A. EXSERTED RADICLE,
B. ENDOSPERM:
'PRIMITIVE' CHARACTERS (SPORNE, 1948; MARTIN, 1947) NOT SEEN IN OTHER AFRICAN TRICHILIA.

TRICHILIA GRANDIFOLIA
(fide BOESEWINKEL, 1981)

1. 1/3 BITEGMIC, 2/3 UNITEGMIC
2. SEED LENGTH 70-100 mm (PACHYCHALAZAL)
3. SARCOTESTAL

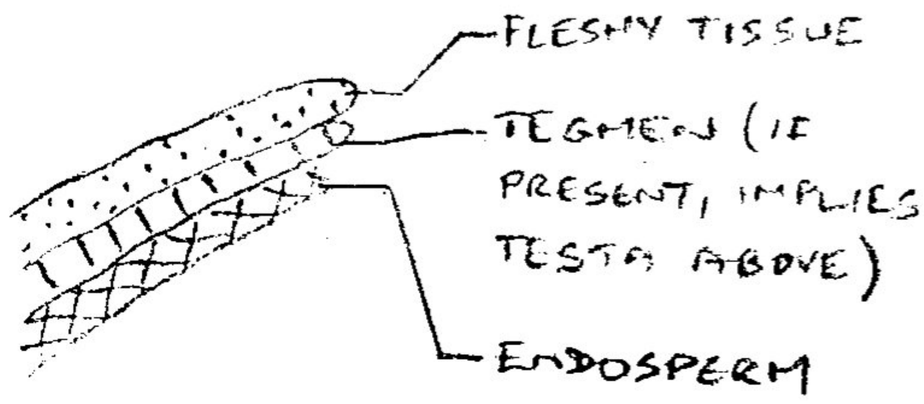



TRICHILIA MONODELPHA, EMETICA & DREGEANA
(& PROBABLY ALL GUINEO-CONGOLIAN SPECIES)

1. COMPLETELY UNITEGMIC (PROBABLY PACHYCHALAZAL)
2. SEED LENGTH 11-25 mm
3. PSEUDO-ARILLATE (PARTLY SARCOTESTAL)

FIG. 5 PHYLOGENETIC SPECULATION IN AFRICAN TRICHILIA: RE-EVOLUTION OF THE 'ARIL'.



of aridity accompanied the warming of the Atlantic ocean. The sea off East Africa remained much cooler, so that it is possible that various mountain ranges in East Africa have acted as refugia though the evidence for this is rather thin (Lovett pers. comm.). Possibly, a small mountainous island such as Saõ Tomé, in the Atlantic might also be buffered against desiccation. The existing Guineo-Congolian species would largely be the result of subsequent, relatively recent speciation from an ancestor resembling T. grandifolia. Indeed, they are closely similar and compared with the variation amongst, for example, the American species (Pennington and Styles, 1981), extremely uniform. If this was the case, it seems likely that the 'arillate' condition has arisen more than once (fig.5).

The seeds of T.grandifolia at 70-100mm long are an order of magnitude larger than those of the East African Group (7-9mm long.). Corner has pointed out that larger seeds are an advantage for establishment in a tropical forest where a seedling may need large food reserves to survive for long enough to have an opportunity to grow, i.e. whilst waiting for a gap to form above it. Boesewinkel (1981) has pointed out that the occurrence of pachychalazy and a highly vascular seed-coat in T. grandifolia is connected with the transport of nutrients to the large embryo. The evolutionary path to T. grandifolia seems clear, but what is it from T. grandifolia to T. emetica and T.monadelpha? Why does T. grandifolia appear a relic and isolated from other African Trichilia species? The answer may lie in the fields of seed predation and seed dispersal. Predation of developing seeds is often overlooked as a selective factor (Herrera, 1984 ). Meliaceae seeds, in my experience, are often infested with insect pests during development. It is possible that the seeds of the Guineo-Congolian group, being smaller but just as highly

PROTO-PSEUDOBERSAMA

(cf. TRICHILIA CAPITATA, PLATE 32)

PSEUDOBERSAMA

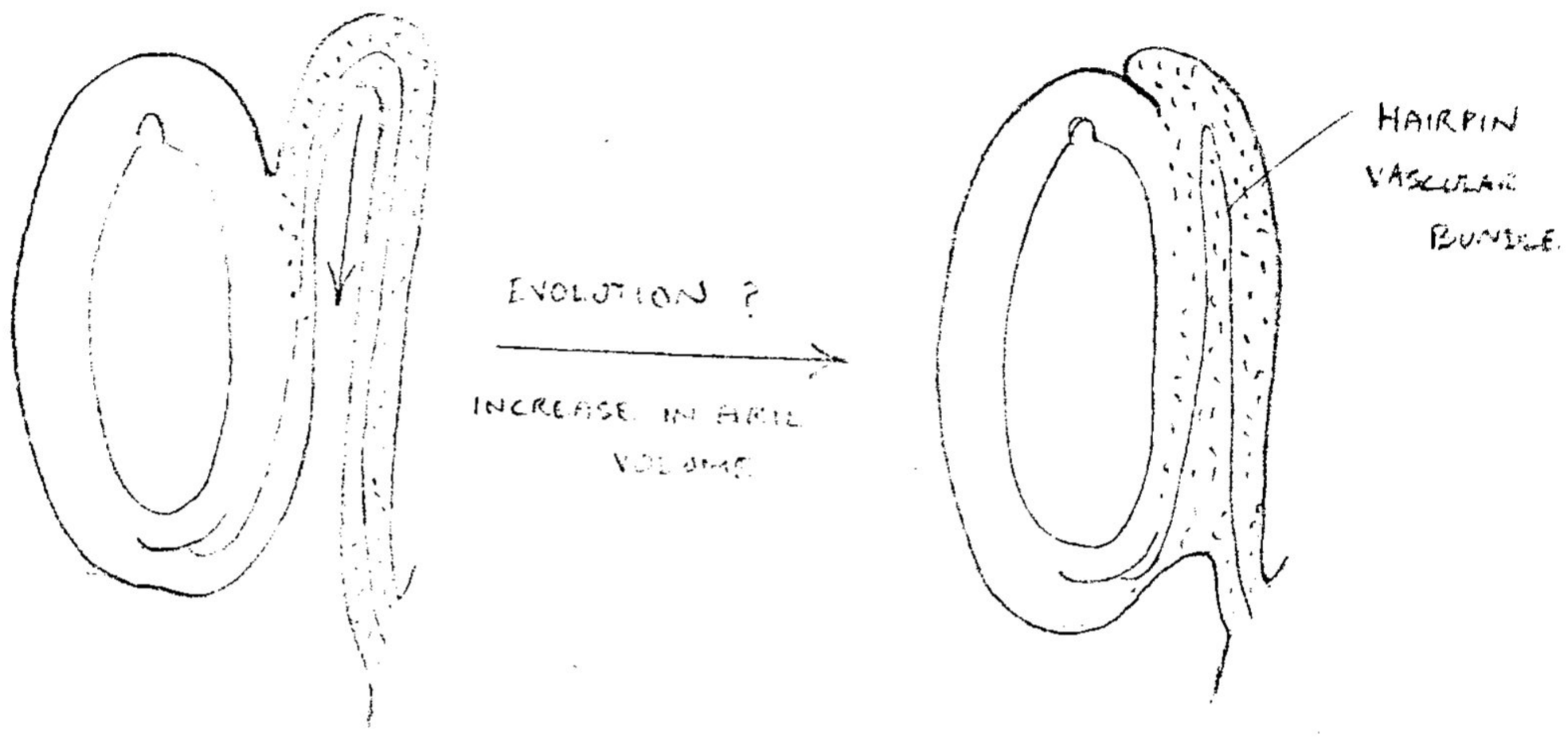



FIGURE 6. PHYLOGENETIC SPECULATION:

DERIVATION OF HAIRPIN VASCULAR BUNDLE IN PSEUDOBERSAMA

FLESHY TISSUE

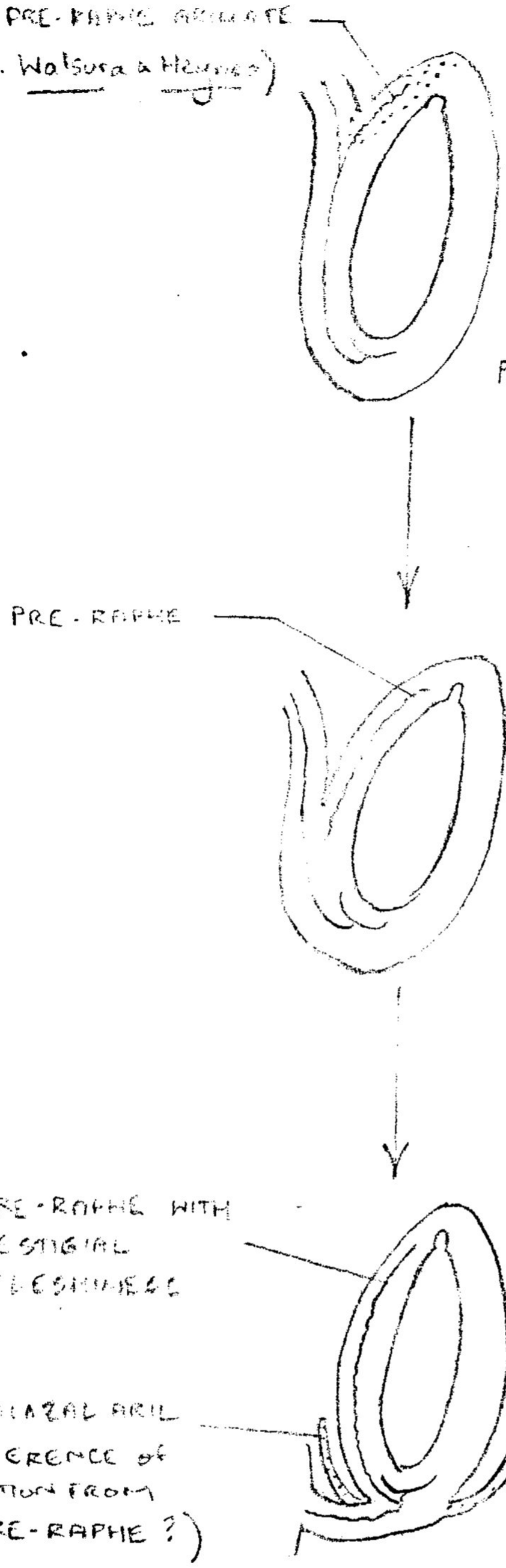
vascularized as their hypothetical ancestor (presumed similar to T. grandifolia) take less time to develop to maturity and are therefore less subject to predator pressure. Alternatively the smaller seed type of the Guineo-Congolian species might favour longer distance dispersal by birds and consequently the greater likelihood of arriving at a gap. The massive seeds of Trichilia grandifolia are surely too large for bird dispersal in Africa (see Ecology). On the other hand, the explanation may purely be that the immediate ancestor of the Guineo-Congolian species was on the mainland to re-colonize when mesic conditions returned after the Pleistocene, whereas the 'grandifolia' type was restricted to the island. With present data one can only speculate.

Evolution of the satellite genera.

The relationship of Pseudobersama with Trichilia in East Africa is undeniably extremely close and it seems that they must share a more recent common ancestor than with any other species of Trichilia. Thus Pseudobersama, if maintained, leaves Trichilia as a paraphyletic group: inadmissible by cladistic methodology (cf. Humbertioturraea/Turraea in Turraeeae). Is Pseudobersama distinct? As far as Trichilia is concerned it is perfectly distinct in its 5(-4)-locular capsules, the sheer thickness of its woody valves and in its hairpin funicular-raphe vascular bundle. All these can be viewed as derived characters. It is only a small step from the 3(-4) locular condition in Trichilia to the (4-)5 locular one in Pseudobersama (or vice versa: the evolutionary polarity is uncertain). The thick, woody, armed capsules are surely a device to reduce predation on immature seeds and the evolution of the hairpin vascular bundle may be correlated with an increase in volume of the fleshy aril, perhaps increasing its attractiveness to dispersing agents

(see fig. 6). It is difficult to be sure of relating the satellite genera to Trichilia since so many of the American Trichilia (the largest and morphologically most variable element of the genus) remain anatomically unknown and it is possible that amongst these exist suites of seed anatomical characters, hitherto unknown in the genus, that are evidence of links with, perhaps Walsura or Heynea. This is considered unlikely, since the two species (picked at random) examined in detail are closely similar in general structure and differ only in minor characters. The evidence suggests that Pterorhachis is the least specialized member of the tribe apart from its stellate hairs and sub-orthotropous seeds, the derivation of which from the anatropous state may be viewed as in fig.7. Pterorhachis shows links with all the other genera in the tribe: it is the only genus which combines the sub-palisade, double thickened exotegmic fibres of the least specialized Trichilia species, and Pseudobersama (East African Group) with the well developed pre-raphe and associated fleshiness of Heynea and Walsura.

As was pointed out earlier, Heynea and Walsura are much more closely related to each other than any other genus; united by the possession of a pre-raphe, funicular-pre-raphe aril and an elongated hilum, none of which characters is reported in Trichilia (at least in Africa). The cytological evidence supports this, since both genera have x=14 of closely similar karyotype, whereas Trichilia have x= 23 or 25 (Khosla and Styles, 1975). The common ancestor of Trichilia and Walsura/Heynea is clearly very distant. To some extent, Heynea and Walsura seem to have evolved in parallel with Trichilia, if the observation of unitegmy (possibly chalazal) in Walsura chrysogyne is correct, since this has clearly occurred independently of the same state in African Trichilia. It is curious that there is no suggestion of indehiscence in Trichilia sensu




PROTO-PTEROROHACHIS

EVOLUTION?

① LOSS OF RAPHE

② LOSS OF PRE-RAPHE / RAPHE FLESHINESS.

PTEKORHACHIS

FIG. 7 PHYLOGENETIC SPECULATION: DERIVATION OF ORTHOTROPY IN PTEKORHACHIS

stricto. Walsura, though largely indehiscent, is clearly only recently so, as the vestigial dehiscence in 'W. rhomboidea' indicates. A line can be traced starting from 'W. rhomboidea' with vestigial dehiscence, thin, largely woody pericarp, with pronounced valve sutures and arillate seeds to Walsura pinnata Hassk. and its allies with a thicker, more succulent and only slightly woody pericarp which seems in the ripe fruit to produce a jelly surrounding the seed proper (testa Terry Clark). In the isolated W. chrysogyne, the pericarp is extremely thick and not woody and the seeds lack a fleshy aril, this function apparently being taken over entirely by the pericarp. On the sparse data available to me, 'W. rhomboidea' would seem to represent the unspecialized end of the genus and W. chrysogyne the most advanced.

The relationship of dehiscent and indehiscent fruited genera.

If Walsura is any indication, indehiscent fruits are derived from dehiscent fruits, since in this instance, indehiscence is correlated with a shift to unitegmy and this state is unquestionably derived from the bitegmic condition. In Walsura, loss of dehiscence accompanies loss of seed fleshiness, and transference of the attractive function to the pericarp. Thus, within a single genus the gap between the two groups of genera considered here is bridged. The question arises, are the indehiscent-fruited genera all derived from a single ancestral indehiscent-fruited genus that has subsequently radiated to give the array of present-day indehiscent-fruited genera or has indehiscence arisen in parallel from several ancestors, perhaps on as many occasions as there are indehiscent-fruited genera? The balance of evidence tends to favour the latter, largely because the seed anatomical data suggests that whilst Ekebergia, for example, shows many similarities to Pterorhachis,

Astrotrichilia clearly has affinities in other directions, perhaps not with any modern dehiscent-fruited genus. It is not necessarily the case that each indehiscent-fruited genus has arisen independently of the others. Lepidotrichilia and Malleastrum for example, show a striking anatomical similarity and this is correlated with morphological similarities: such as valvate corolla aestivation. Possibly they arose from a common indehiscent-fruited ancestor.

It should be emphasized that these lines of affinity are rather tenuous, far more so than those drawn in the fleshy-seeded group of genera. This is because the transition to an indehiscent fruit seems linked with a reduction in the number of taxonomic characters in the seed-coat, either by the crushing in cell layers (e,g. Cipadessa where the bitegmic seed-coat is reduced to only two cell layers thick) or by the shift to unitegmy and the concomitant loss of the testa and tegmen and all the structures they contain, e.g. Owenia, Lepidotrichilia and Malleastum (integuments completely lost). It is noticeable that, as a proportion of species surveyed in this tribe, unitegmy occurs far more frequently in the indehiscent-fruited genera (60%) than the dehiscent (30%). Whether indehiscence directly favours unitegmic development (or perhaps vice versa) or whether, both being advanced characters, there is simply a greater probability of them tending to occur together in corresponding taxa, is difficult to answer. Unitegmy by loss of an integument through absorption and crushing in a bitegmic seed is only to be expected where the endocarp takes over the protective function of the seed-coat and makes the latter partly redundant. But although this condition is approached in Cipadessa, most of the unitegmic seed-coats in the tribe, insofar as one can judge without conducting exhaustive developmental studies, are pachychalazal.

A possible advantage of a pachychalazal seed-coat has already been postulated above under 'the fleshy-seeded genera' as more rapid development of the seed through greater vascularization and hence more rapid supply to the embryo. It is difficult to construe how this might be an advantage in Owenia unless development of mature seed is constrained by pest pressure or the duration of a growing season. In any case these factors are not directly linked to the possession of indehiscence or an endocarp. A further potential advantage of the pachychalazal state is that it might be superior mechanically to the bitegmic state. Some bitegmic seed-coats have greater strength through various developmental routes. In Heynea, the testal O.E. has become mechanical through developing a palisade. In Pseudobersama, the exotegmen has developed additional layers. In Walsura the exotegmen has, in addition, developed a 'cross-ply' structure of undoubted additional strength. However, a pachychalaza, with its high vascularization and associated fibres and tannin-filled cells might also be stronger than a primitive bitegmic seed, where only a single layer of short fibres or sub-palisade cells forms the protective layer. This hypothesis may also explain the presence of the pachychalaza in 'giant' seeds (e.g. Trichilia grandifolia) since, whereas a bitegmic rigid seed wall might be adequate for the postulated small ancestral seed when scaled up, it would be inadequate unless additionally thickened and strengthened (see the example of Humbertioturraea and Turraea).The advantage of a vascularized seed-coat is that not only can it be thicker, but the very nature of the mixture of vascular bundles and parenchyma confers a more flexible and less directional strength to the seed-coat: it is far less likely to crack than a bitegmic seed-coat is, though the latter may be harder: an important consideration during the dispersal phase. this matter is

considered further under 'Ecology'. Whilst the switch to a unitegmic seed-coat (putatively pachychalazal) might be considered advantageous on mechanical grounds in those indehiscent-fruited genera lacking a pyrene, for example Malleastrum, Lepidotrichilia (endocarp barely differentiated in L. volkensii) or indeed Walsura, its presence cannot be explained in Owenia (with a very thick endocarp) on this basis. Owenia is not alone. Pachychalazal seeds (of known developmental origin) have been demonstrated in other families with a thick putamina, for example Mangifera (Anacardiaceae) by von Teichman et al. (1988).

From the foregoing, it is clear that whatever the explanation, most seed-coats in indehiscent-fruited genera of this tribe are generally either unitegmic and/or highly crushed if our sample is at all representative. The exceptions in this tribe are Ekebergia and Astrotrichilia. The explanation might be that they are only relatively recently indehiscent and that they have not yet acquired a typical pyrene seed-coat (crushed or unitegmic), much as in Walsura, where the relatively recently (as presumed here) indehiscent W.pinnata remains comprehensively bitegmic, whilst the more completely indehiscent W. chrysogyne (further reduced endocarp and sutures, thick fleshy pericarp) appears unitegmic. Perhaps a delay is to be expected: but this is all speculation. Indeed, sparing dehiscence (suggesting that indehiscence has only recently been achieved) has been reported in Astrotrichilia (Leroy, 1958c). It would be interesting to investigate the development of the seed from the ovule in these two taxa to determine whether a vestigial aril (often present early in the development of the fertilized ovule) is formed and later lost. Certainly, none is visible in the mature seed. Pennington (pers. comm.) has reported a case in Sapindaceae where the mature seed is non-fleshy and dispersed in a dry, winged, indehiscent

fruit, yet the developing ovule has a well-marked funicular aril. It would be interesting to find out whether there is a parallel in Meliaceae.

ECOLOGICAL ASPECTS

In order to determine the functional significance (if any) of the different seed-coat structures related above, it is important to know something of their dispersal ecology. It may be that particular types of fleshy seed appendage, seed-coat structure or fruit type are associated with different modes of dispersal. Pannell and White (1985) and Pannell and Koziol (1987) have shown that in Aglaia (Meliaceae-Aglaieae) two distinct fruit syndromes occur. The first obtains in species with dehiscent fruits dispersed by birds,these fruits are brick red or pink outside, and contain seeds with orange-red, lipid-rich arils. The birds remove and eat individual seeds and subsequently pass or regurgitate them, cleaned of the 'aril'. The second sort occurs where the fruits are dispersed primarily by primates. These have an indehiscent, orange, pinkish-orange or brown pericarp and the seed is surrounded by a gelatinous, translucent, sugar-rich 'aril' that firmly adheres to the seed-coat. The fruit is opened by the animal, the seeds extracted and, because of the nature of the seed-coat, swallowed whole. The first state is regarded by Pannell as primitive, the second as derived.

Where fleshy seeds occur in Trichilieae, they seem, from those sampled here, almost always of the first sort and rarely of the second, so it is difficult to test in this tribe whether there are any anatomical characters that might correlate with each of the two syndromes. However, Walsura does have fruits of the second, primate-dispersed syndrome in such species as W. pinnata. This has fawn, indehiscent fruits with a translucent gelatinous 'aril' firmly attached to the testa, whilst that

of Heynea trijuga is completely free of it . This discrepancy agrees with the two syndromes and makes ecological sense: in a bird-dispersed seed it is no disadvantage for the aril to be loosely attached in that the whole is consumed and the aril separated in the gut, probably the gizzard, whilst being carried, before the main body of the seed is ejected. If, in a primate dispersed seed the aril were loosely attached, it is likely that, being dextrous, the animal would simply remove the aril and deposit the seed body under the parent tree, so that effectively, there would be no dispersal. An adherent, gelatinous aril is far more likely to be swallowed whole, so that it is likely to be dispersed at some distance from the parent tree (see e.g. Pannell & Koziol, 1987). Both Heynea trijuga and Walsura pinnata seem to be bitegmic, yet their seed-coats differ greatly in various anatomical characters. Do these differences have any functional significance?

It is plain that, whilst the Heynea seed is protected by a testal O.E. palisade, that in Walsura is much more strongly protected, and at two levels rather than one. Whilst the testal O.E. is strengthened by radial thickenings, it is further immensely strengthened by the arillar I.E. that adheres above (see plate 38 N) and has larger wall thickenings. The second level is that of the exotegmen. In Heynea, the tegmen lacks exotegmic fibres and does not in any case fully encapsulate the embryo, whereas in Walsura it consists of a cross-ply arrangement of eight layers of fibres and is clearly immensely tougher. Ecologically, this would be advantageous, since a bird's digestive tract is often likely to be less destructive than that of a primate (see e.g. Pannell and Koziol, 1987; Crome, 1975). Primates frequently gnaw seeds whilst feeding in a way that birds, lacking teeth, do not (Pannell & Koziol, 1987). Thus, if Heynea is effectively bird dispersed and Walsura pinnata is primate dispersed, as

seems likely if unproven, then Pannell's syndromes do hold in this tribe and there are correlated anatomical characters.

It is curious that in this tribe, the second Aglaia syndrome only occurs in Walsura and that this, like Aglaia is a Indomalesian genus. Is this merely coincidence, or does the environment there predispose selection towards Pannell's primate syndrome?

Eight other genera remain to be considered. Do other syndromes obtain in the tribe; does the first syndrome always hold? To answer this, it is necessary to examine what is known of the animals that eat Trichilieae seeds. Pannell and White (1985) have thoroughly reviewed the literature pertaining to seed dispersal in the Meliaceae. Many of the references below are listed there. Trichilia emetica (see plate 29A) in South Africa is reported as being consumed by seven species of bird, baboons, monkeys, Nyala and also by fish such as Barbel (Palmer and Pitman, 1972:1075). Seeds of the closely allied T. dregeana are eaten by starlings according to Dowsett-Lemaire as cited in Pannell and White (1985), and in western Uganda by both hornbills and blue-tailed monkeys according to Struhsaker (pers. comm.). 'Arils' of Trichilia prieuriana are listed as an important source of food for chimpanzees in Gabon by Pannell and White, 1985). Of the 'East African Group', nothing is known of potential dispersal agents. The fruits of Pseudobersama with their thick woody valves and warts are highly protective of the seeds and yet extremely showy (plate 33) . The seeds are believed by Pannell and White (1985) probably to be bird-dispersed, but it is just as likely that they are attractive to primates. In America, where most species of Trichilia occur, far less is known of the dispersal biology than in Africa. Trichilia martiana C.DC. (Trichilia cuneata Radlk.) in Costa Rica has been reported as being a food item of 13 species of bird by Leck (1969)

and of a further two species by Foster and McDiarmid (1983). The latter go on to analyse which species are 'specialist' (four species of bird) and which 'opportunistic'(the remainder) frugivores, what the nutritional value of the aril is and the allocation of resources in the components of the fruit represented by dry weight. Wheelwright et al. (1984) mention that seeds of Trichilia havanensis Jacq. are occasionally eaten in Costa Rica by the long tailed manakin.

In Madagascar, seeds of Trichilia sp. 2 (Cheek, s.n.) are consumed by a large black bird with a loud raucous call given on the wing according to Merona (pers. comm.) and at least one other species of Trichilia occurs on a large offshore island on which no primate occurs naturally (pers. obs.) and might well be bird-dispersed. About 10% and 60% respectively of fruit samples were infested with insect larvae.

Nothing is known of dispersal in Pterorhachis.

The seeds of various Walsura spp. in Sarawak are consumed by primates, including gibbons (T. Clark, pers. comm.) whilst in Brunei, Heynea seeds dangle from the capsule on a red 'aril' (in this case, surely the placenta) according to Ashton (exsicc. at FHO). This is in classical bird-dispersed fashion (see e.g. Corner, 1949).

The indehiscent-fruited genera are less well observed, excepting Ekebergia. According to Phillips (1927:222), the fruit of E.capensis is eaten and dispersed in Knysa, South Africa by seven species of bird, and to a lesser extent by baboons, monkeys and bush pigs. Whilst in the Mau escarpment, locals report that black and white colobus monkeys as well as birds eat the fruit (pers. comm.).

The small orange, sweet, juicy fruits of Lepidotrichilia volkensii (see plate 41) are probably eaten by birds in upland Kenya (pers. obs.) but nothing is known of the Malagasy species. Fruits of Malleastrum gracile

are consumed by Sifaka Lemurs (Propithecus verreauxii) in Ankarafantsika, Madagascar according to Pettersen (pers. comm.) though one would imagine that bird-dispersal is also likely. Indri indri (the largest lemur) consumes the fruits of Astrotrichilia sp. in Analamazotra, but the latter are often unripe and unlikely to be dispersed far according to Jon Pollock (pers. comm.). Owenia fruit is reported to be eaten by emu in Australia, where they are known as 'emu apples' according to Harms (1940). Nothing is known about the dispersal biology of Cipadessa, but its small juicy fruits are possibly bird-dispersed.

From the above, it can be seen that fruits of the 'bird' Aglaia syndrome are far from all eaten by birds. Primates and fish account for almost as many observed instances of seed consumption as birds for African Trichilia. Here the question of co-evolution between the dispersal agent and the dispersed must be considered. An important review of this subject is given by McKey (1975). He draws a distinction between 'opportunistic frugivores' and 'specialized frugivores' the latter completely dependent on fruits for their nutrition, the former, as their name suggests, merely using them to supplement their diet as they become available. His hypothesis, based largely on neotropical bird dispersal and particularly papers by Snow, draws attention to the distinction between water and carbohydrate-rich fruits with many small seeds eaten by opportunistic species, and oil and protein-rich fruits usually containing only a single large seed, that are consumed by specialized frugivores that may have co-evolved with their dispersers, the two being mutually dependent on each other.

Naturally, intermediate fruit types, eaten by both frugivore types occur. In such cases, where careful and extended studies have been made, the specialized frugivores do seem to do the best job of dispersal as

Howe and Primack (1975) have shown with Casearia nitida Jacq. (Flacourtiaceae)- a genus with similar seed presentation to that of many Meliaceous genera with 'arillate' seeds and dehiscent capsules. Trichilia martiana also seems to fall into the intermediate category. Foster and McDiarmid (1983) state that only four out of 15 species of birds feeding on its seeds are specialist frugivores: perhaps only these are the real dispersers. Should a plant species become dependent on a single specialized 'specialized frugivore' and the latter disappear, extinction is possible. The usual example given is that of Calvaria and the Dodo, but a more convincing example is that of Phylica arborea an apparently ant-dispersed species in South Africa (Breytenbach, 1986). But if a fruiting tree is observed over a period of time, and animals are recorded eating the seeds or fruits, then which are the 'specialized frugivores', that are the 'real dispersers'? Janzen (1981) in investigating the postulated seed dispersal by Tapir of Enterolobium sp. and Cassia grandis L. found that all of the latter were destroyed by the tapir's digestive system before they were defaecated! Until careful investigative work of the same type is performed in the Trichilieae, there is no way of being certain what their 'real' dispersers are. It is quite possible that most of the animal 'dispersal' candidates listed above, are in fact predators, either destroying the seeds like the tapir, or not dispersing them effectively. For all the knowledge we have of reproductive biology in this tribe it may be that the 'real dispersers' are long extinct, that the species propagate vegetatively (as in another tribe the Turraeeae from rootstocks, e.g. Turraea: pers. obs.) or that seed dispersal is entirely a matter of serendipity! Until this work is done, it is clear that an assessment of the functional significance of seed-coat anatomical characters in the tribe (such as that of Heynea/Walsura) must

remain largely hypothetical. It is tempting to group fruit types into syndromes of primate-dispersed, bat-dispersed, and bird-dispersed on the evidence of morphology and presentation, as van der Pijl (1969) has done. But to use this as a basis for research is fraught with danger as Boucher (1981) has illustrated with the case of Swartzia cubensis (Britton & P. Wilson) Standley which, although it falls perfectly into van der Pijl's bird-dispersed syndrome, is undoubtedly dispersed in Costa Rica by Spider Monkeys.

## THE AGLAIEAE

This tribe was erected by Pennington and Styles (1975). They distinguish it on the basis of the stellate hairs (or peltate scales), the globular or cyathiform staminal tube, the absence of a prominent nectary, the baccate fruits, the sarcotestal rather than arillate seeds, the superposed cotyledons and included radicle usually seen in the species that comprise this tribe.

The tribe consists of five genera: Sphaerosacme, monotypic in the Himalaya; Reinwardtiodendron with seven species distributed from India to New Guinea, Aphanamixis with three species distributed from India to the Solomon Islands; Lansium with three species from Peninsular Thailand to Lesser Sunda Islands; Aglaia, the type genus with over a century in Indomalesia and neighbouring regions (Mabberley, 1985; Pennington and Styles, 1975).

The first two genera have never, it seems, been investigated seed anatomically, and I have not been able to trace any material suitable for seed anatomical work at Oxford. The third has been intensively investigated by Corner (1976,1:186) who shows that the seed of A. polystachya (Wall.) R.N.Parker (as 'A. grandifolia Bl.') is largely pachychalazal, with the testa and the raphe-like part fleshy. Corner (1976, 1:190) also investigated Lansium domesticum Corr. This too is partly pachychalazal, but shows an anti-raphe perichalaza and occasional sclerotic cells in the tegmic mesophyll, the latter two characters not encountered in any of the species presented here. The genus Aglaia with over a hundred species is represented by many fruit collections at Oxford, but insufficient time was available to investigate this immense genus, the largest in the family. Corner, who presents descriptions of three species (Corner, 1976,1:186) indicates a wide range of organization types, 'from arillate to exarillate, to perichalazal and pachychalazal with sarcotesta'. The seeds of this genus certainly warrant intensive research and are probably worth investigating as a thesis topic on their own.

The predominantly pachychalazal construction and the nature of seed organization types in this genus as presented by Corner (see above) suggest a close affinity with the Guareeae.

# CHAPTER EIGHT

## GUAREEAE

### INTRODUCTION

The species of Guareeae differ from most other Meliaceae in their usually entire, cylindrical staminal tube with anthers inserted inside (rather than at the rim), nearly always well-developed nectary and generally discoid style-head (Pennington and Styles, 1975).

Pennington and Styles who erected this tribe (1975) recognize 11 genera within it: Heckeldora with one species in West Africa; Cabralea with one variable species in the Americas (Pennington and Styles, 1981); Ruagea with five species in the Americas, Turraeanthus with possibly three species in tropical West Africa, Guarea with about 35 species in tropical America and five in tropical Africa (Pennington and Styles, 1981); Chisocheton from Indomalesia with 51 species (Mabberley, 1979, who includes Megaphyllaea which Pennington and Styles maintained); Synoum with one or two species in Eastern Australia; Anthocarapa with one or two species in E. Malesia and W. Pacific (Mabberley, 1985); Pseudocarapa with one species in Sri Lanka (Mabberley, 1985); Dysoxylum with c. 60 species from the Indomalesian region eastwards to Australia, Polynesia and New Zealand.

Despite the size of this tribe, I have been unable to trace any investigation of its seed anatomy, apart from Corner's work (1976,1:188-190). Corner investigated Guarea guidonia (L.) Sleumer ('G. trichilioides'), describing it as probably pachychalazal, two species of Chisocheton (both pachychalazal but with testa and tegmen persisting)

and seven species of Dysoxylum in which he traces a sequence from bitegmic arillate species to pachychalazal sarcotestal species and describes the usual Meliaceae integument 'markers' from the bitegmic species: testal O.E. with crystals and fibrous exotegmen. Material was available for all the genera mentioned above, except Anthocarapa. In addition, material was available of Leplaea, recognized by some as a monotypic genus though reduced to Guarea by Pennington and Styles (1975).

It was possible to investigate two genera, Chisocheton and Dysoxylum in particular detail ( more than ten species examined in each), because of the range of material available in spirit. Both show the range from arillate to sarcotestal and from partly chalazal to completely chalazal seed-coats. For these reasons, they are discussed first, despite the fact that the plates and descriptions are presented in the sequence of Pennington and Styles' generic monograph (used here as the framework for evaluation). It is convenient for the purpose of this discussion to divide the remaining genera into two groups: firstly, those with bitegmic seeds which appear arillate, from dehiscent capsules, i.e. Cabralea, Ruagea, Synoum and Pseudocarapa, of which one species of each was examined, and secondly those with apparently unitegmic, sarcotestal seeds, often from indehiscent fruits, i.e. Heckeldora (two collections), Turraeanthus (three collections, two species) and Guarea (several species and collections). Chisocheton was, as stated in Chapter 2, the first genus investigated in the course of this study (for explanation, see there), so was the most intensively investigated of all genera. Consequently, pericarp anatomy and indumentum (plate 66b) and seed-coat micromorphology (plate 66a) were assessed as sources of taxonomic characters, but were found, in comparison with seed anatomy, to be of

PLATE 51

HECKELDORA LATIFOLIA

FRUITS: INDEHISCENT, ROSTRATE, SUB-MONILIFORM, WITH SUCCULENT ORANGE PERICARP CONTAINING WHITE SARCOTESTAL SEEDS.


51
10ths
1
2
3

PLATE 52

HECKELDORA LATIFOLIA

A FRUIT DISSECTED TO REVEAL SEEDS: NOTE RAISED MICROPYLAR EXOSTOME (LOWER WITH EXSERTED RADICLE: PRECOCIOUS GERMINATION ), TRANSLUCENT SEED-COAT WITH VEINS VISIBLE.

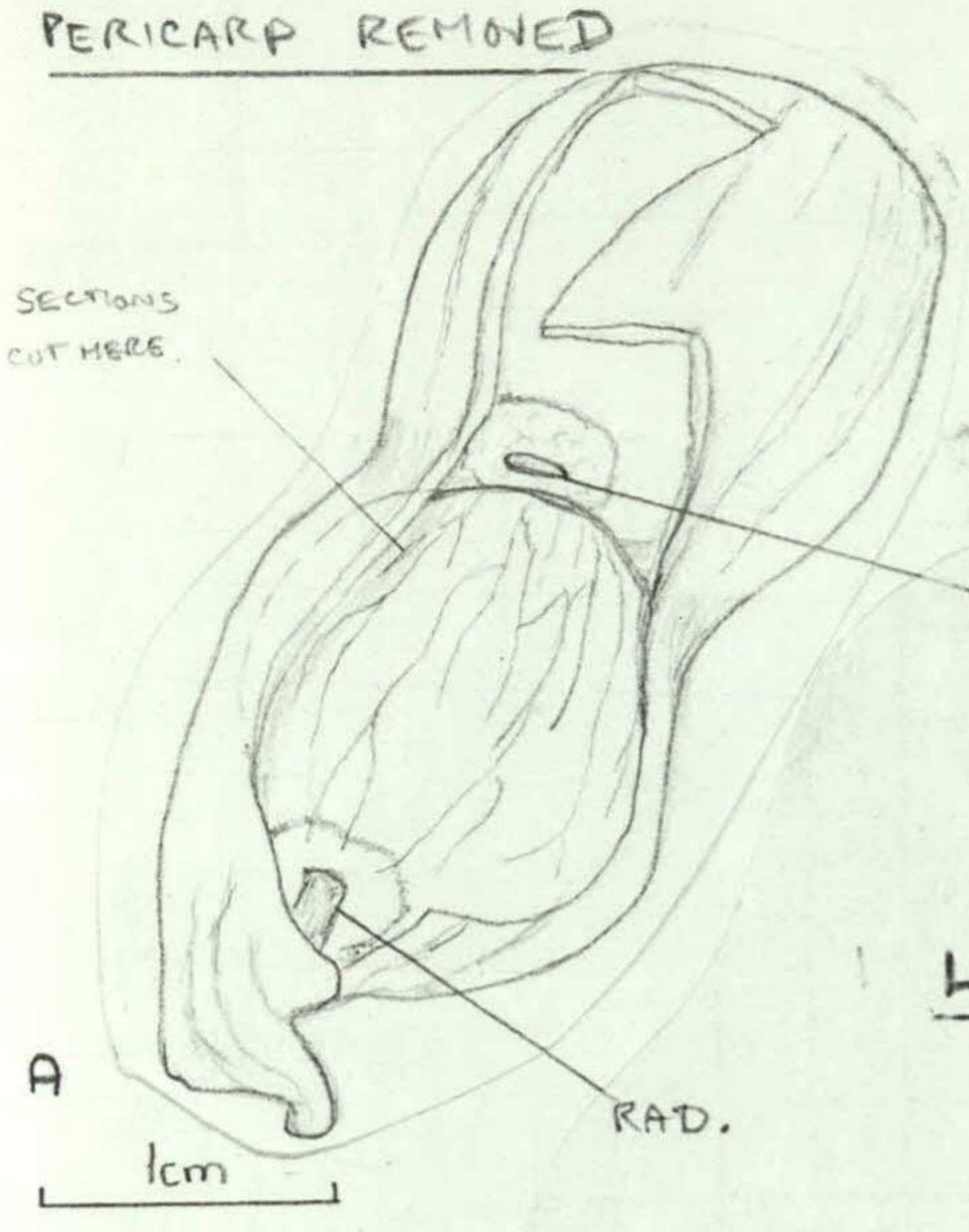
B-C VARIATION IN FRUITS: SINGLE-SEEDED (B) TO FOUR-SEEDED (C), FRUIT, LATTER SUB-MONILIFORM.

D WHOLE SEED. NOTE DISTAL MICROPYLE UNITED WITH PERICARP, SWELLINGS NEAR PLACENTA AND PARIETAL PLACENTA.

E SEED-APPARENTLY ORTHOTROPOUS.

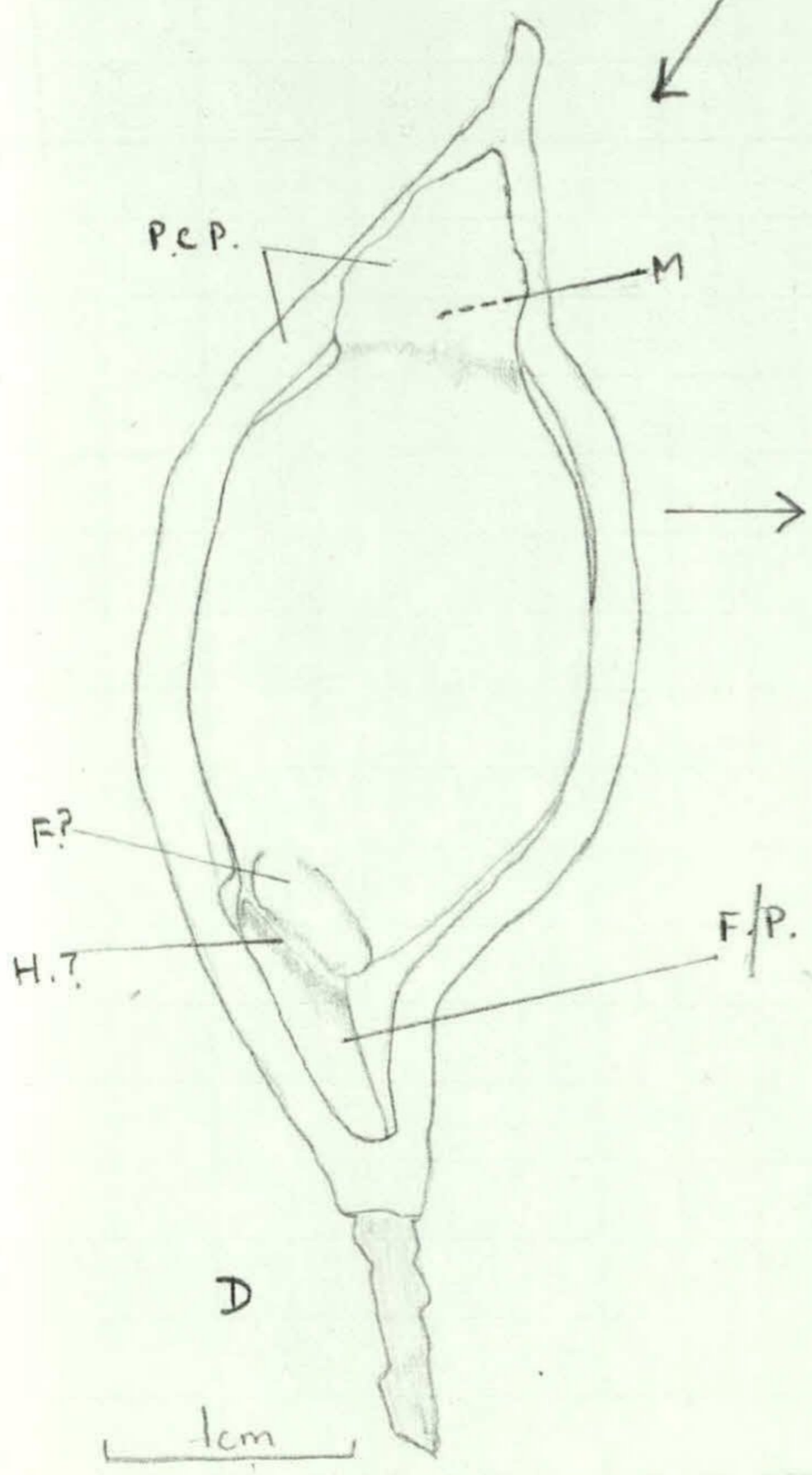
# Heckeldora latifolia

## 2-SEEDED FRUIT, PARTS OF PERICARP REMOVED

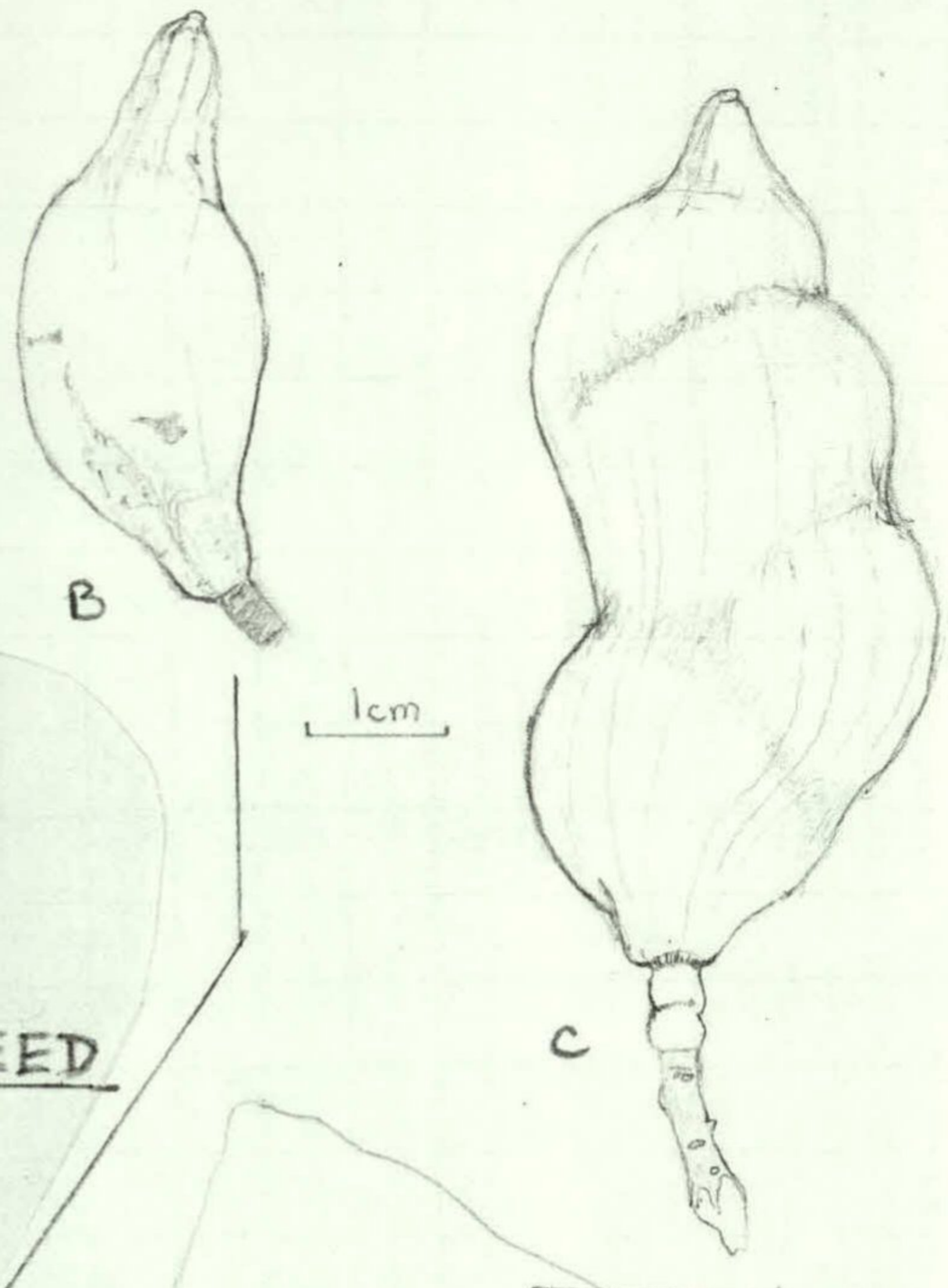



## L.S. SEED

## FRUIT (1 SEED) PART PERICARP REMOVED




## VARIATION IN FRUIT SHAPE & SIZE



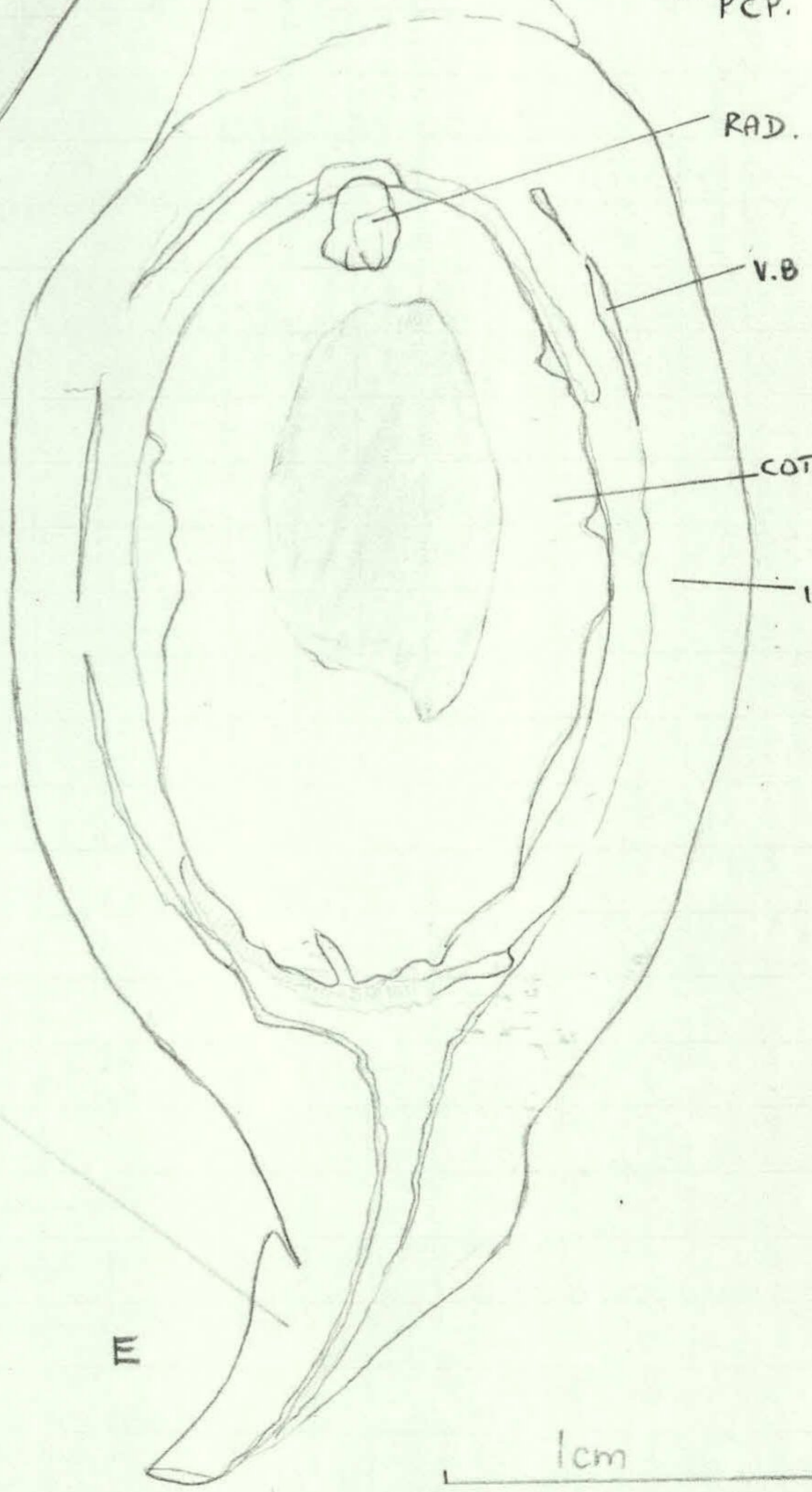



PLATE 53

# HECKELDORA LATIFOLIA

A-D SEED-COAT ANATOMY. UNITEGMIC (PACHYCHALAZAL?)

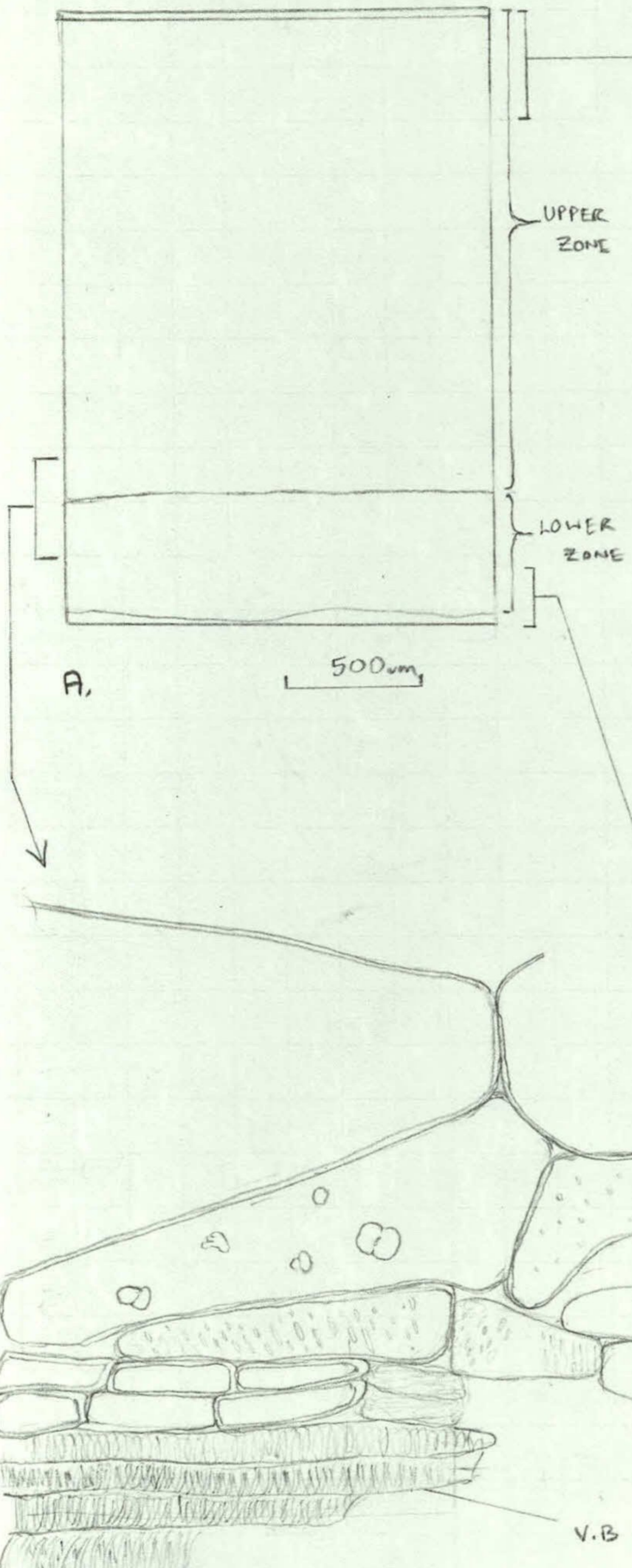
UPPER PART FLESHY: AERENCHYMATOUS, THIN-WALLED PARENCHYMA.

LOWER PART: WITH VASCULAR BUNDLES AND SCLEREIDS.

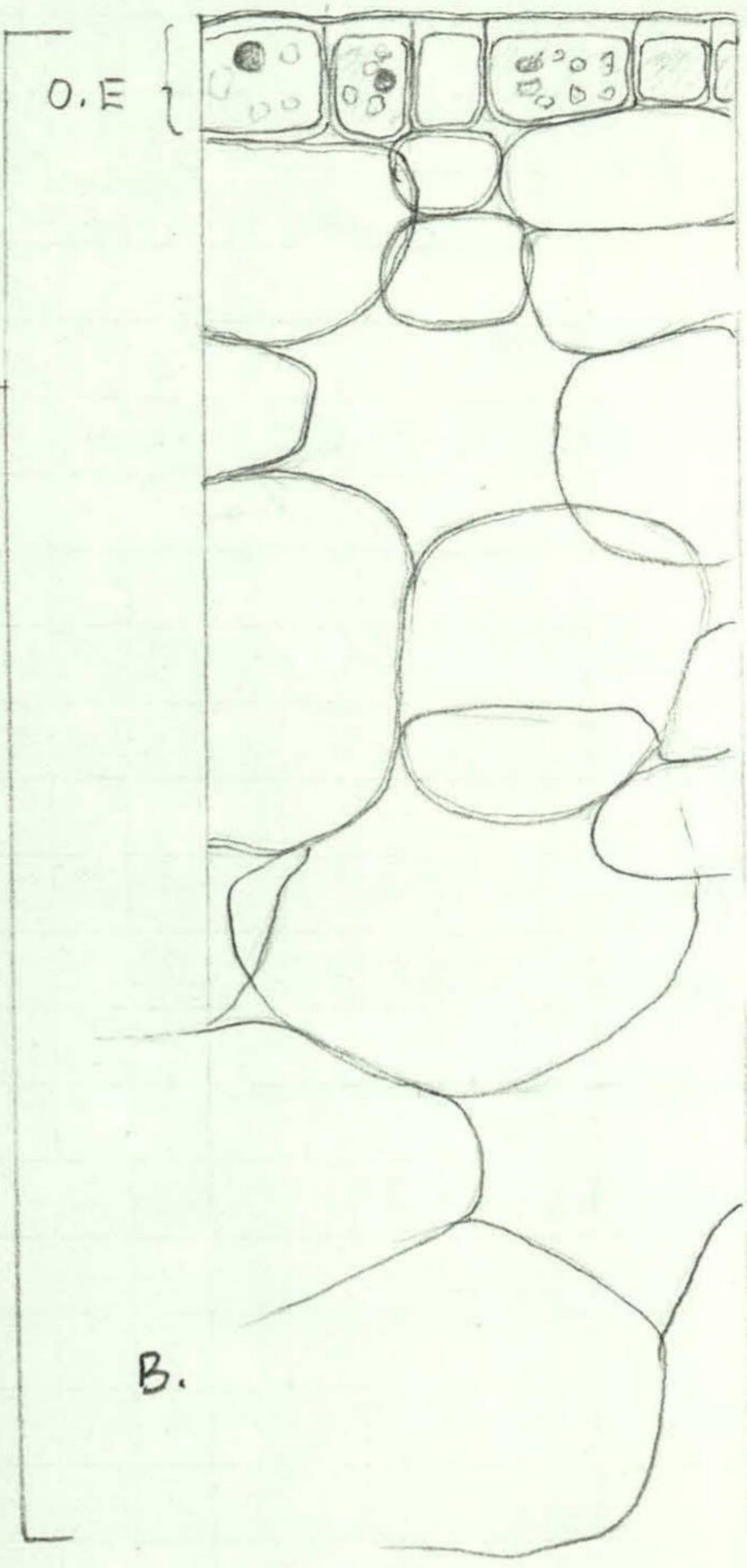
# Heckeldora latifolia

## Tissue Plan

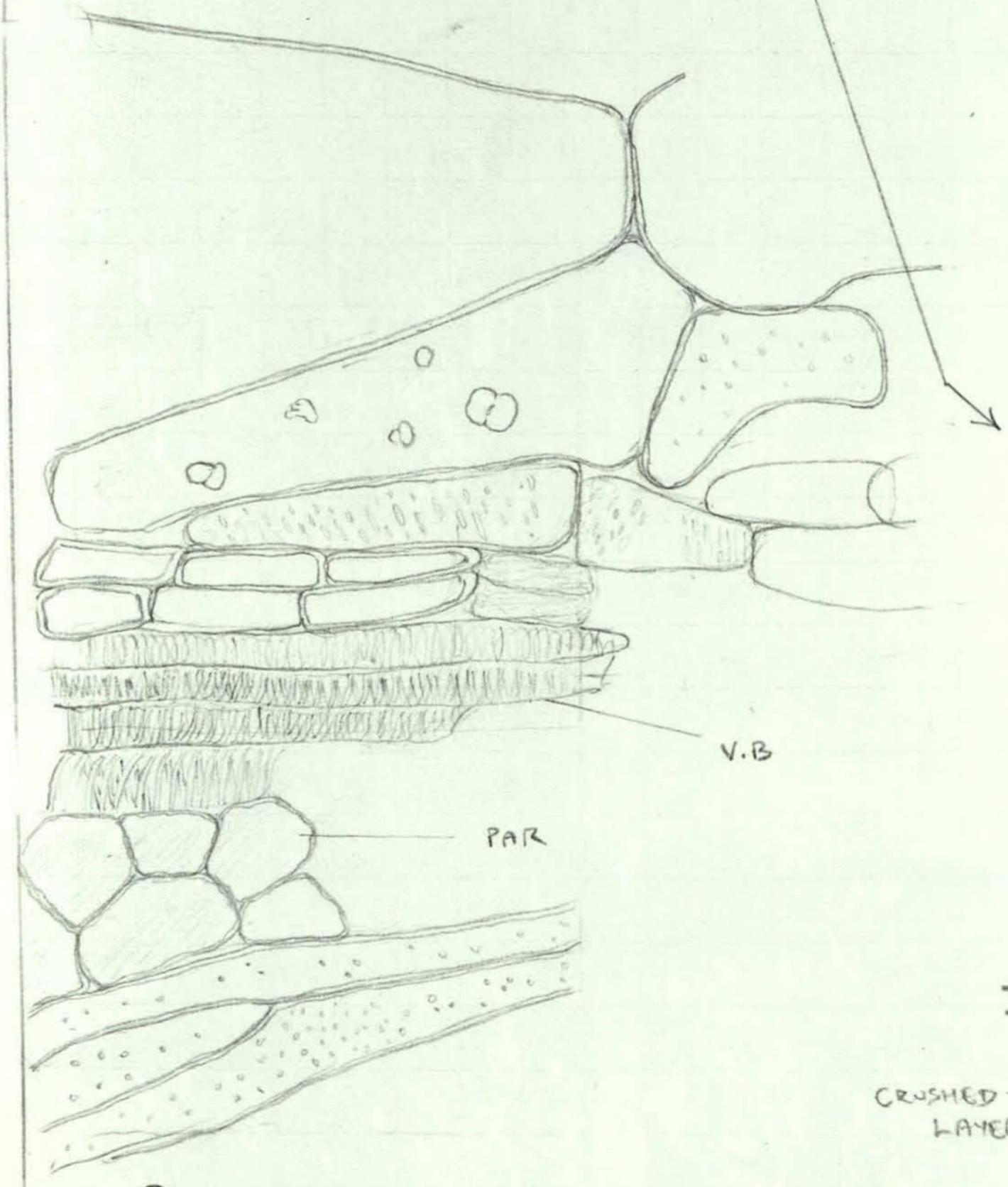
### L.S. Seedcoat



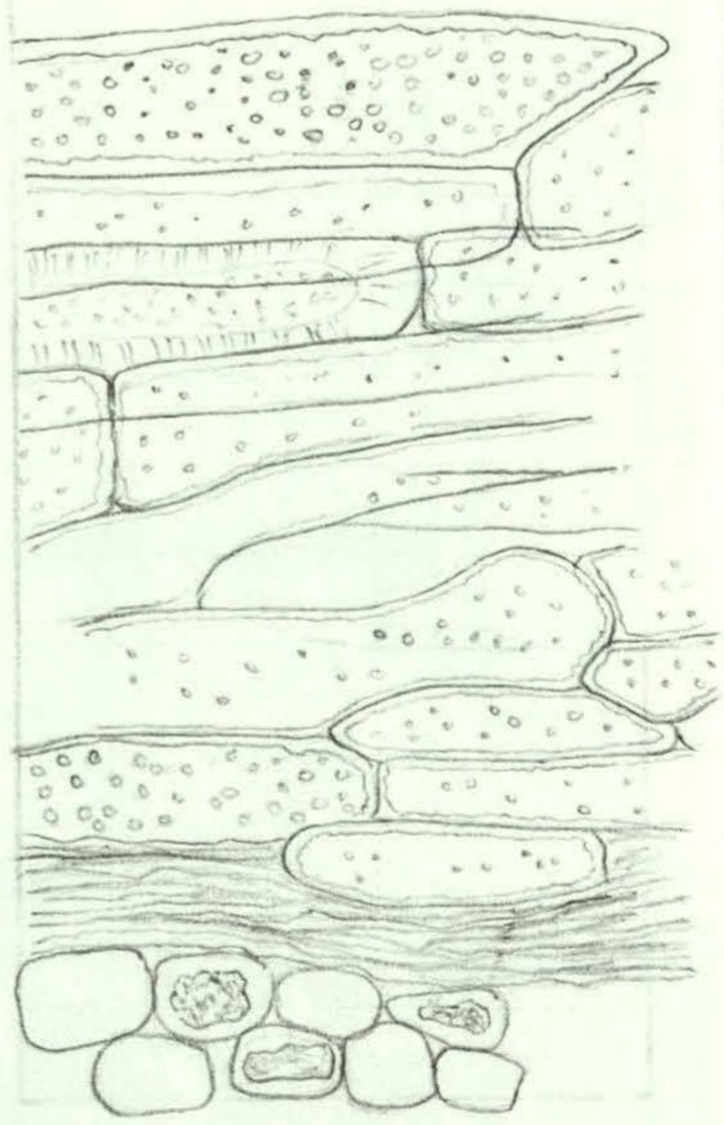

A.




B.




C.




D.

much less use in this case. Pericarp anatomy proved comparatively unorganized and difficult to interpret. Pericarp indumentum proved to be of the same basic structure and differed from one species to another only in quantitative characters (except one group of species with stellate indumentum: Sect. Rhetinosperma) such as degree of cuticular sculpturing, length and density, the latter two having been already assessed and used appropriately in the taxonomy of the genus by Mabberley (1979) and the former being of relatively little taxonomic importance. Seed micromorphology proved slightly more revealing in that, although most of the seeds had isodiametric, polygonal testa cells with tabular outer periclinal walls exhibiting no sculpturing and slightly raised anticlinal walls (not illustrated), some did show what appeared to be coarse cuticular sculpturing (e.g. C. lasiocarpus (Miq.) Valeton, plate 66b-A) so thick as to obscure the testa cell margins, whilst in other species there appeared to be intercellular gaps between the testa cells which, in C. granatum Mabberley are extended polygonal (plate 66b-B). Owing to the fleshy or immature nature of the available material in this genus, the testa surface proved highly susceptible to desiccation artefacts (see e.g. plate 66b-C: C. longistipitatus (F. M. Bailey) L.S. Smith ) but these were reduced using critical point drying techniques.

## RESULTS

### Heckeldora latifolia Pierre

This description based on D.Thomas s.n., Cameroun, 1985 and 1986.

Collector's notes: none available.

GROSS MORPHOLOGY

Fruit an indehiscent rostrate berry, irregularly long-ellipsoid with constrictions between seeds, sub-moniliform. 40-70mm long, 16-26mm wide. Rostrum 5-15mm long.

Pericarp orange, with low longitudinal ridges pronounced at rostrum, 2mm thick, succulent. Endocarp absent.

Single locule, 1-4 seeded, placentation basal (one seed) or parietal (second to fourth seeds), the placental vascular bundles carried up from the base to individual seeds. Seeds orthotropous, sub-elliptical to shortly and regularly ellipsoid, little faceting (pericarp wall distends), 17-24mm long, 12-18mm broad. Hilum and micropyle at poles, seed-coat swollen at both. Micropyle ± circular, c.0.5mm in diam., often adnate to pericarp, sometimes with radicle far-exserted (precocious germination). Hilum ill-defined, seed detaching below the swellings or with a funicular-placental stipe to 4mm long. Seed-coat white, translucent, marbled with veins and thus resembling a pickled onion. 1.5-2(-3mm at poles) thick, fleshy. Endosperm absent. Cotyledons collateral, longitudinal. Radicle c.1mm wide, 1.5mm long, exserted.

ANATOMY

Testa and tegmen not distinguished, seed-coat unitegmic. Lower part of fibrous, pitted cells, upper of thin walled parenchyma, the two intermingling at the boundary and vascular bundles occurring in both. seed-coat probably pachychalazal.

Cuticle: thin, c.1um thick, even, colourless.

O.E. single layer of small prostrate to columnar rectangular cells 18-35um high and 20-56um wide, o.p.w. slightly convex, colourless, c.5um thick, other walls c.2um. Lumina with cytoplasm and plastids.

Upper zone: very thick (1250-2500um thick) of numerous layers of small but mostly very large, thin-walled (c.1.5um, pale yellow), prostrate,

rounded polygonal parenchyma cells, sometimes with crystalline inclusions, lumina colourless. Cells 20-140um high, 35-350um wide. Large intercellular air spaces. Vascular bundle present in lower layers.

Lower zone: largely of sclereids, some vascular bundles ( in upper part) and packets of parenchyma. Very irregular in thickness, but up to 500um thick. Parenchyma cells polygonal, isodiametric 40-45um diam., or extended and prostrate, c.40um high and 60um wide; thin walled, contents colourless. Sclereids prostrate, usually shortly fibrous, but variable: from 42um high, 105um long to 17um high, 380um long. Walls dark straw yellow, 2-4um thick, pits numerous, round or slightly scalariform. Upper layers of lower zone sclereids with parenchyma of upper zone.

Crushed layer c.20um thick.

?PERISPERM 1-3 layers, rounded rectangular cells with thick colourless walls (4um) and dense, dark cytoplasm. 20-30um wide, 10-20um high.

VARIATION

Three collections were examined.

The first, D.T. 1985, was probably slightly immature. Parenchyma of upper layers slightly smaller (immaturity ?). Parenchyma of upper layers slightly smaller. Vascular bundles were well developed, but in the lower zone, relatively few sclereids, where these present long and fibrous, parenchyma dominating.

The second, D.T. 1986 was taken from a fruit with precocious germination, hence assuredly mature. Anatomical description above based on. Sclereids very diverse in length.

The third, Onochie,s.n., Nigeria, a poor spirit specimen. Here the upper zone and O.E. had collapsed beyond redemption. Probably due to desiccation. But the lower zone well preserved, 350um thick. Densely

packed sclereids of same character (wall thickness, colour, pitting etc.), but mostly long and fibrous, 500-600um long.

Cabralea canjerana (Vell.) Mart. ssp. canjerana

This description based on TDP and Budowski 10105.

Collectors' notes: 'Fruit 5cm diam., pale brown; with dense large pale lenticels. 5-valved dehiscent revealing white interior of fruit and 5 orange-brown seeds partially surrounded by fleshy orange arillode. Pericarp rather soft, containing sticky white latex. Endocarp thin cartilaginous'.

GROSS MORPHOLOGY

Fruit a weakly dehiscent (1-) 5-locular capsule, spherical to slightly obovoid, to 45mm diam.. Surface weakly verrucose. Pericarp rather thick, 3-9mm, fibrous fleshy, lined with a pellicular transparent endocarp, which, at maturity, often detaches with seeds. Placenta well developed, c.25mm long, broadest at the apex, c.11mm wide.

Seeds (1-)2 per locule, placentation ± collateral, axile, but rotation of each differs by c.90 degrees, so seeds superposed in locule. Raphe-aril well developed, largely or completely enveloping the integument of each seed and partly interlocking with the neighbouring seed's aril, so the two detach from the placenta as one unit (although tissues not continuous). The twin seed unit appearing as an elongated bean, to 22mm long, 14mm radially, 12mm tangentially, slightly pandurate in middle, with a weak dorsal ridge and terminal beak, hila central, ellipsoid 4-6mm long, 2-3mm wide, longitudinally orientated, 0-2mm apart, always separated by a double epidermal layer.

PLATE 54

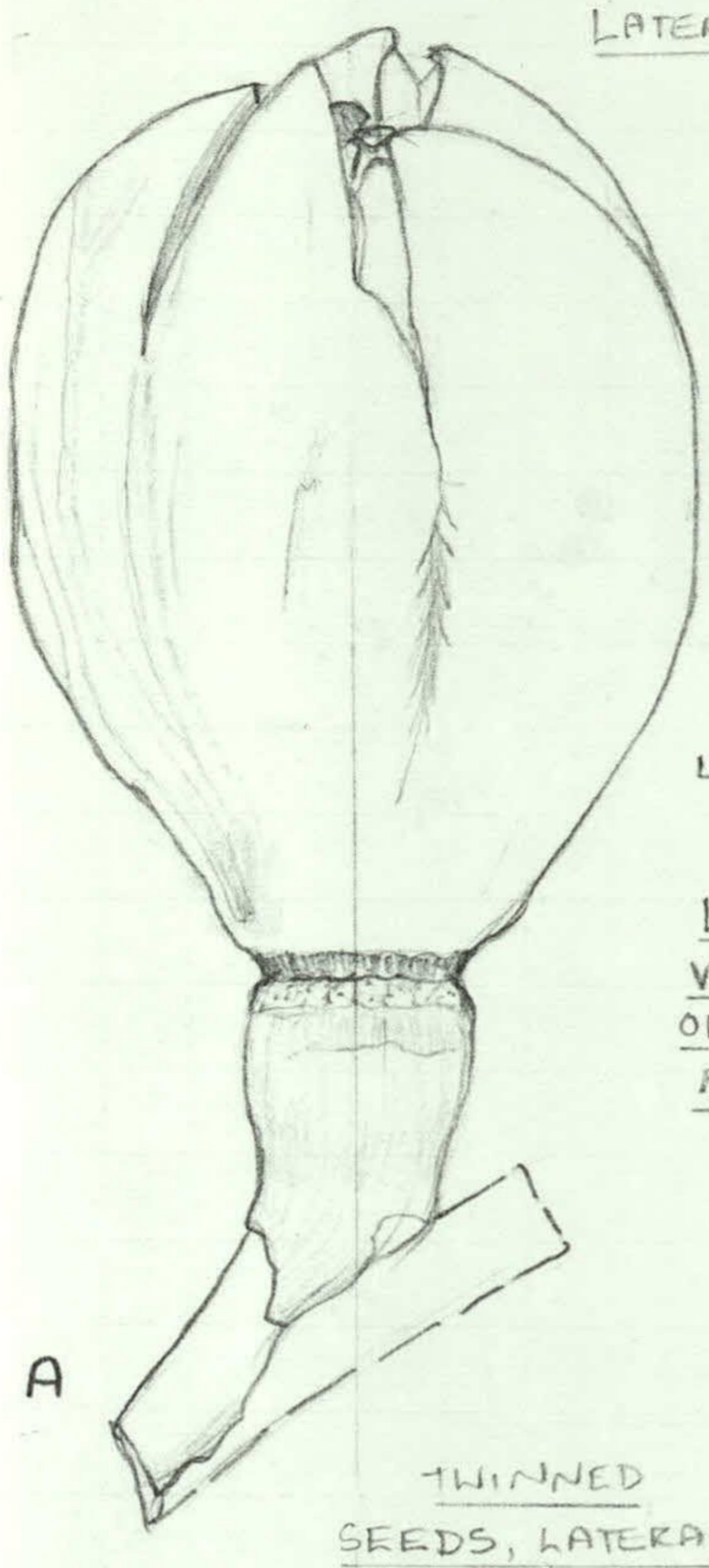
A-D CABRALEA SP. (SOURCE UNKNOWN). NOTE LOCULICIDAL, DEHISCENT FRUITS, THE TWO SEEDS OF A LOCULE UNITED BY THEIR ENTWINED ARILS.

E-N CABRALEA CANJERANA (TDP AND BUDOWSKI 10105). SEEDS DISSECTED TO SHOW NATURE OF FLESHY APPENDAGE: FUNICULAR-RAPHE(-CHALAZAL)-ARILLATE. NOTE NARROW RAPHE SCAR, SMALL CHALAZA (<10% OF SEED-COAT SURFACE.)

# Cabralea sp.

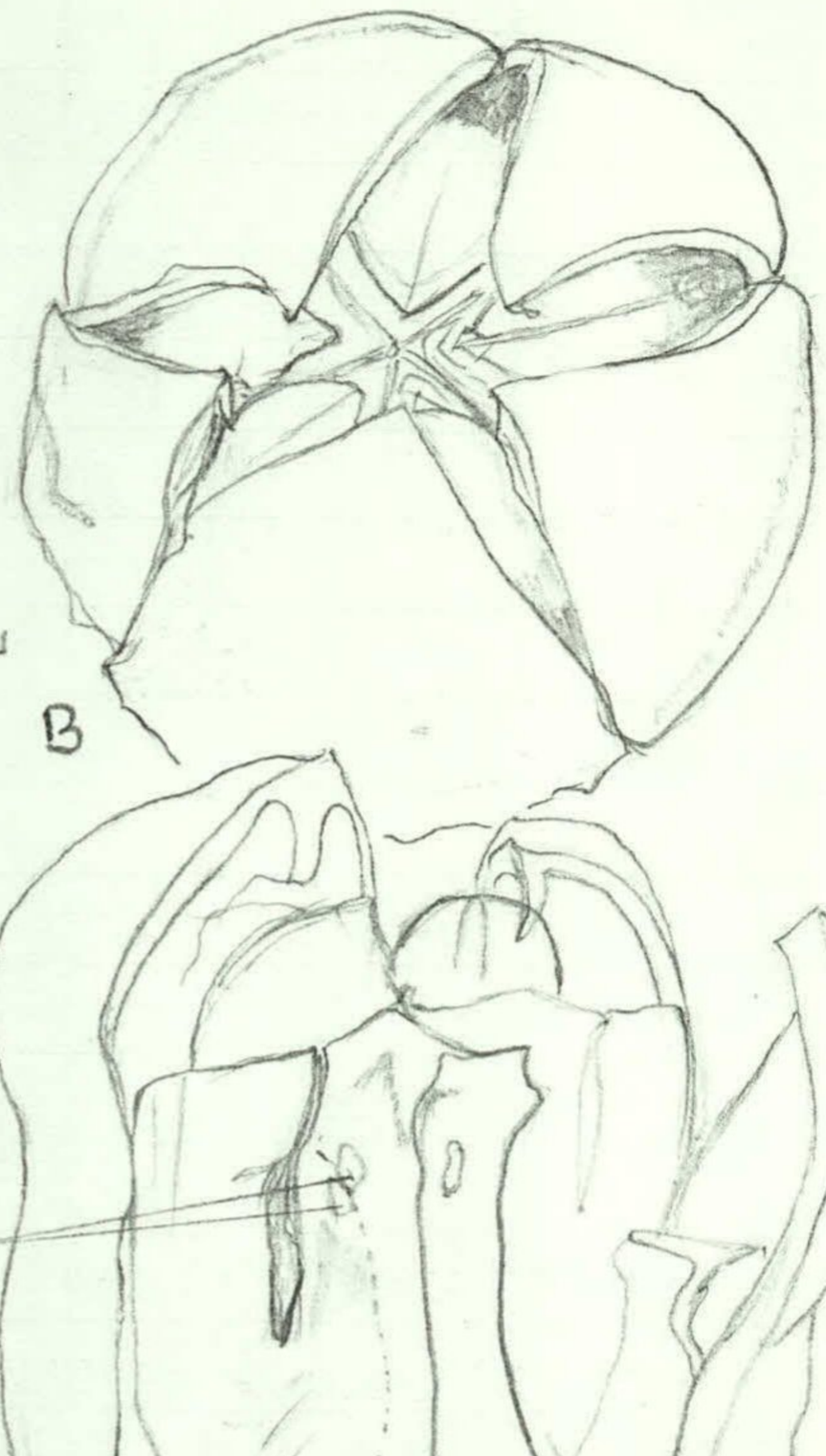
LATERAL VIEW FRUIT

PLAN VIEW FRUIT



A

1cm



B

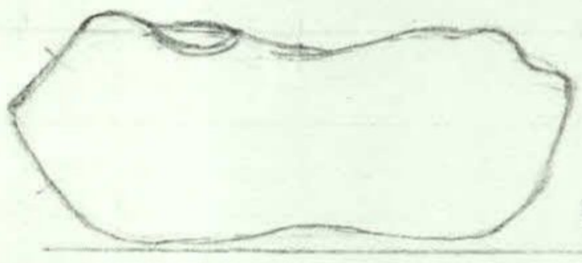
LATERAL VIEW FRUIT, ONE VALVE REMOVED

H. SCARS.



C

TWINNED SEEDS, LATERAL VIEW



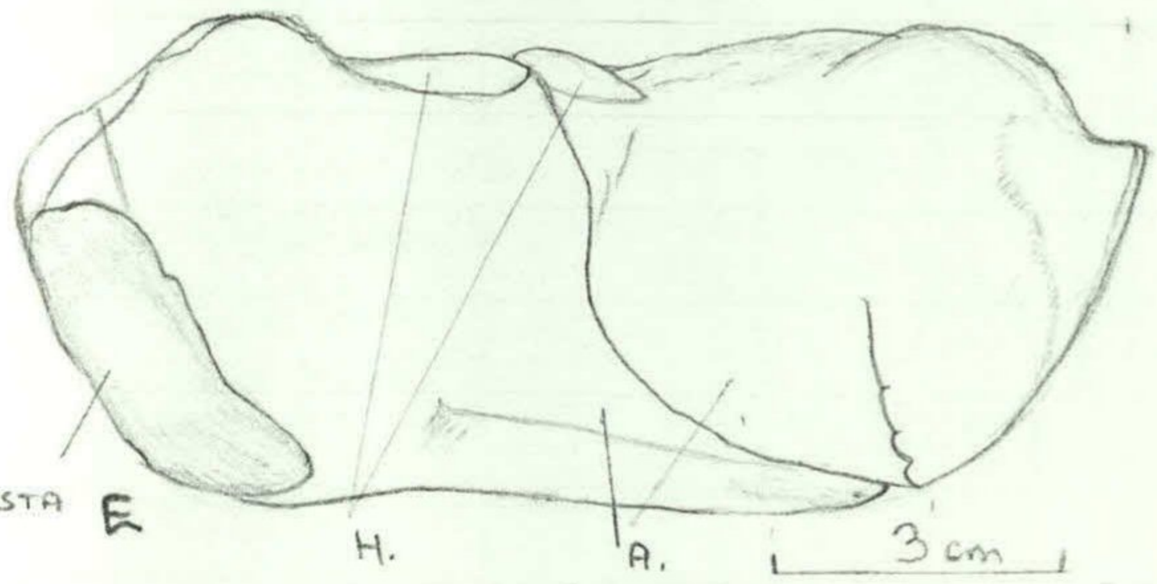
D

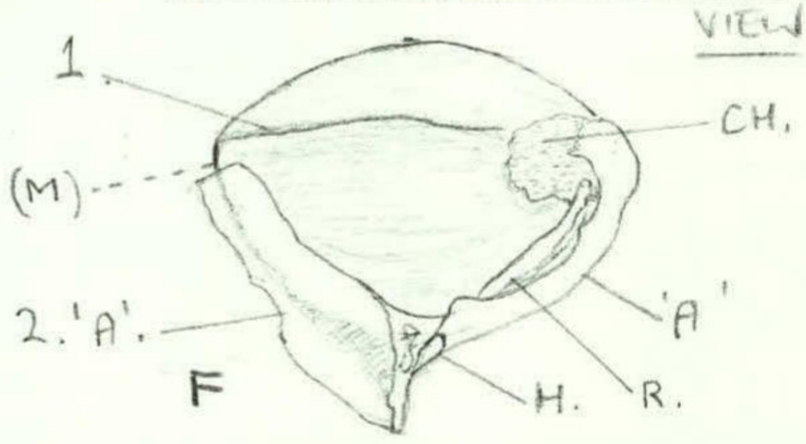
2cm

## Cabralea canjerana

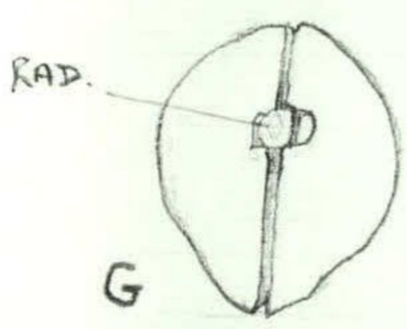
SEED 'ARIL' PART REMOVED

LATERAL - CHALAZAL - VENTRAL VIEW

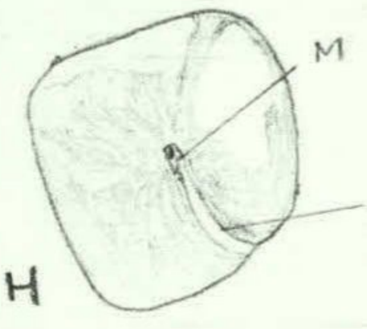


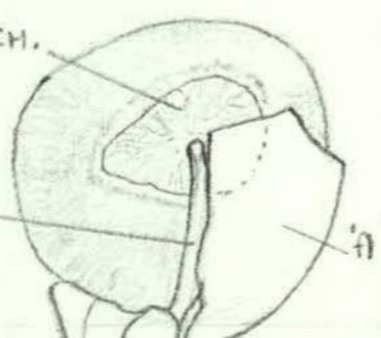

EMBRYO. MICROPYLAR END




SEED MICROPYLAR END

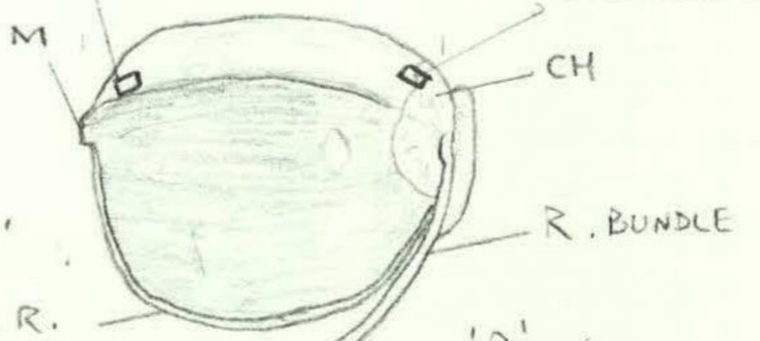



CHALAZAL END

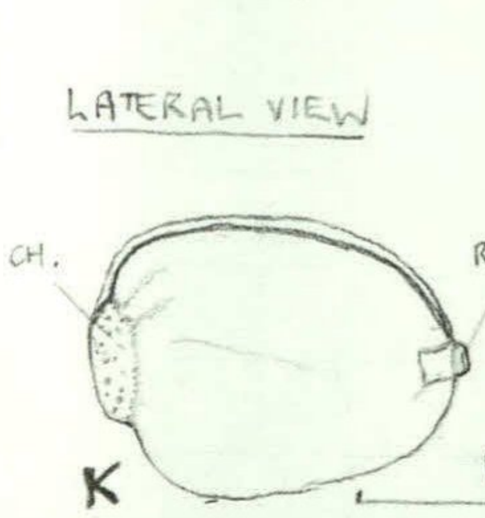



SEE PLATE 2

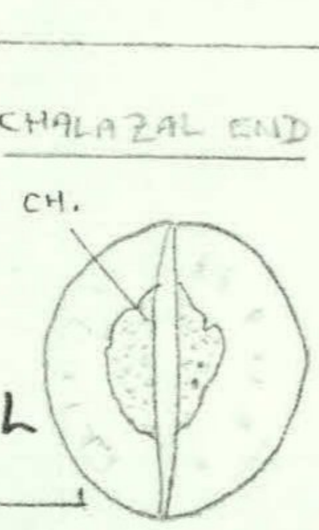
LATERAL VIEW



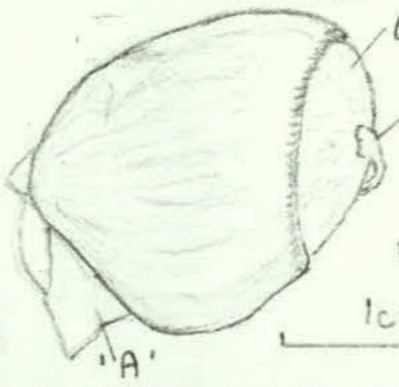

LATERAL VIEW




CHALAZAL END




DORSAL PLAN VIEW




VENTRAL PLAN VIEW

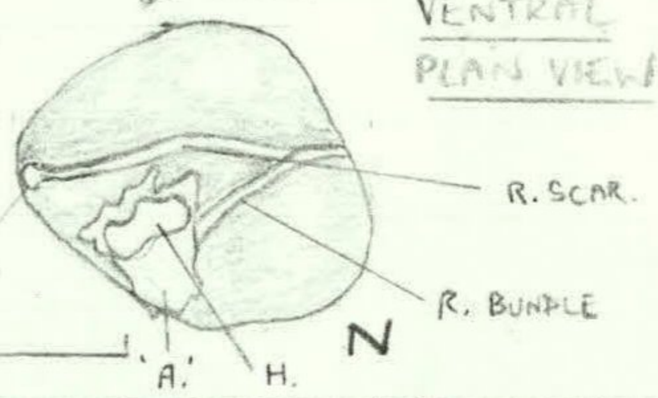


PLATE 55

CABRALEA CANJERANA

(TDP AND BUDOWSKI 10105)

SEED-COAT ANATOMY: NOTE BITEGMIC CONSTRUCTION

TYPICAL MELIACEOUS ANATOMY, SUB-CUBOIDAL

TESTAL O.E., FEW-CELLED TESTAL MESOPHYLL,

SMALL-CELLED TESTAL I.E. WITH CALCIUM

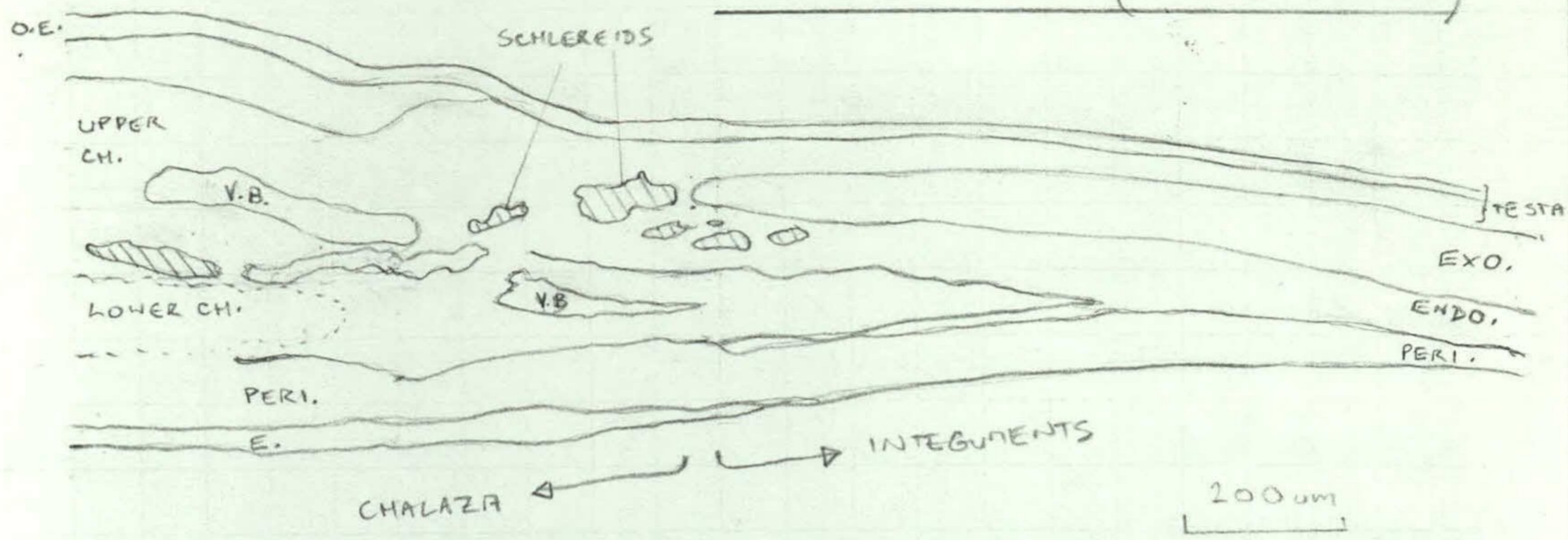
OXALATE CRYSTALS, LONGITUDINAL EXOTEGMIC FIBRES,

PARENCHYMIC ENDOTEGMEN.

# Cabralea canjerana

## L.S. CHALAZA: INTEGUMENTS

### TRANSITION ZONE (TISSUE PLAN)




## T.S. INTEGUMENTS

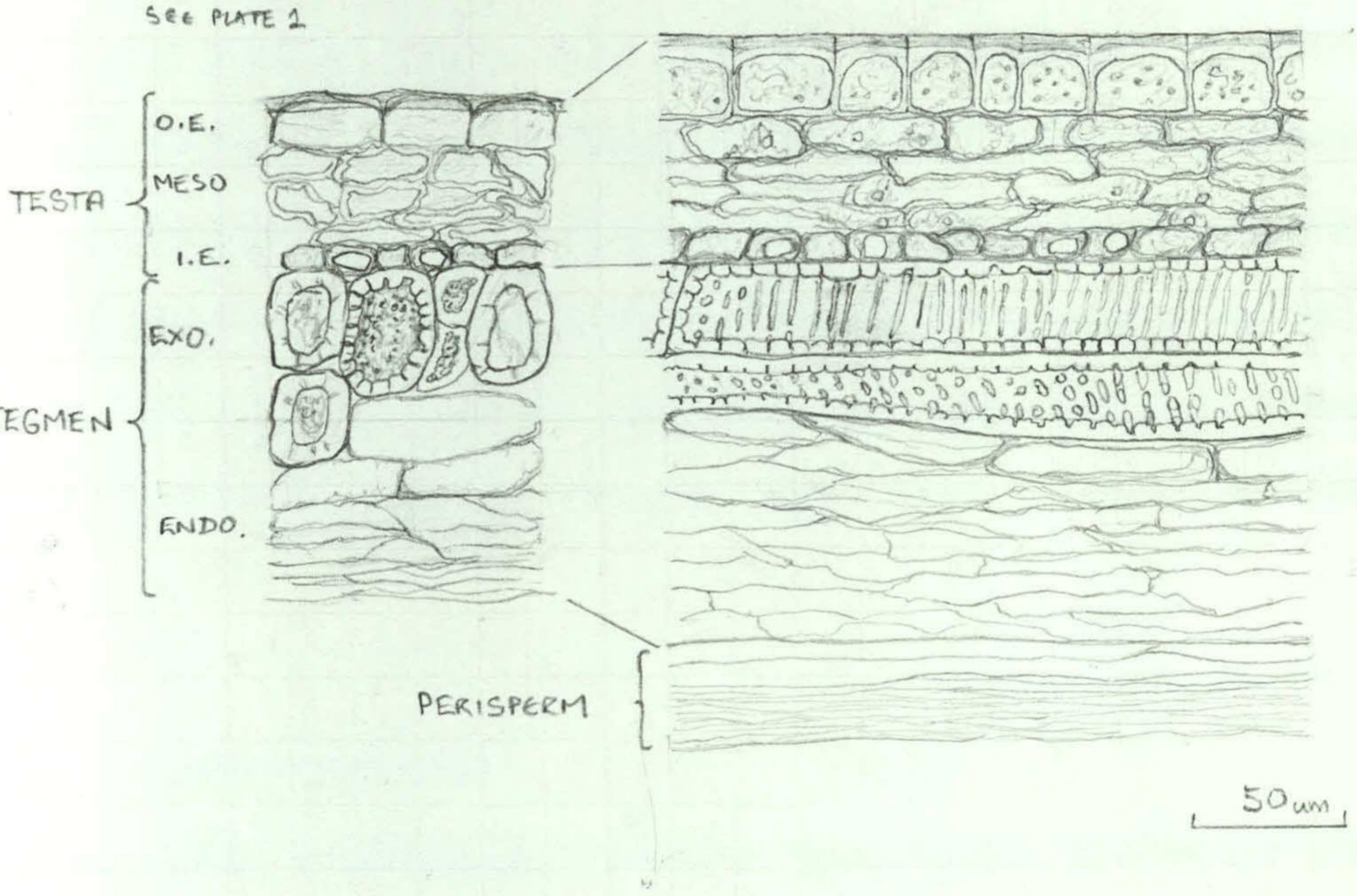
### NEAR MICROPYLE (± CRUSHED)

SEE PLATE 1

## L.S. INTEGUMENTS

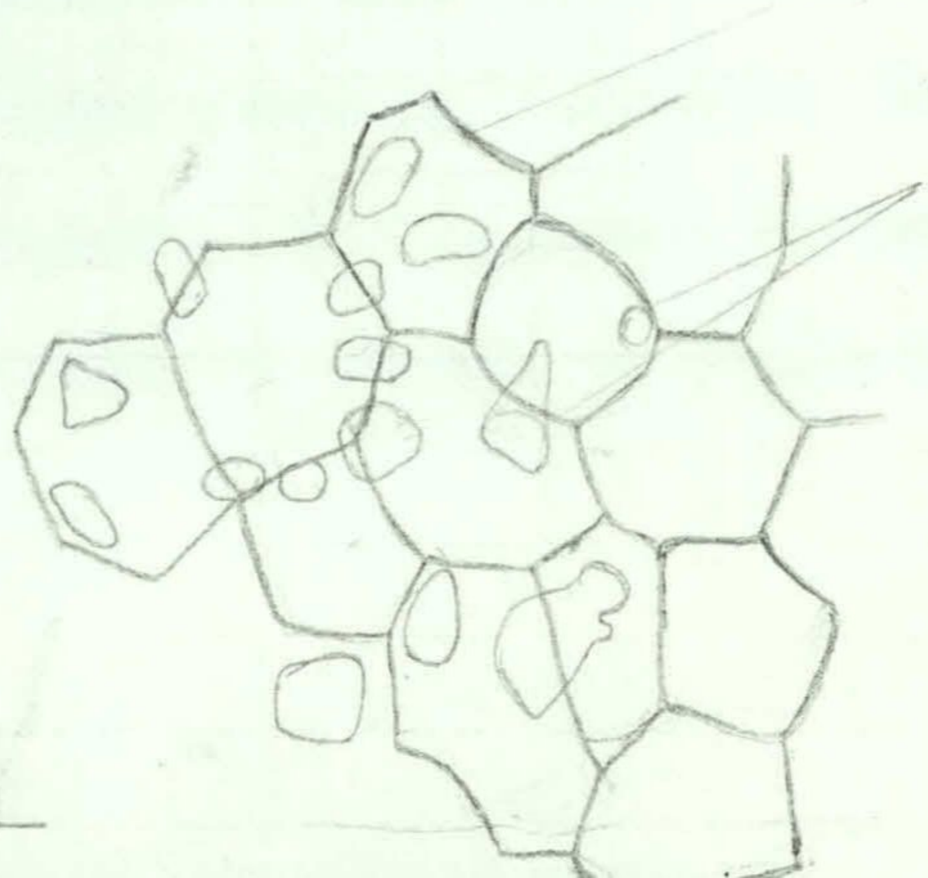
### NEAR CHALAZA (UNCRUSHED)

SEE PLATE 1




## TESTA (PARADERMAL VIEW)

O.E. LARGELY ISODIAMETRIC POLYGONAL CELLS.



INTERCELLULAR SPACES OF ± AERENCHYMATOUS TESTAL MESOPHYLL.

50 um

Where one ovule aborts, the dark, flattened, atrophied integument, c.3-5mm long is surrounded by a considerable aril, hilum about quarter normal size.

Both upper and lower seeds (excluding raphe-aril)shortly ovoid to ellipsoid, slightly oblique, not completely regular, 14-15mm long, 8-10mm wide, surface glossy chestnut brown. Chalaza at blunt end, superficially barely detectable as a slightly sunken ± isodiametric or longitudinally extended area, 4-7.5mm long. Micropyle a small apiculus almost opposite chalaza. Raphe scar white, 1-1.5mm broad, runs sinuously from centre of chalaza across the most shallowly curved surface of the seed to the micropyle. Raphe-aril up to 1mm thick, envelopes each seed, interlocks and overlaps (up to 30%) that of its neighbour. It carries the exserted raphe bundle which enters the hilum 2/3-3/4 the distance along scar from CH. to M. Upper seed usually naked of aril on uppermost, outer part. seed-coat c.0.1mm thick, endosperm functionally absent. Cotyledons plano-convex, radicle exserted, 2mm long, 3mm wide between cotyledons. Outer, cut surface of cots. with layer of small cavities.

ANATOMY

TESTA

cuticle: c.0.5um thick,even.

O.E. single layer of prostrate, shortly rectangular to shortly columnar cells,

14-45(-70)um wide, 20-28um high, with a thick, 3-4um, internally concave, chestnut coloured o.p.w., other walls thin, relatively colourless. Lumina with coarsely granular contents. In paradermal view, 4-8-sided isodiametric polygonal (c.5% extended 2:1 polygonal near the chalaza, but percentage increasing towards micropyle.)

Mesophyll c.5 cells thick, small, aerenchymatous (best seen in paradermal view), prostrate elliptic-rectangular cells, 35-49um wide, 9-13um high, walls relatively thick, pale brown. Lumina packed with dense grey translucent cytoplasm, occasionally with lipid globules. Few airspaces. This tissue usually crushed to a layer 30um thick in mature seed-coat, except close to chalaza.

I.E. not readily differentiated from the layers above. Sparsely crystalliferous, short, prostrate elliptic cells c.9um high, 20um wide. Crystals translucent, c.6um long, variously orientated.

TEGMEN

Exotegmen of 2-3 layers of long, longitudinal fibres with predominantly square ends, walls 5-7um thick, pale gingerish in colour, remarkably untapered along their length, with dense scalariform pits transverse or slightly oblique to fibre axis and 6-20um long, 1-3um wide. Fibres 210-455um long in LS, 20-32um wide in TS, 31-38(-42)um high, in TS appearing shortly columnar, elliptic (rarely isodiametric, circular).Fibres not densely packed, especially in lower layer.

Endotegmen of largely crushed and absorbed, colourless cells forming a zone c.65um thick. Uncrushed cells are rare, c. 70um wide, 9um high, thin walled.

PERISPERM apparently represented by a thin zone of crushed cells c.30um thick.

CHALAZA

seed-coat 2-3 times thicker than integuments.

O.E. and sub-O.E. mesophyll as in testa, but O.E. cells more usually columnar.

Upper chalaza of very small, prostrate elliptic cells c.14um wide, 9um high, lumina filled with dense grey cytoplasm, cell boundaries difficult to discern. c.200um thick.

Embedded in this are:

a. Vascular bundles; at the uppermost layers in the centre of chalaza, but at lowermost layers at rim of chalaza, being confluent with endotegmen.

b. sclereids; prostrate, in intermittent clusters, c.45um long, c.25um wide, with walls c.4um thick. Confluent with exotegmen.

Lower chalaza c.100um thick of larger, prostrate, shortly elliptic (to spherical) cells c.15um high, 20um wide, usually filled with tannin or black granular cytoplasm.

Ruagea glabra Tr. and Planch.

This description based on Pennington and Poveda 10132, Costa Rica.

Collectors' notes not available.

GROSS MORPHOLOGY

Fruits one to three locular dehiscent capsules, spherical to very slightly obovoid, 20-25mm long, 20-28mm wide, surface glabrous with scattered corky verrucae. Valve sutures very slightly depressed. Style persistent or not, slightly raised or sunken. Pedicel 4-9mm long, 4-5mm wide. Pericarp 1.5-2.5mm thick, outer part fleshy-leathery, the endocarp cartilaginous as a toenail.

Central column with three distinct vascular bundles projecting from edges and top, c.10mm high, 3mm broad.

Seeds 1-3 per fruit, glossy, chestnut brown, broadly ellipsoid, sl. flattened dorsi-ventrally, c.16mm long, 12mm broad and 8mm wide. The

L32

PLATE 56

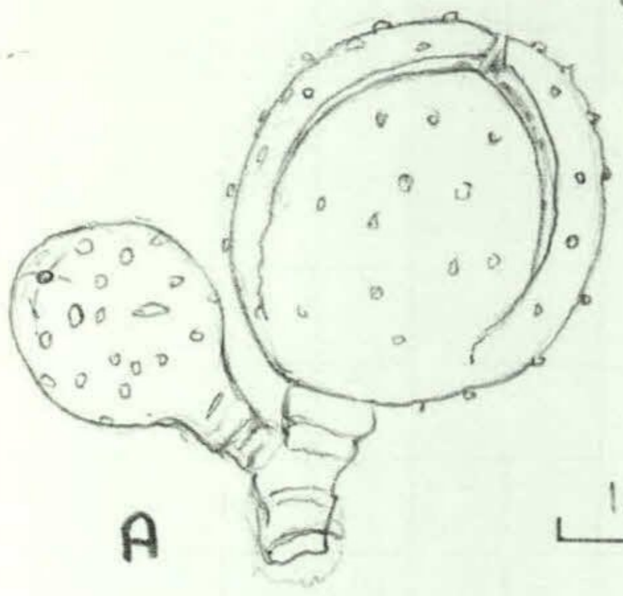
RUAGEA GLABRA

A-C FRUITS; LOCULICIDALLY DEHISCENT, WARTY SURFACE.

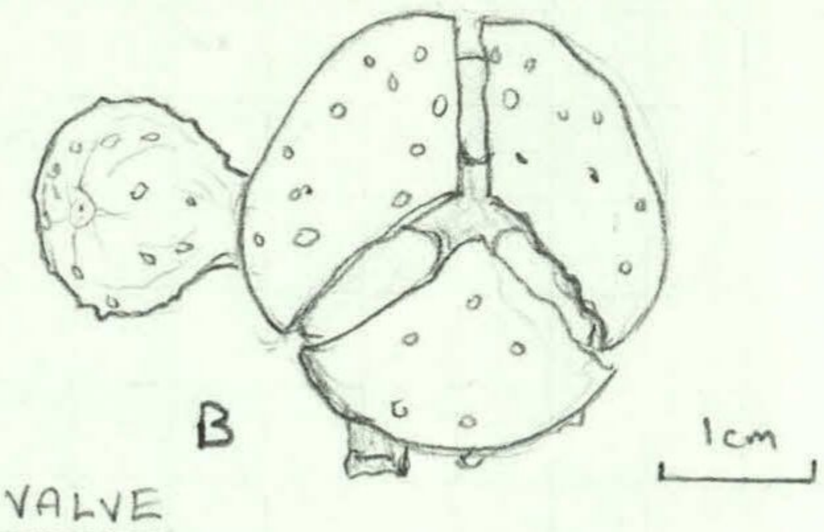
D-M SEEDS; NOTE BROAD RAPHE SCAR. RAPHE-CHALAZAL-ARILLATE TO PARTLY SARCOTESTAL.

# Ruagea glabra

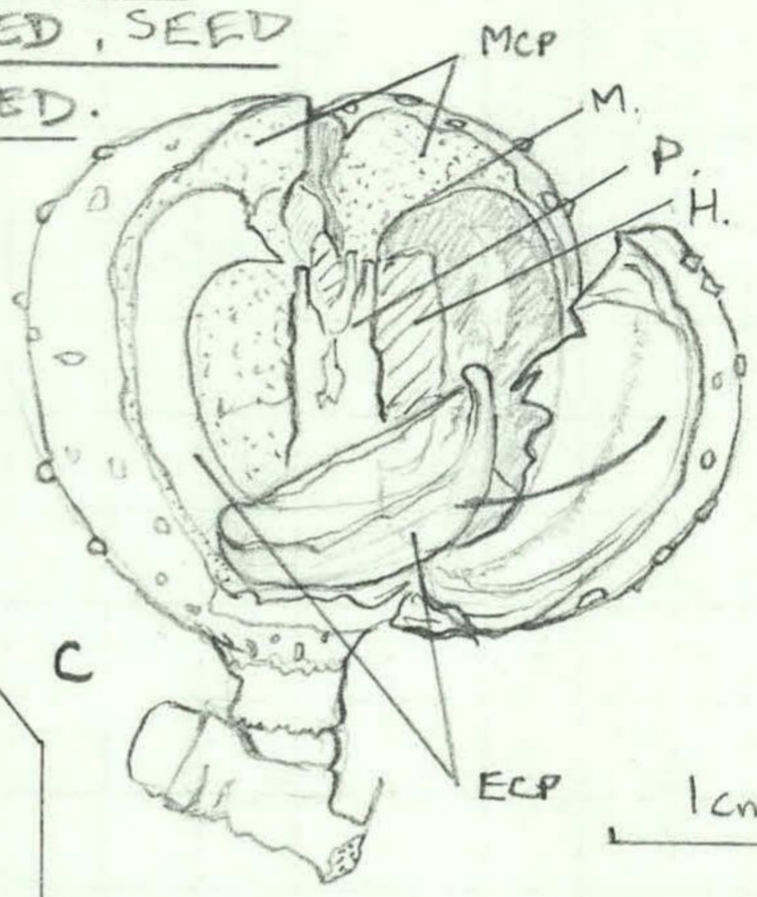
LATERAL VIEW FRUIT




PLAN VIEW FRUIT

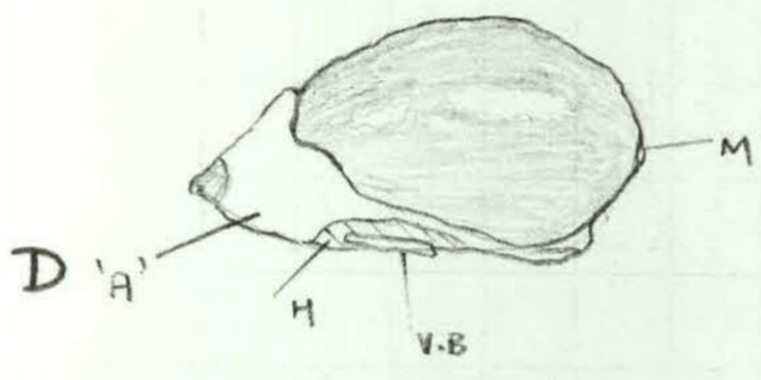



FRUIT. VALVE DISPLACED, SEED REMOVED.



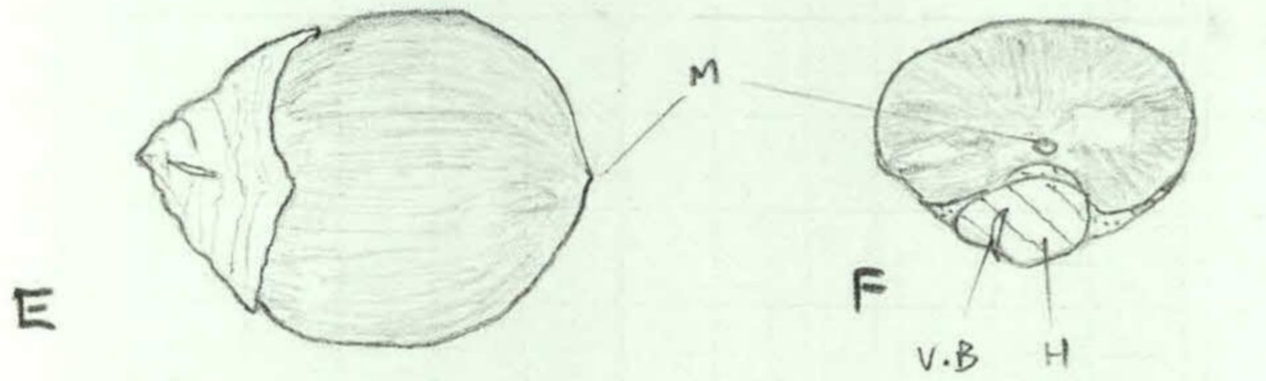

SEED. FLESHY PART ATTATCHED

LATERAL VIEW



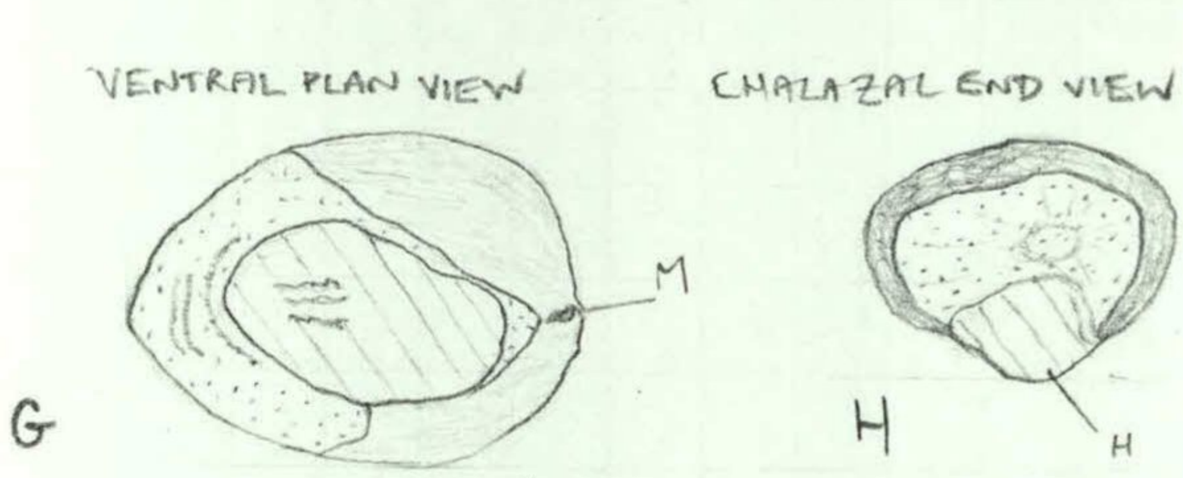

DORSAL PLAN VIEW

END VIEW. MICROPYLE




VENTRAL PLAN VIEW

CHALAZAL END VIEW

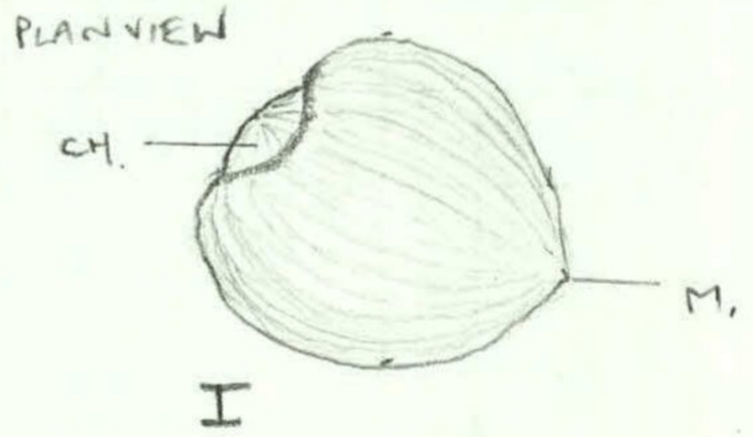



HARD SEED SURFACE = FLESHY SEED SURFACE = HILUM

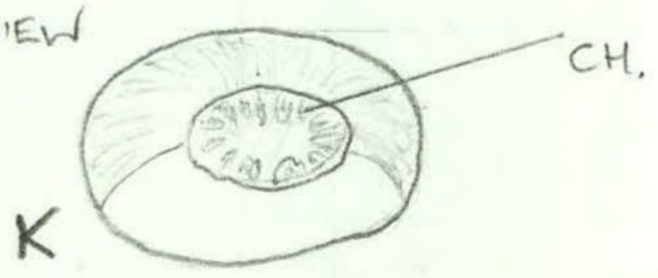
SEED. FLESHY PART REMOVED

1cm

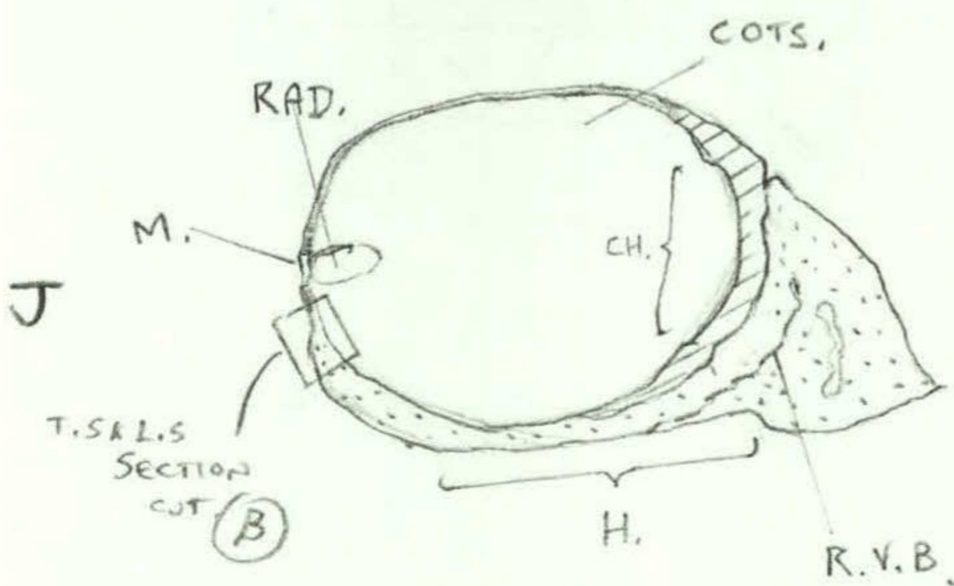
DORSAL PLAN VIEW




CHALAZAL END VIEW



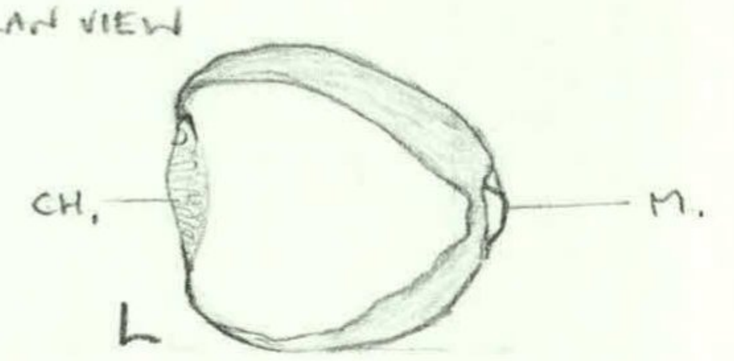

L.S. SEED




SCHLEREIFIED CHALAZA = FLESHY TISSUE.

1cm

VENTRAL PLAN VIEW



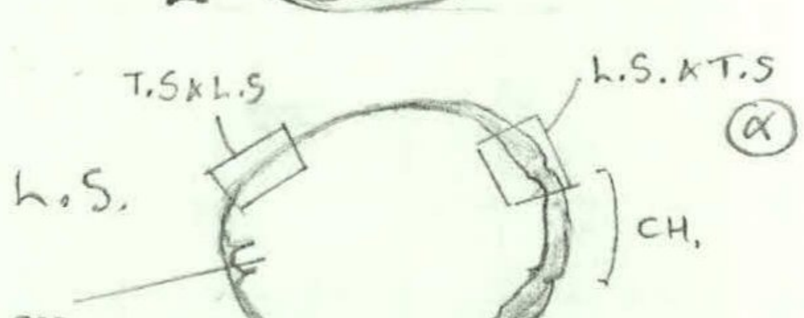



PLATE 57

RUAGEA GLABRA

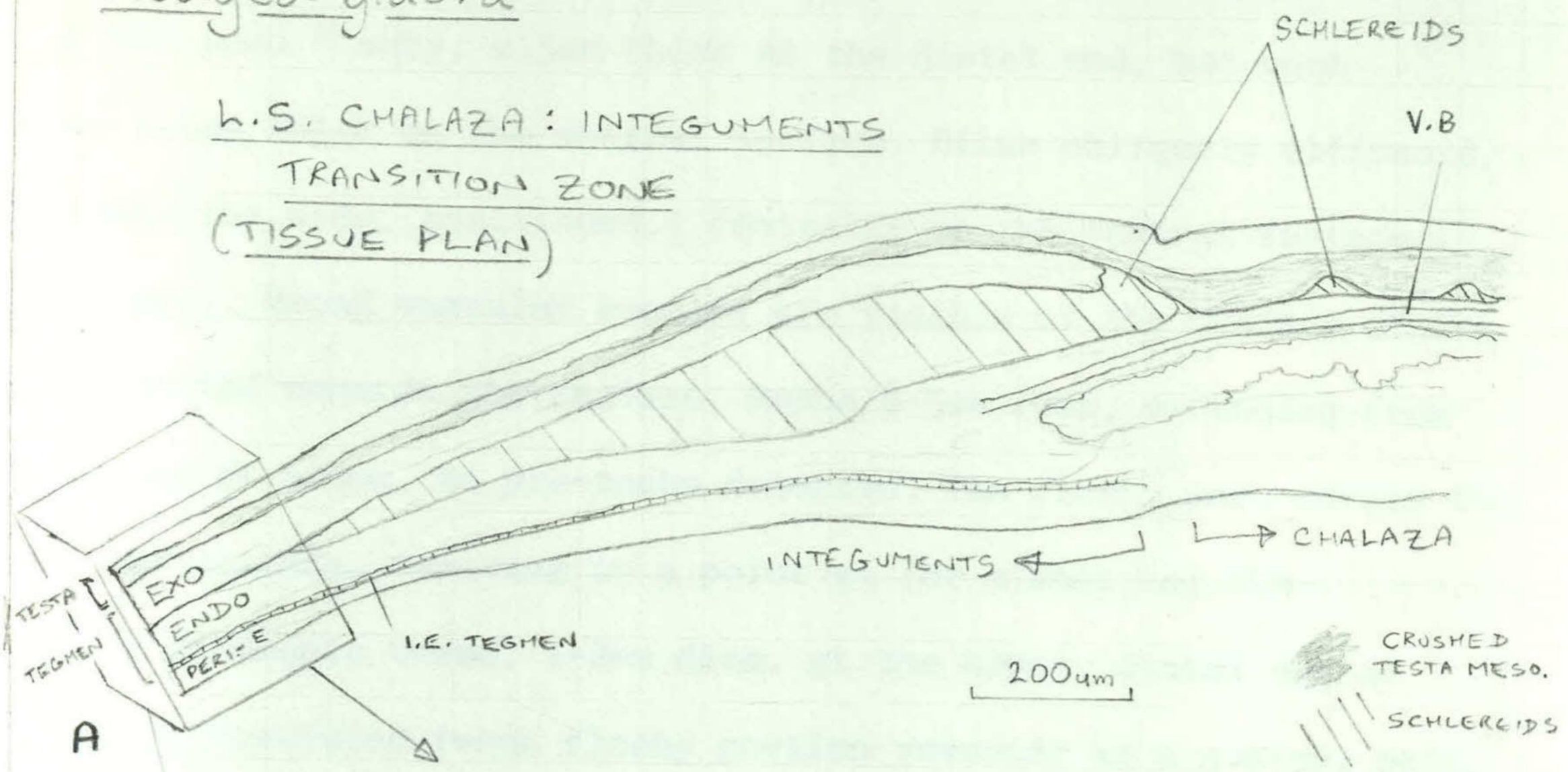
A-E SEED ANATOMY: NOTE BITEGMIC CONSTRUCTION,

EXOTEGMIC FIBRES COLUMNAR IN T.S.,

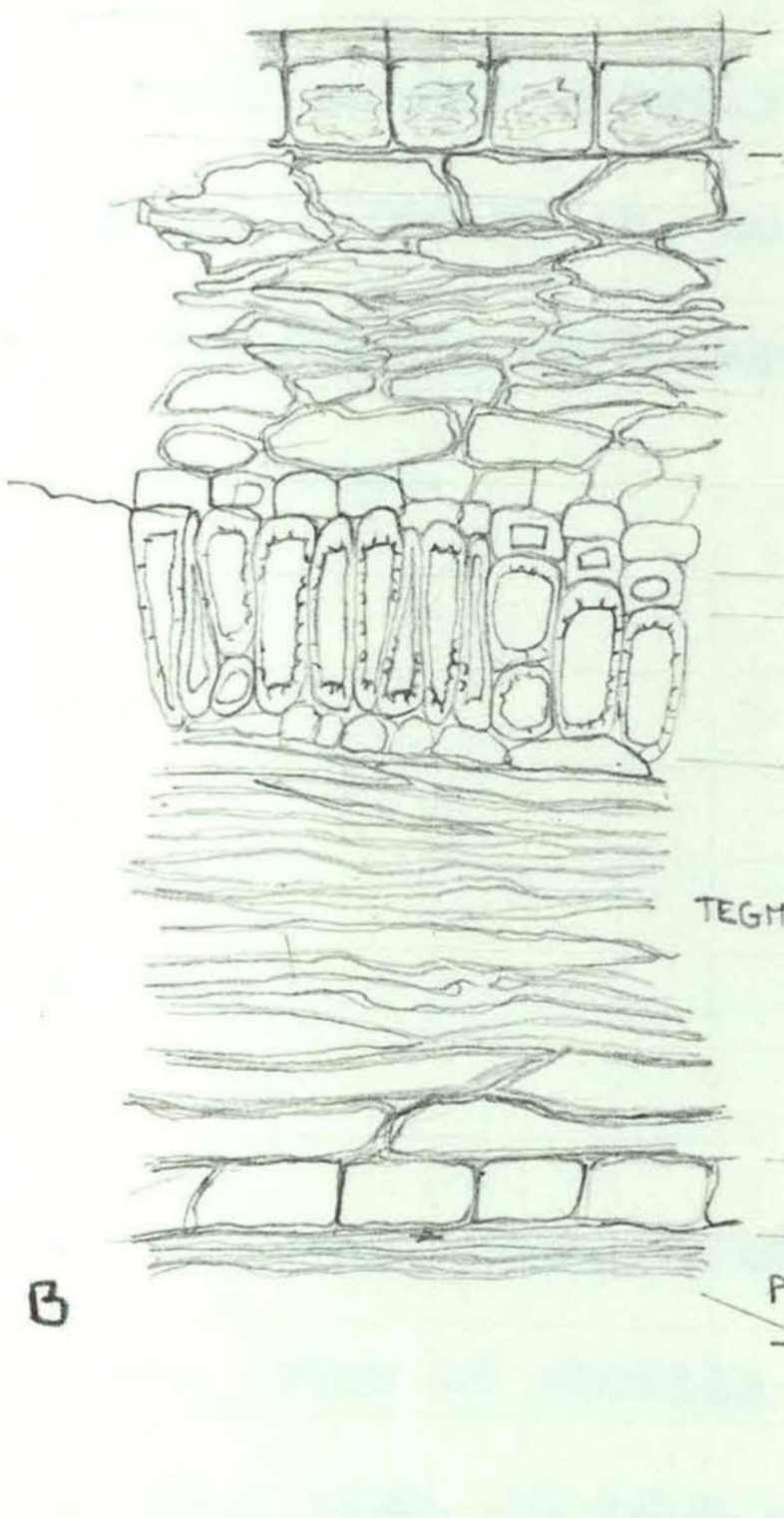
CRYSTALS ONLY INTERMITTENT IN CELLS OF TESTAL I.E.

# Ruagea glabra

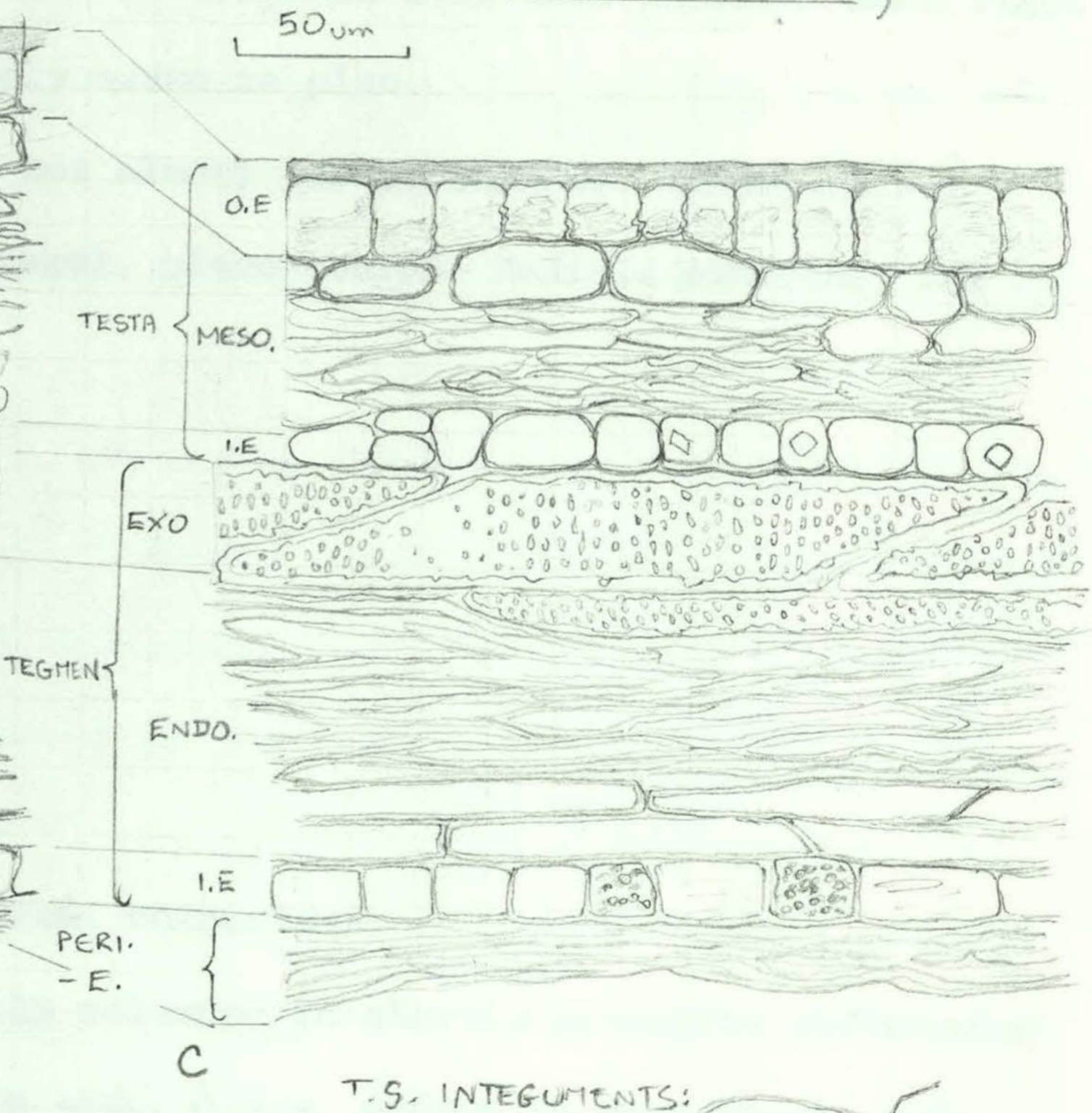
## L.S. CHALAZA : INTEGUMENTS TRANSITION ZONE (TISSUE PLAN)



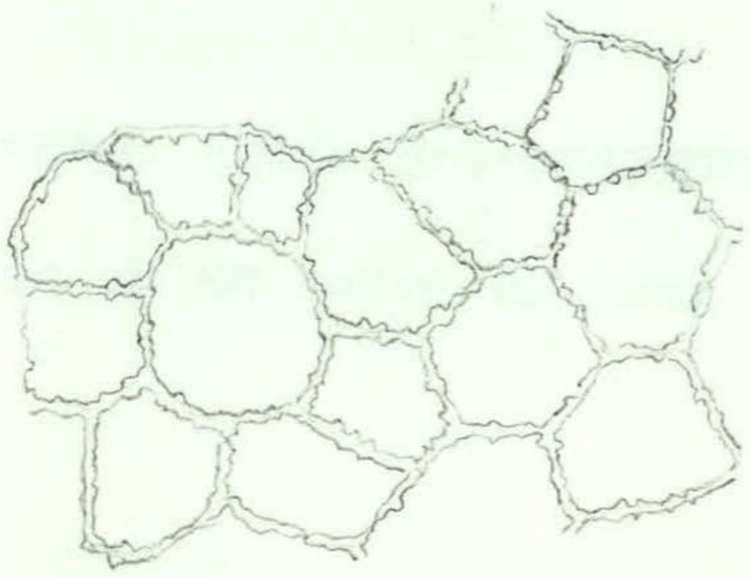

## T.S INTEGUMENTS (α)



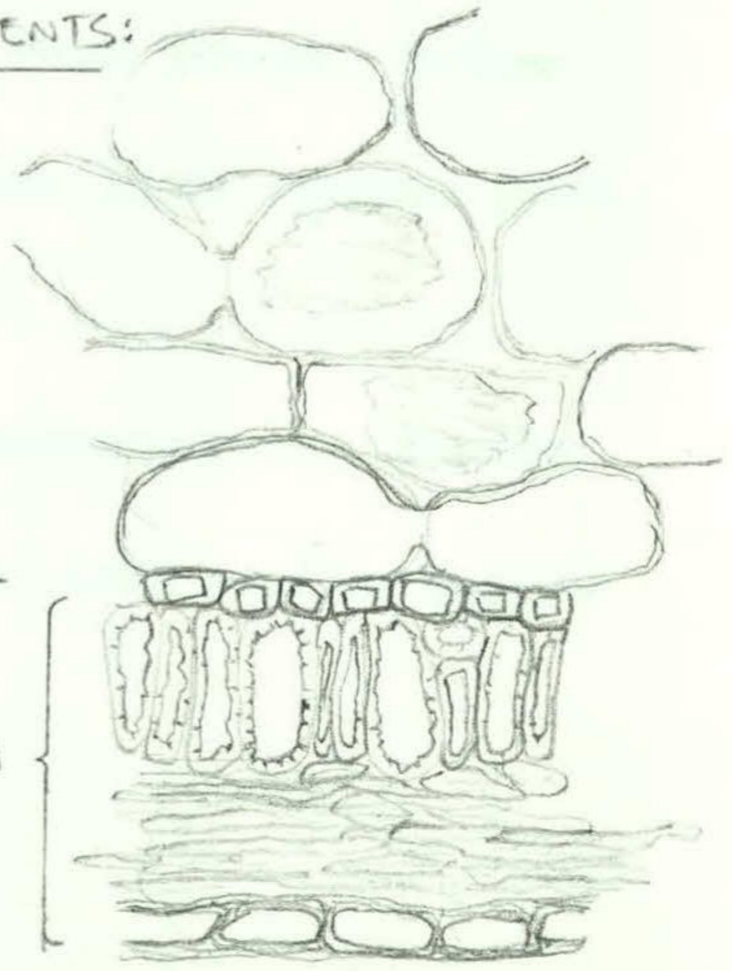

## L.S. INTEGUMENTS (α) (NEAR CHALAZA)




## O.E. TESTA (PARADERMAL VIEW)




## T.S. INTEGUMENTS: (MICROPYLE, 'SARCOTESTAL')



lower (proximal with respect to fruit) third together with the central part of the seed fleshy, c.5mm thick at the distal end, but much thinner, c.1mm thick on the ventral surface. Hilum obliquely ellipsoid, c.9mm long, 7mm wide, positioned ± centrally on the ventral surface (fleshy part). Broad vascular bundles are visible at the surface of the hilum, directed towards the chalaza. Raphe 4-5mm long, extending from chalazal end of hilum. No pre-raphe detected. The fleshy part covers the chalaza and extends, tapering to a point at (or almost to) the micropyle. Micropyle broad, 1-2mm diam. at the blunt, distal end of seed. Chalaza revealed (when fleshy portion removed) as a sunken, matt, darker, transversely ellipsoid area , 5.5-7mm broad, 4mm high at the proximal end. The fleshy layer is thickest over this portion. When flesh removed, seed appears broadly ovate in plan.

Seed-coat c. 0.2mm thick, but almost 1mm at chalaza. Endosperm not detected. Cotyledons collateral, plano-convex. Radicle exserted, 2mm long, 1.25mm broad.

ANATOMY

INTEGUMENTS

TESTA

Cuticle: extremely thin, <1um, colourless.

O.E. single layer of shortly columnar to shortly prostrate rectangular cells, 18-35um high, 14-42um wide. O.p.w. medium to dark brown, 6-7um thick. Anticlinal and i.p.w. thin, 2-3um thick. Lumina with sparse pale brown contents.

In paradermal view, cells 5-7-polygonal, usually isodiametric, rarely extended and then up to twice as long as broad. Anticlinal walls appear

as though finely pitted or slightly ribbed, but this not apparent in LS or TS.

Mesophyll. Very variable:

Dorsal, non-fleshy seed-coat. 4-8 layers thick, all but the uppermost usually (e.g. dorsal surface from chalaza to micropyle) crushed to a very dark zone 25-30um thick. Uppermost layer of prostrate ellipsoid cells 14um high, 40um wide with thin contents, walls c.1-2um thick.

Ventral surface. For the larger part, it is this zone that proliferates to form the fleshy part of the seed-coat, the cells uncrushed, ± aerenchymatous, up to 20 layers thick and much larger than in the non-fleshy integument. In L.S., cells prostrate elliptic with pale to medium brown walls and contents, to 91um wide, 42um high. On the non-fleshy ventral surface, the mesophyll declines to only 3-4 uncrushed cell layers thick, the cells far smaller.

I.E. a single layer of robust, markedly uncrushed, rounded rectangular (prostrate or shortly columnar) cells 8-17um high and 9-24 um wide. Anticlinal walls thin, c.1um but o.p.w. often as well developed as o.e, to 9um thick, but pale brown. Contents colourless, but usually each with a single rhombic to rounded translucent endocrystal up to 14um long. These largest and most numerous on the ventral surface of the seed.

TEGMEN

Exotegmen a single (rarely two) layer of longitudinal fibres 122-330um long, fusiform in longitudinal and paradermal views, end walls highly tapered. In T.S, columnar to 35um high, 12-19um wide. Walls 3-7um thick, very pale yellow, highly translucent. Heavily pitted with small transverse elliptic pits 1-3um long, c.5-8 thick on each anticlinal wall.

Mesotegmen c. 10 layers thick, completely crushed near the micropyle (to a zone 25um thick), and in this seed, all but the lower three layers largely crushed, even near the chalaza. These of rather large, prostrate elliptic cells c.110um wide, 14um high, walls pale brown, c.2um thick. No contents.

I.E. a single layer of robust, shortly rectangular (prostrate or erect) cells, which resist crushing even near the micropyle. Cells 14-22um high, 21-40um wide. Contents sparse, but occasionally densely dark granular. Walls brown, 2-3um thick.

PERISPERM-ENDOSPERM

Probably represented by the amorphous zone of crushed material up to 30um thick below the tegmic I.E.

CHALAZA

Can be conveniently divided into two zones:

Upper fleshy zone, to 5mm thick corresponding and confluent with mesophyll of the testa (for description q.v.).

Lower sclerenchymatous zone, to 1.1mm thick, corresponding with the tegmen, but many more layers thick and more homogeneous. Largely of short prostrate sclereids 50-70um wide and 14-28um high, with walls 5-7um thick, sometimes with orange contents. Interspersed are parenchyma and vascular bundles.

Turraeanthus mannii Baill.

This description based on Cheek et al. 948 and Thomas s.n.

Collector's notes: 'fruits fully mature, pericarp glossy, orange, thin and succulent; seed white with crisp succulent coat, cotyledons green'.

# PLATE 58

## TURRAEANTHUS MANNII

(CHEEK ET AL 948)

A FRUITS, MATURE. NOTE ORANGE, SUCCULENT, INDEHISCENT PERICARP, IRREGULARLY DISTENDED BY SEEDS. X 1.

B FRUIT & SEED DISSECTED. NOTE BASAL INSERTION OF SEED. THICK, WHITE, SUCCULENT SARCOTESTA & GREEN COTYLEDONS X 2.


A
B

PLATE 59

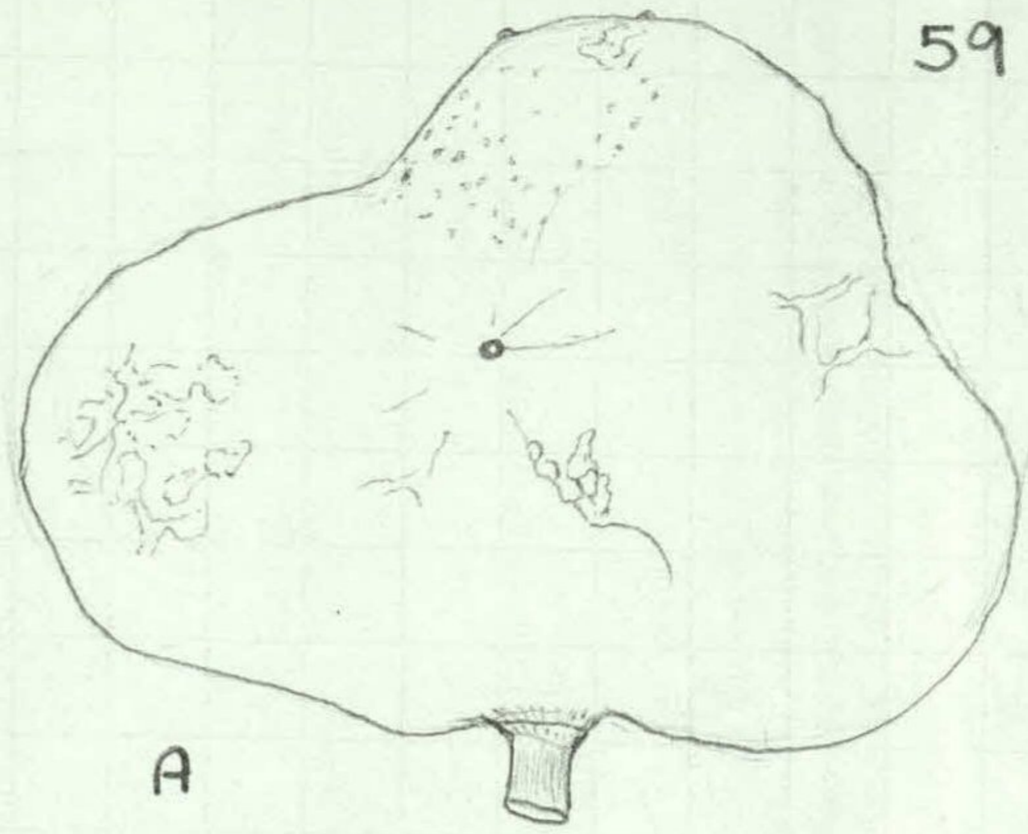
(A-CHEEK 948, OTHERS THOMAS S.N.)

TURRAEANTHUS MANNII

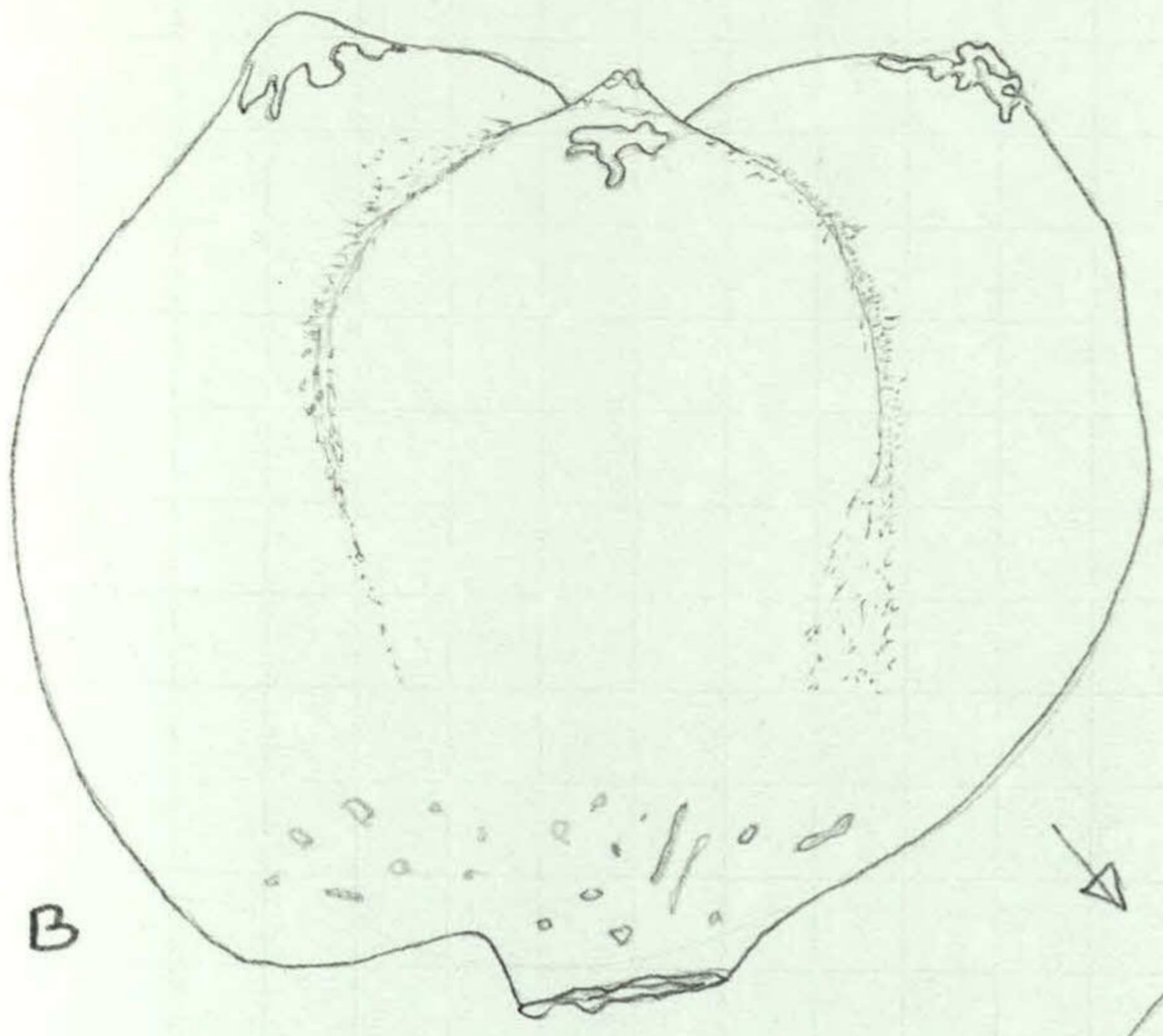
A-I FRUITS AND SEEDS. NOTE SEED ORIENTATION.

# Turreanthus mannii

FRUIT : LATERAL VIEWS

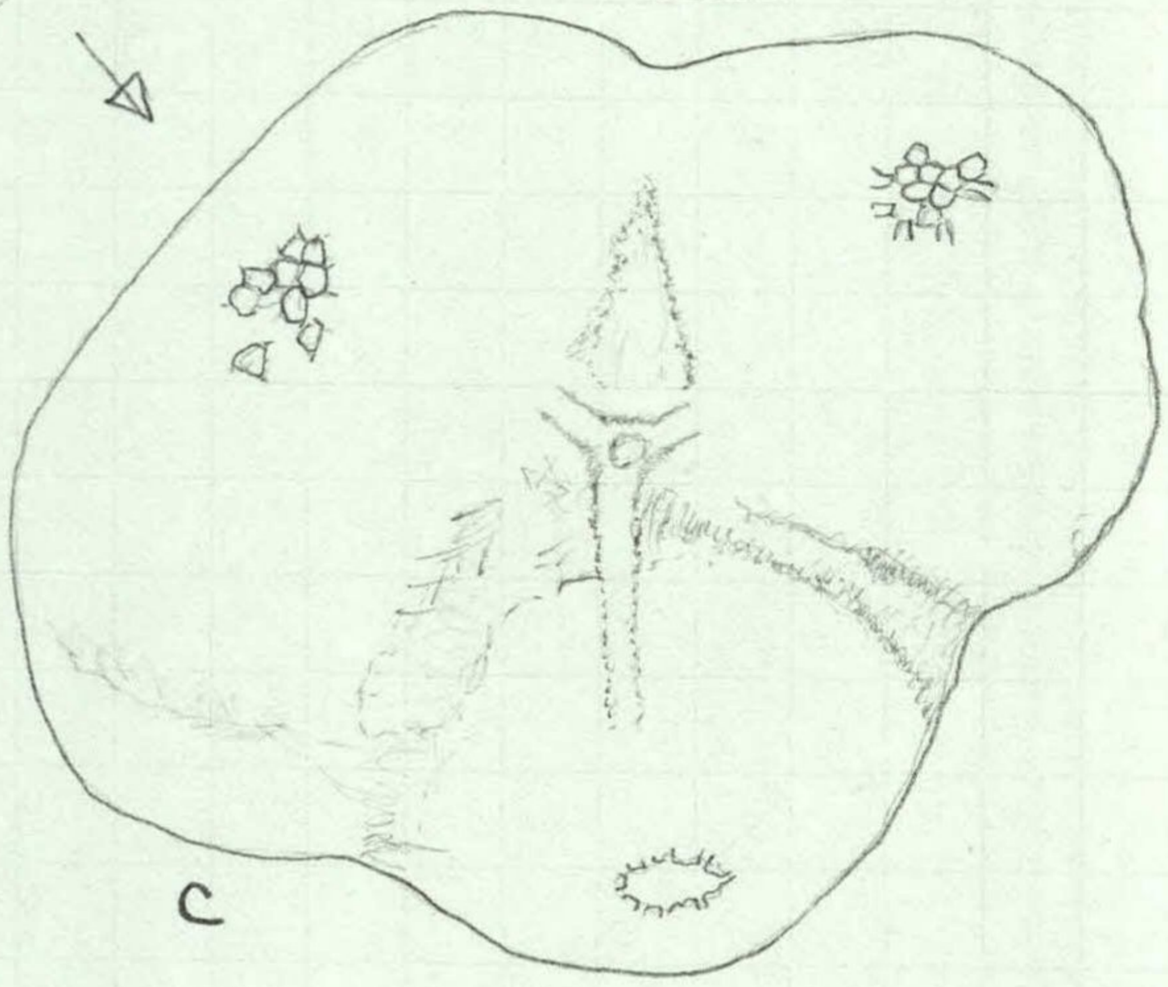


A



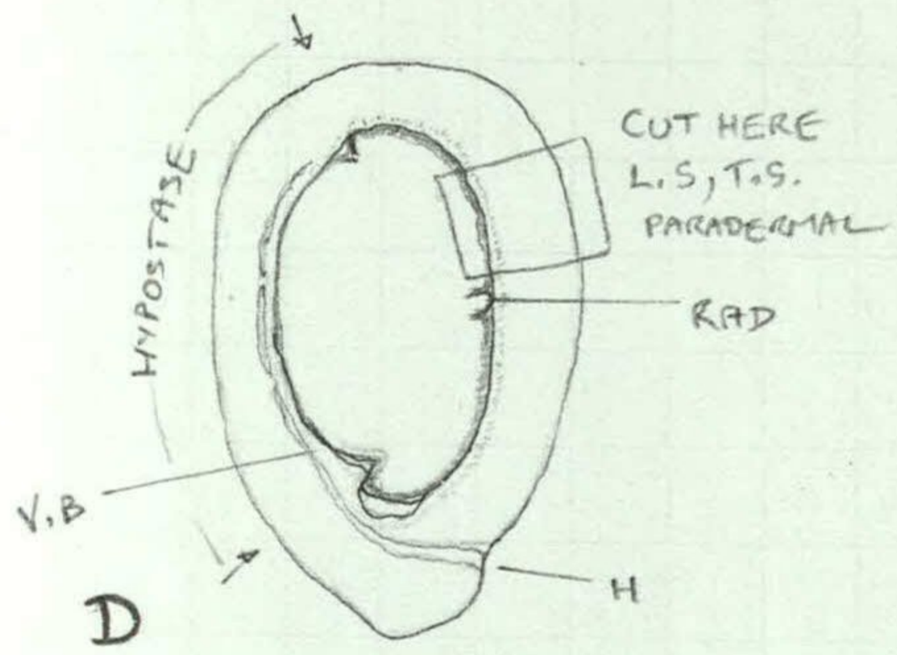
B

FRUIT : PLAN VIEW



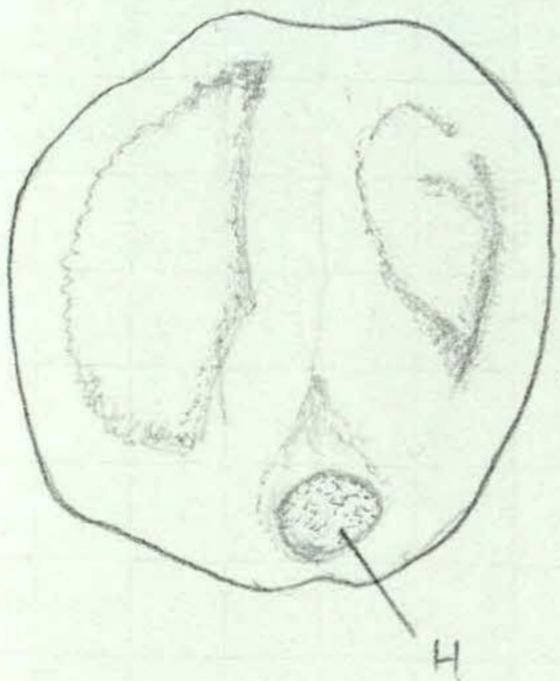
C

SEED L.S



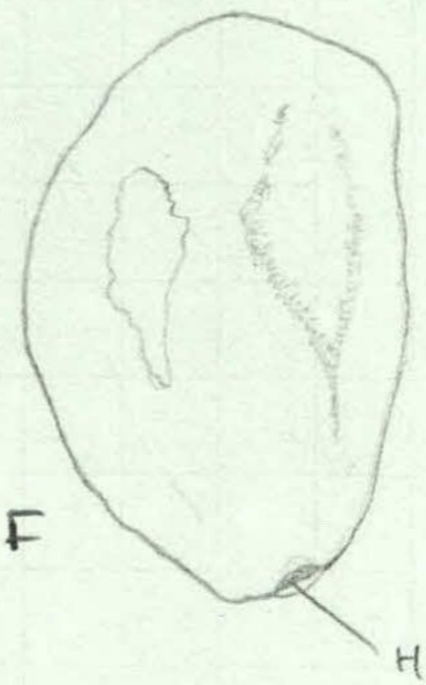

D

SEED VENTRAL VIEW



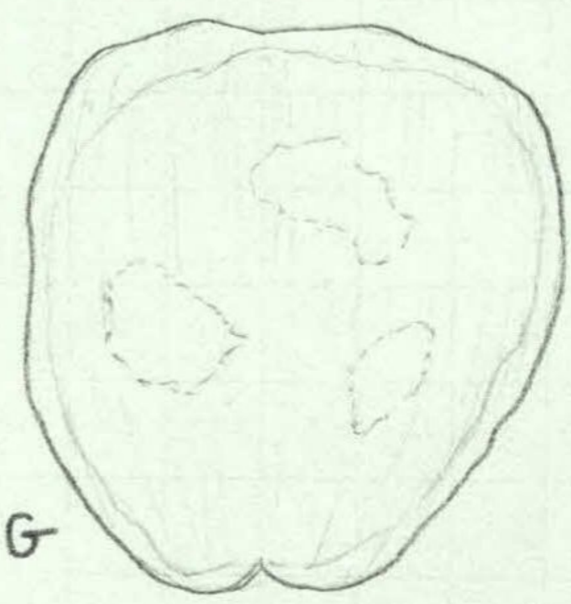

E

LATERAL VIEW




F

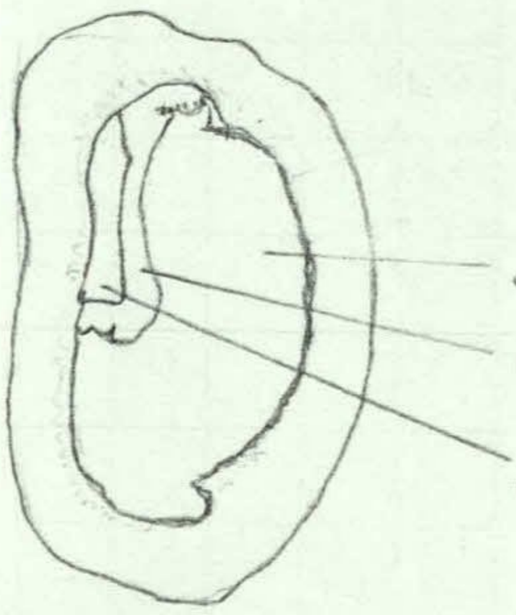
DORSAL VIEW



G

SEED L.S.

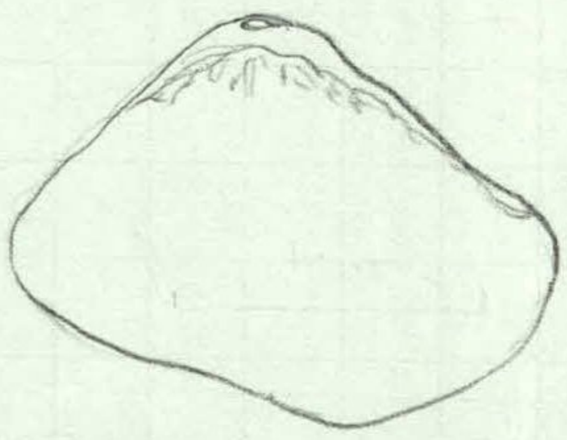
(PRECOCIOUS GERMINATION)




H

1cm

SEED PLAN



I

PLATE 60.

(CHEEK 948)

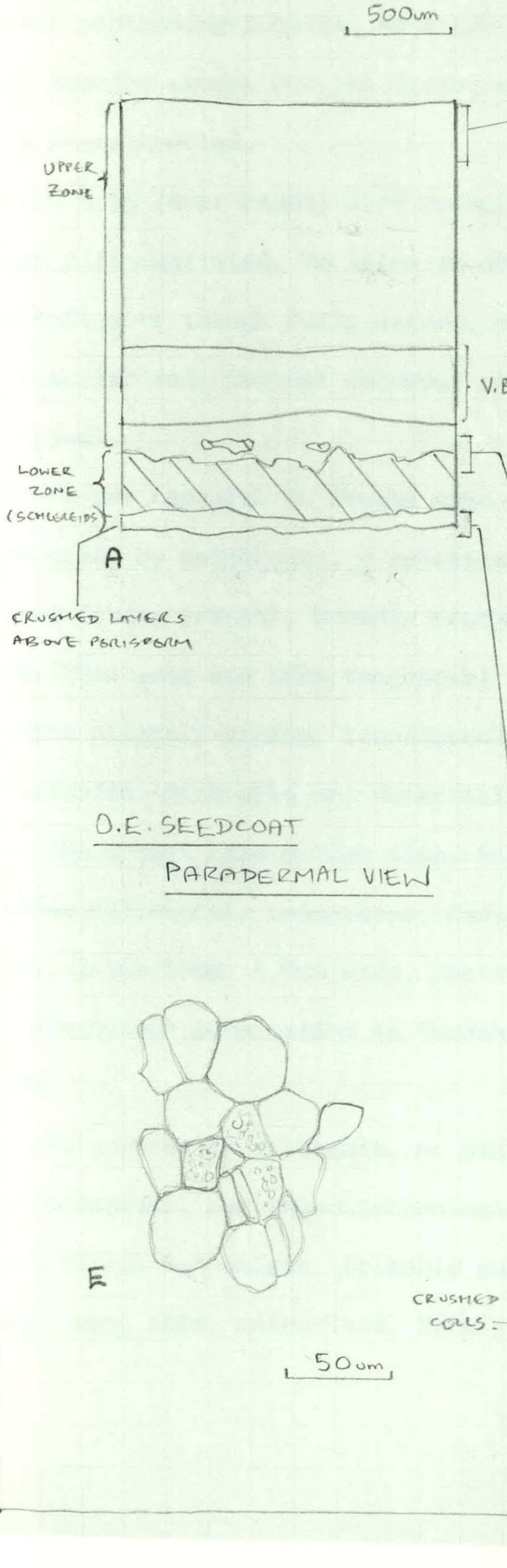
A-D SEED ANATOMY. NOTE UNITEGMIC (PACHYCHALAZAL?) CONSTRUCTION, UPPER PART FLESHY, LOWER WITH LIGNIFIED CELLS. LATTER WITH VERY UNUSUAL THICKENINGS . VASCULAR BUNDLES ABOVE SCLEREIDS.

# Turraeanthus mannii

## L.S. SEEDCOAT




## L.S SEEDCOAT: TISSUE PLAN




## O.E. SEEDCOAT

### PARADERMAL VIEW

GROSS MORPHOLOGY

Fruit an indehiscent 3-locular berry, broader than long and widest distally. But 1 (-2) locules usually abort so fruits irregularly 2-3-lobed, 15-35mm wide, 20-25mm long. In perfect fruits (regularly 3-lobed), 35-40mm broad, 30mm long. Style base swollen, but sunk between the three protruding locules. No stipe or rostrum. Pericarp glossy yellow, smooth, except for the distal surface of the three protruding locules where knurled.

Pericarp 0.75 (over seeds)-2(-4 exceptionally, near testa)mm thick. No endocarp differentiated. No lines of dehiscence noted. Fruits indehiscent even though fully mature, with seeds germinating. Septa soft, vascularized. Central columnar placentae absent, placentation axile, basal.

Seeds 0-2 per capsule. In fruits with aborted locules where seed shape unconstrained by neighbours, ± spherical, c.15mm diam.. In fully developed fruits (rarer), broadly orange -segment shaped, 10-11mm radial breadth, 19mm long and 18mm tangential breadth.

Seed-coat slightly glossy, translucent-white, 2-3mm thick. Hilum 3-4mm diam., rounded. Micropyle not detectable. Hypostase apparently a convex area on the dorsal face c.12mm diam. Endosperm apparently absent. Cotyledons collateral, transverse. Radicle slightly included (by 0.5-1mm), 2.5mm long, 1.5mm wide, centripetal. Often further extended due to precocious germination in (undehisced) fruit.

ANATOMY

Seed-coat apparently unitegmic, no distinct testa and tegmen. A lower zone of sclereids, but these intermingle with parenchyma above and no distinct testal I.E exists. Probably pachychalazal.

Cuticle: very thin, colourless. Barely detectable.

O.E. a single layer of small prostrate, rounded rectangular to square cells. (TS and LS). o.p.w. slightly convex, straw-coloured,c.2um thick. Lumina with colourless cytoplasmic contents. In paradermal view, polygonal to rectangular.

Upper parenchymatous zone very thick, c.1500um, of colourless, thin-walled parenchyma cells. Cells polygonal, rather angular, isodiametric or columnar, 50-90um wide, 50-100um high. Lower part heavily vascularized, with fibres up to 400um thick. Here, the parenchyma smaller, isodiametric, polygonal, c.40um diam. Below the vascular , cells smaller still, matching sclereids in size. Parenchyma with thin (c.1um thick) pale yellow walls and colourless lumina.

Lower zone of sclereid layers, 200-300um thick. Cells shortly radially to longitudinally extended angular-elliptic sclereids 50-65um long and 35-50um broad. Thin-walled (c.2um) with thin scalariform to spiral thickenings.

A zone of crushed cells 10-50um thick, below the sclereids.

?PERISPERM

Intermittently present, 0-4 layers thick. Cells sub-isodiametric, 4-5 angled, 26-31um wide, 14-30um high, walls thick, but colourless, lumina with dark, densely granular contents.

VARIATION

Thomas s.n.

seed-coat thicker, upper zone to 2200um thick; Parenchyma cells larger, usually columnar (radially elongated) to 140um high.

Lower zone to 350um thick, sclereids 20-40(-70um) long, 15-20um broad (slightly smaller than first colln.). Identical thickenings.

Crushed zone absent.

?Perisperm absent.

Guarea glomerulata

This description based on D.Thomas 4429

Collectors notes: not available.

GROSS MORPHOLOGY

Four locular dehiscent capsule, strongly four-lobed in plan view, to 18mm wide, 14mm long, stipe 2-3mm long, covered by persistent calyx. Fruit apex sunken, style persistent, cylindrical c. 1.5mm wide, c.2mm long. Broad ridges flank each valve suture. Capsule surface strongly tomentose. Pericarp 2mm thick at sutures, stiffly cartilaginous endocarp.

Seeds one per locule, axile-pendulous, ellipsoid in dorsal plan and lateral views, 11mm long, 8mm wide, 7.5mm deep. Surface medium-pale brown, slightly fleshy, especially on the ventral surface near the hilum. Hilum ± isodiametric, c.2mm diam. often with a smaller cavity where vascular bundle enters. Micropyle at apical end (w.r.t. fruit) of seed, obscure, a small slit c.0.5mm long.

Seed-coat c. 0.3mm thick, except the fleshy ventral surface, c.1.5mm thick.

Endosperm effectively absent. Cotyledons unequal, the dorsal c.1/10th the size of the ventral. Radicle included by c.1.5mm, c.0.5mm wide and 1.5mm long, medium brown.

ANATOMY

Seed-coat appears unitegmic (testa and tegmen are not markedly differentiated). Cuticle: extremely thin, apparently colourless. O.E. a single layer of prostrate, shortly rectangular to shortly columnar cells (L.S., T.S.) with concave o.p.w. yellowish brown, 5-7um

PLATE 61

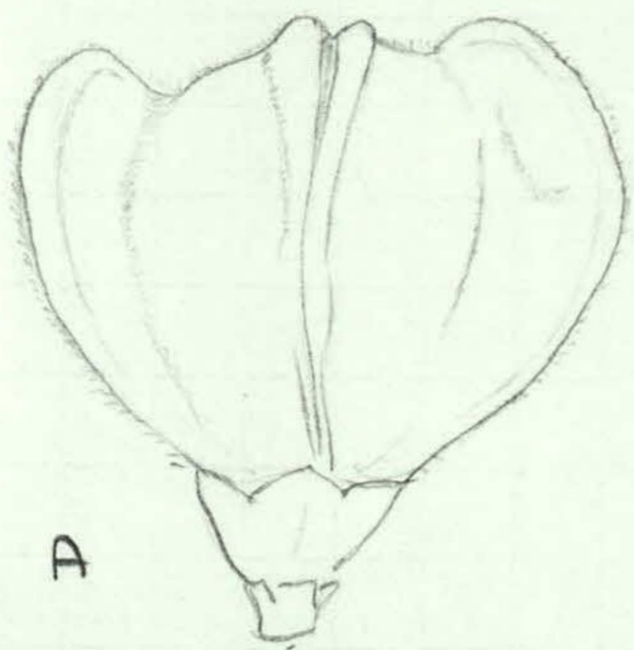
GUAREA GLOMERULATA

A-C FRUITS: DEHISCENT.

D-H SEEDS: SARCOTESTAL

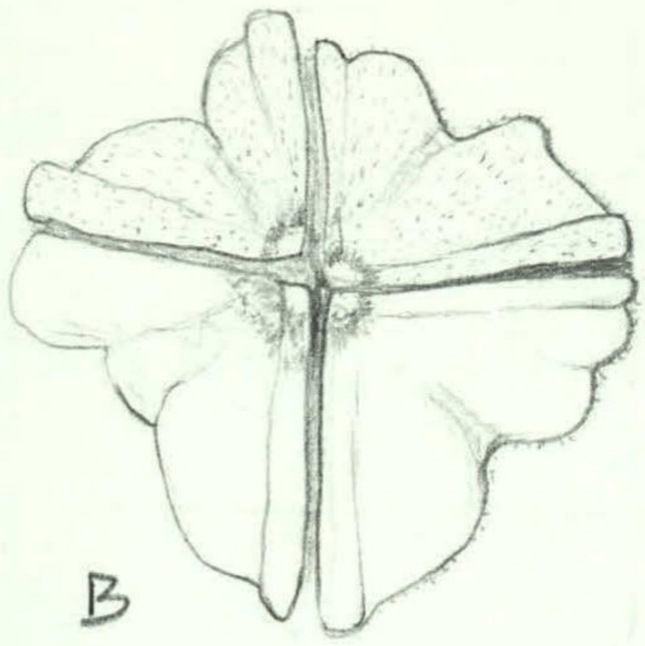
# Guarea glomerulata

FRUIT. LATERAL VIEW



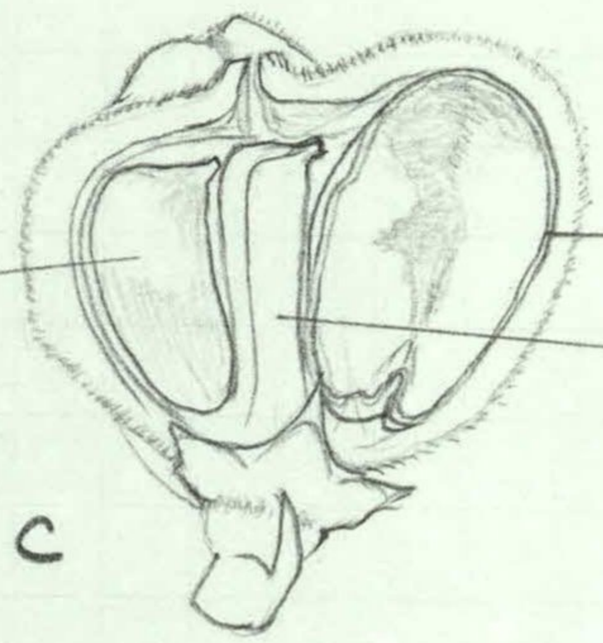
A

FRUIT. PLAN VIEW



B

FRUIT. LATERAL VIEW - (TWO VALVES REMOVED)

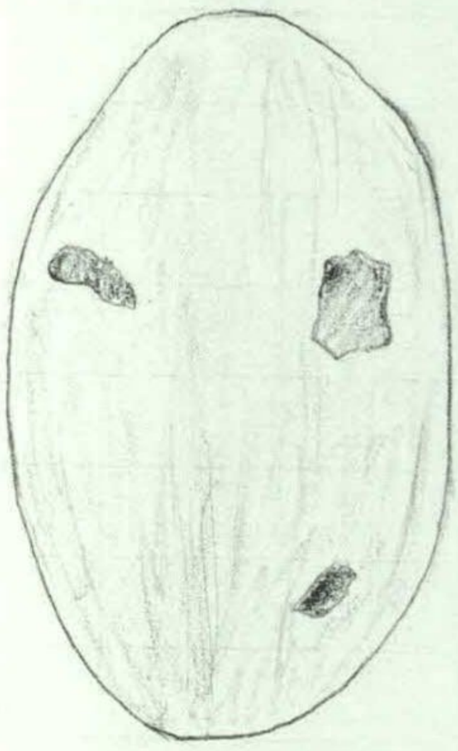



C

1cm

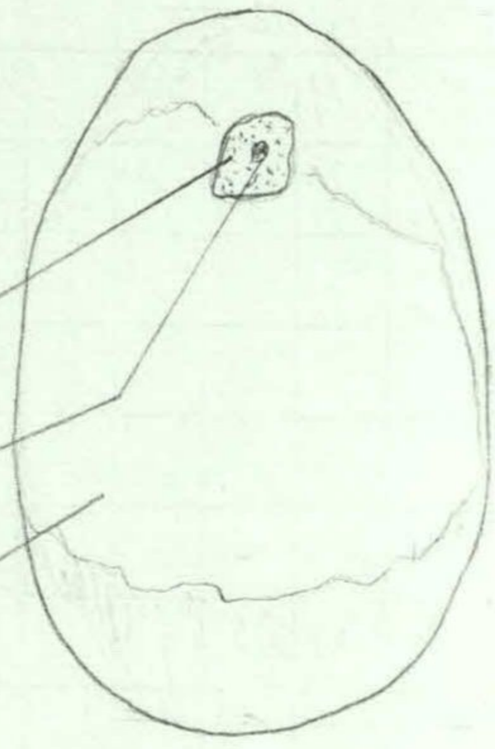
SEED DORSAL PLAN VIEW.

SEED, LATERAL VIEW

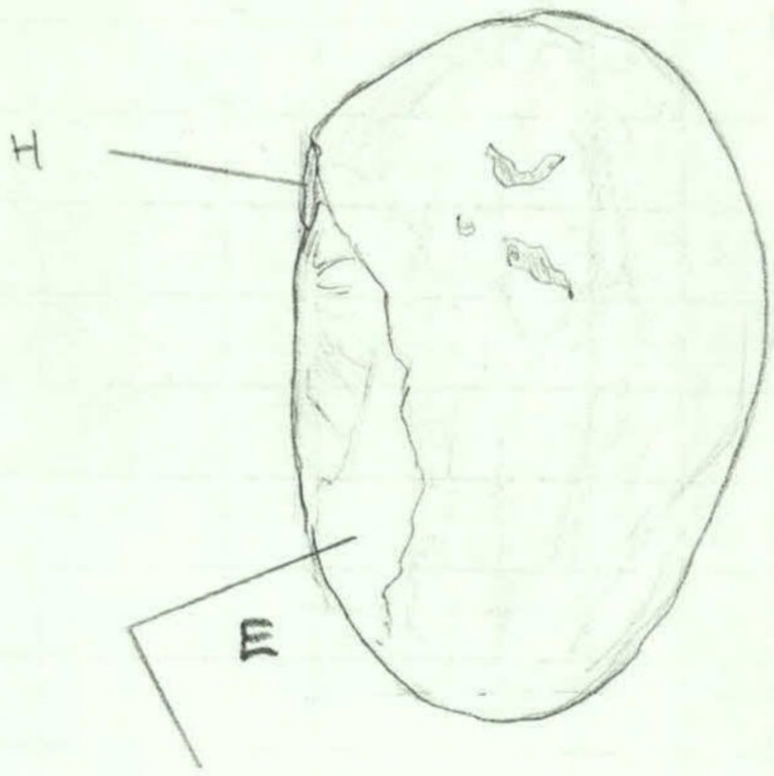


D

VENTRAL PLAN




F




L.S. SEED

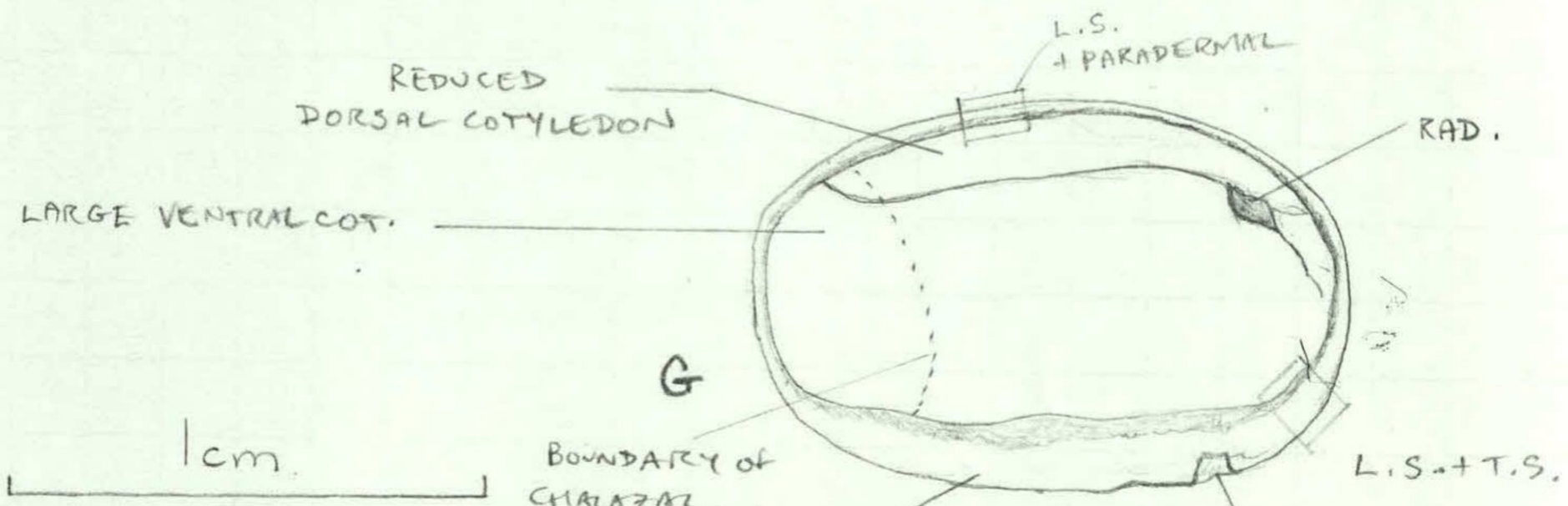


PLATE 62

GUAREA GLOMERULATA

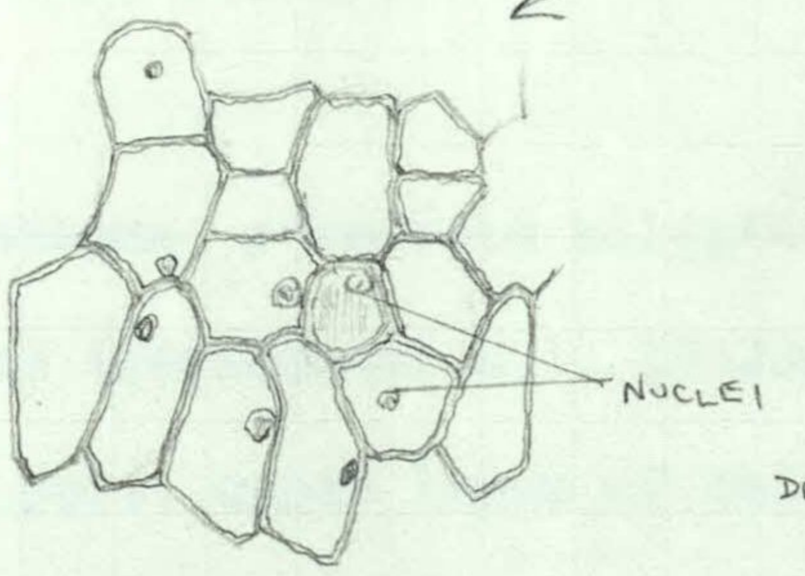
A-D SEED ANATOMY: UNITEGMIC. NOTE DIFFUSE LONGITUDINAL FIBRES, (C & D): INDICATIVE OF A LARGELY LOST TEGMEN?

NOTE ABSENCE OF SCLEREIDS AND TANNINIFEROUS CELLS, VASCULAR BUNDLES PRESENT, BUT NOT SHOWN HERE.

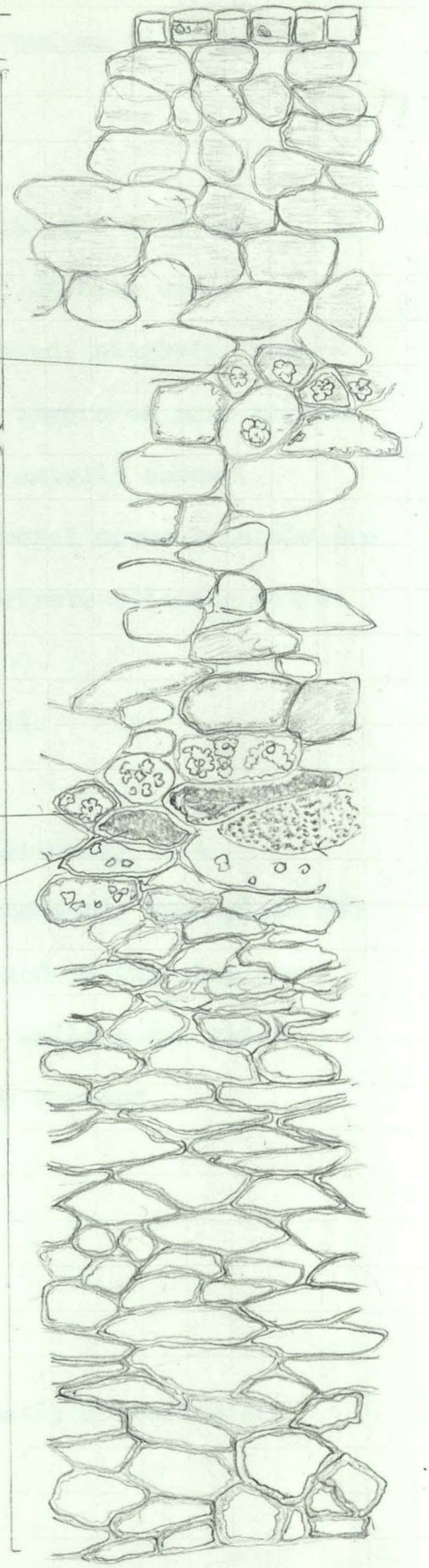
# Guarea glomerulata

## L.S. SEEDCOAT
MICROPYLAR END, VENTRAL

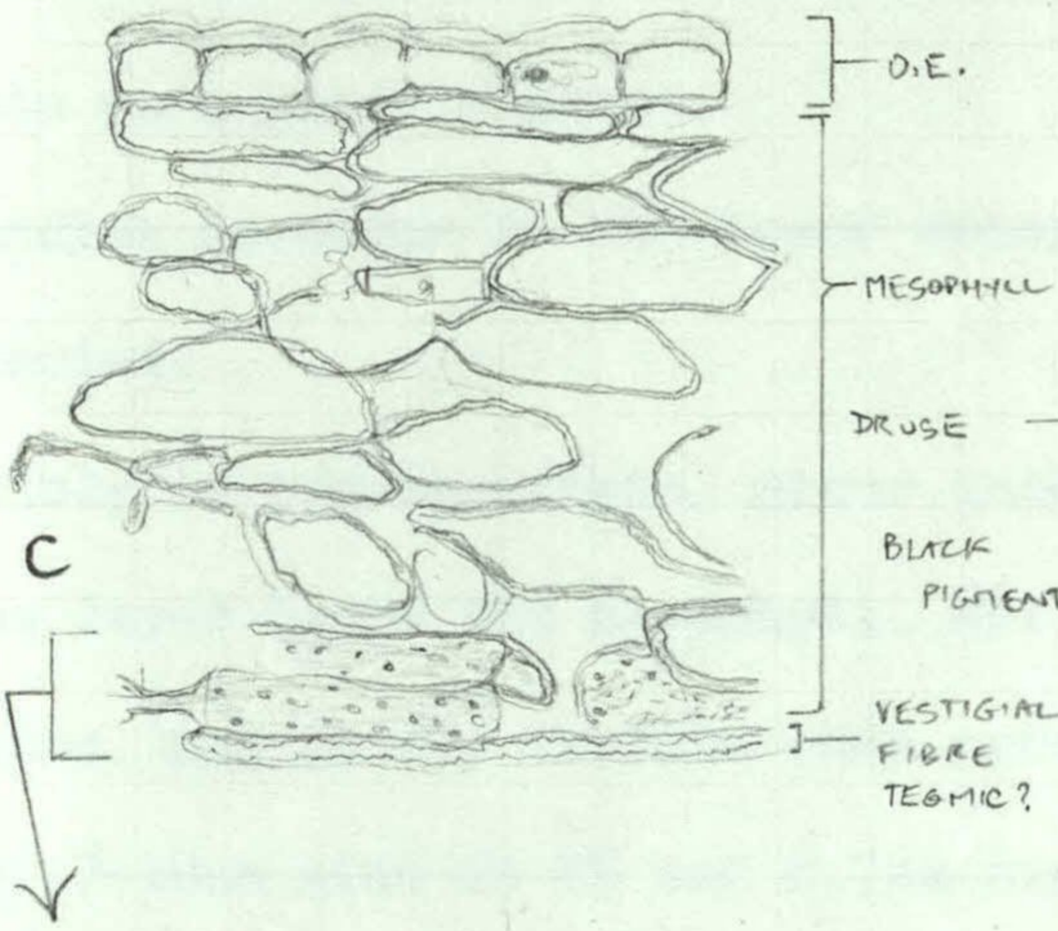
## O.E. SEEDCOAT
PARADERMAL S.




B

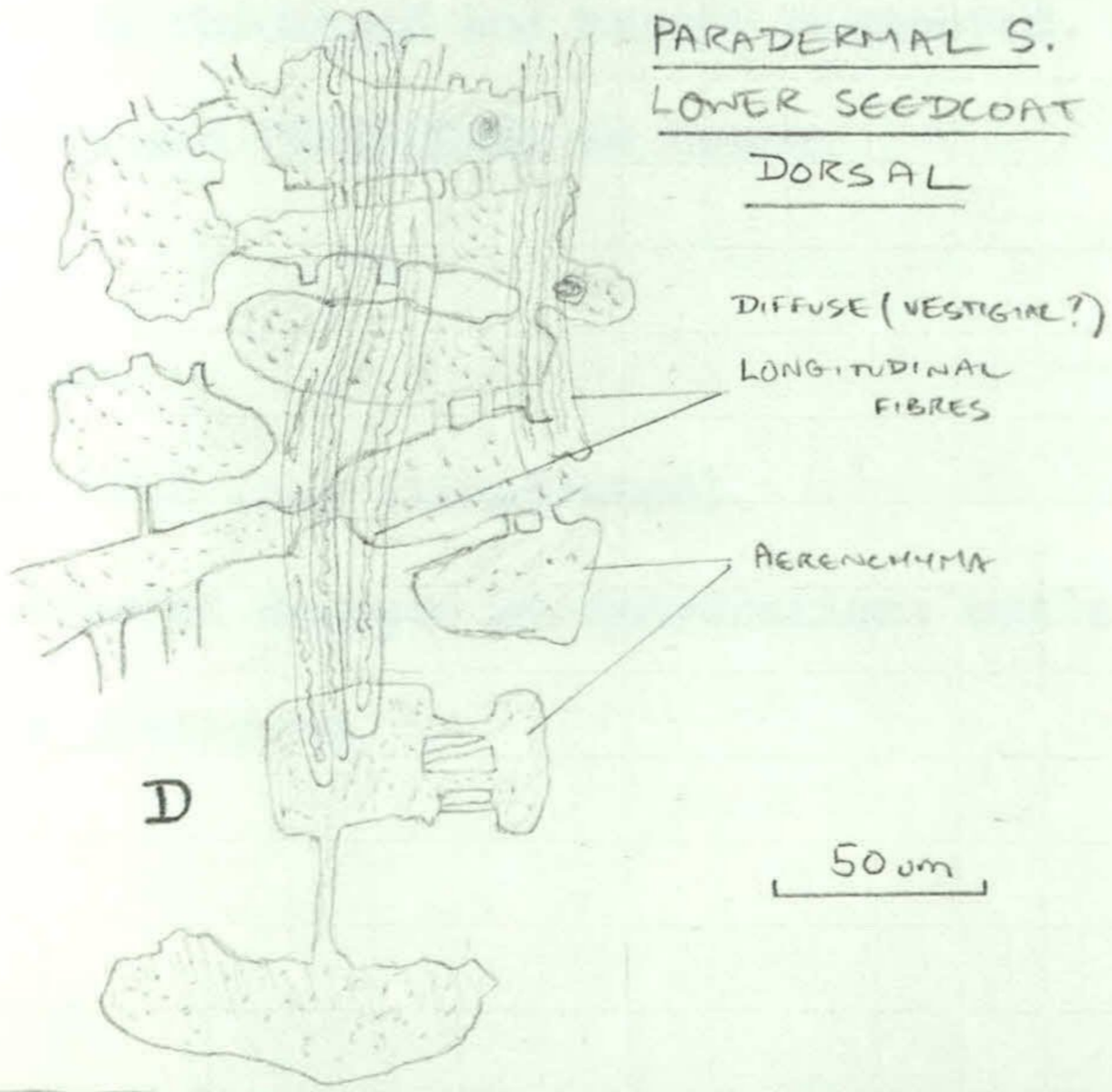



## L.S. SEEDCOAT
CHALAZAL END, DORSAL




C

## PARADERMAL S.
## LOWER SEEDCOAT
## DORSAL




D

50 um



A

thick. Anticlinal walls much thinner (1-2um). In paradermal view, isodiametric to slightly extended (<2:1), 4-7 sided polygonal. Lumina occasionally with sparse cytoplasmic contents. Cells 22-40um wide, 17-29um high.

Mesophyll 7-10 layers thick on dorsal surface, but up to 45 layers on the fleshier ventral surface.

Cells aerenchymatous, prostrate elliptic (TS, LS) and isodiametric to rounded polygonal (paradermal s.). 14-22um high, 25-65um wide.

In the ventral part, upper layer of thinner-walled, slightly larger cells with thin, pale brown contents. The lower layers of more angular, compacted cells with thicker walls and contents usually absent.

Idioblasts. Small isodiametric cells with 1-several druse crystals are common, scattered as idioblasts. occasional prostrate elliptic cells contain tannin or a black pigment.

Vascular bundles do occur in the lower mesophyll.

I.E. Not detected.

Fibres, possibly of tegmic origin, occur intermittently in a discontinuous layer below the mesophyll. Not detectable (see plate 62) in all sections, and barely visible when presented in LS, they are c.200um long, 7-10um wide in TS and c.7um high, walls c.3um thick, irregularly thickened and barely pigmented. Ends rounded.

ENDOSPERM and PERISPERM: No trace.

VARIATION

D.Thomas 4236 (not illustrated).

This material damaged by dehydration: cells mostly distorted and contents destroyed.

O.E. Cells shorter (12um high). O.p.w. orange-brown.

Mesophyll. cells more highly prostrate elliptic, commonly to 90um wide, 9um high; but this probably due to dehydration.

Druse cells not detected.

Fibres as in Thomas 4429: extremely diffuse and insignificant.

Guarea (Leplaea) mayombensis Pellegr.

This description based on Cheek et al. 1009

GROSS MORPHOLOGY

Sparingly dehiscent (3-) 4-locular capsule, irregularly spherical in plan view, spherical with a stout stipe in side view. Fruits 75-125mm wide, 90-100mm long, stipe 22-37mm broad, 12-15mm long.

Pericarp with numerous raised longitudinal, rarely continuous ridges, 4-7mm thick. Endocarp not detectable, septa soft. Placenta 3-4mm thick.

Seeds one per capsule, placentation axile, pendulous.

Orange-segment-shaped by compression. 60-75mm long, 38-55mm broad, 32-40mm deep. Rarely, hemispherical where two locules abort. Seed-coat orange, fleshy, 1-2mm thick. Micropyle, raphe and chalaza not visible. Hilum large, white, apical on dorsal face, ± rhombic to 2cm wide, 3cm long. Endosperm absent. Embryo transversely orientated, cotyledons collateral. Radicle 7mm long, 1mm wide included by 1-2mm.

ANATOMY

This description made from ripe seeds, which, owing to their extreme fleshiness sectioned poorly. Consequently this description is a composite from a large number of poor sections and macerations.

Seed-coat apparently unitegmic, no distinct testa and tegmen. A lower zone of fibrous cells, but these appear to intermingle with the

# PLATE 63

## GUAREA (LEPLAEA) MAYOMBENSIS

A SINGLE, GIGANTIC SEED. NOTE HILUM X 1.

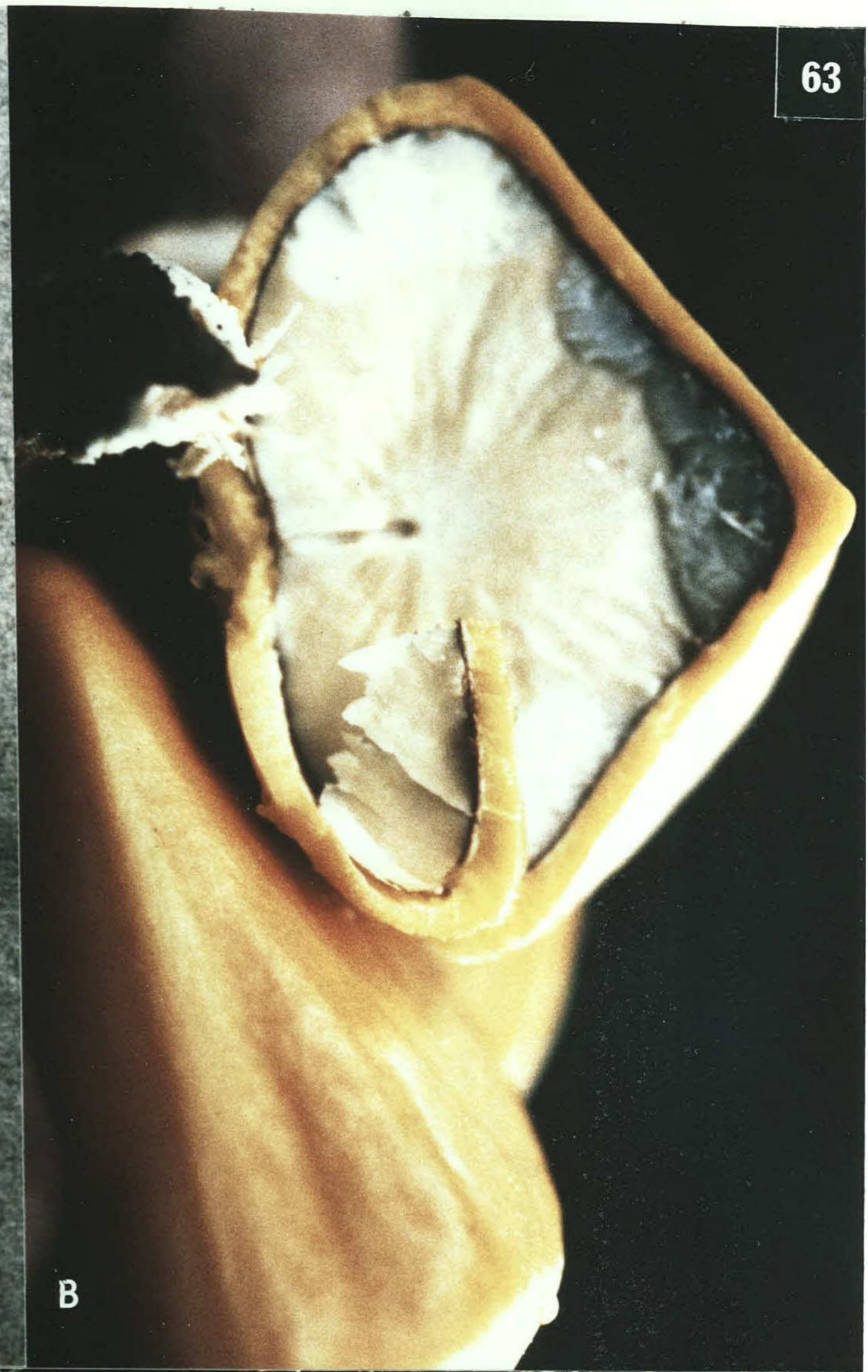
B SEED IN T.S. NOTE THICK, FLESHY SARCOTESTA (TASTES MILDLY PLEASANT) AND ORIENTATION OF EMBRYO X1.75

C- FRUITS: NOTE DEHISCENCE DOES OCCUR IN FALLEN FRUITS , BUT ONLY OLD ONES, ONCE SARCOTESTA HAS ROTTED.

X 0.3



A



B



C

PLATE 64

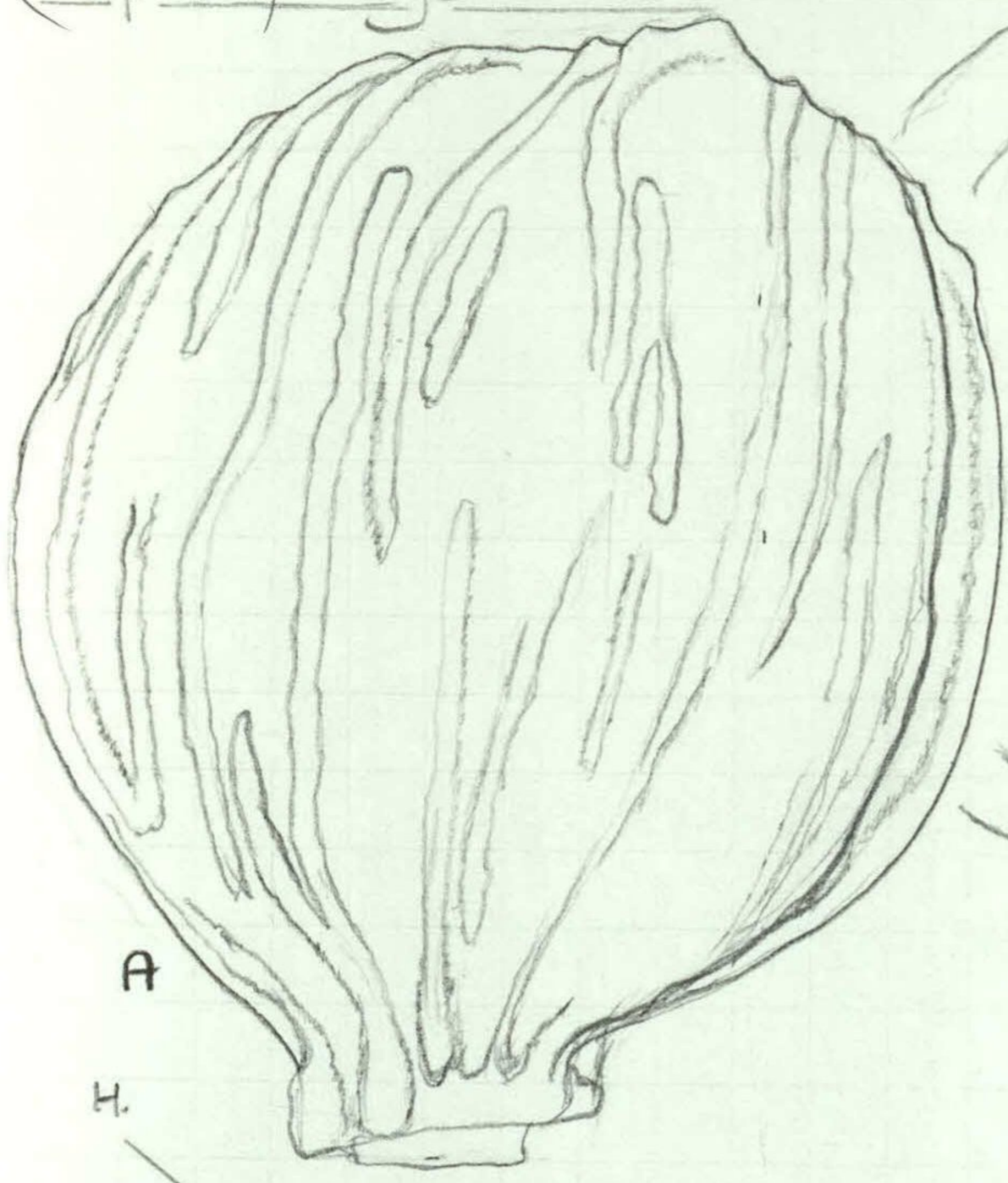
GUAREA (LEPLAEA) MAYOMBENSIS

A-B FRUITS, NOTE LONGITUDINAL RIDGES ON PERICARP.

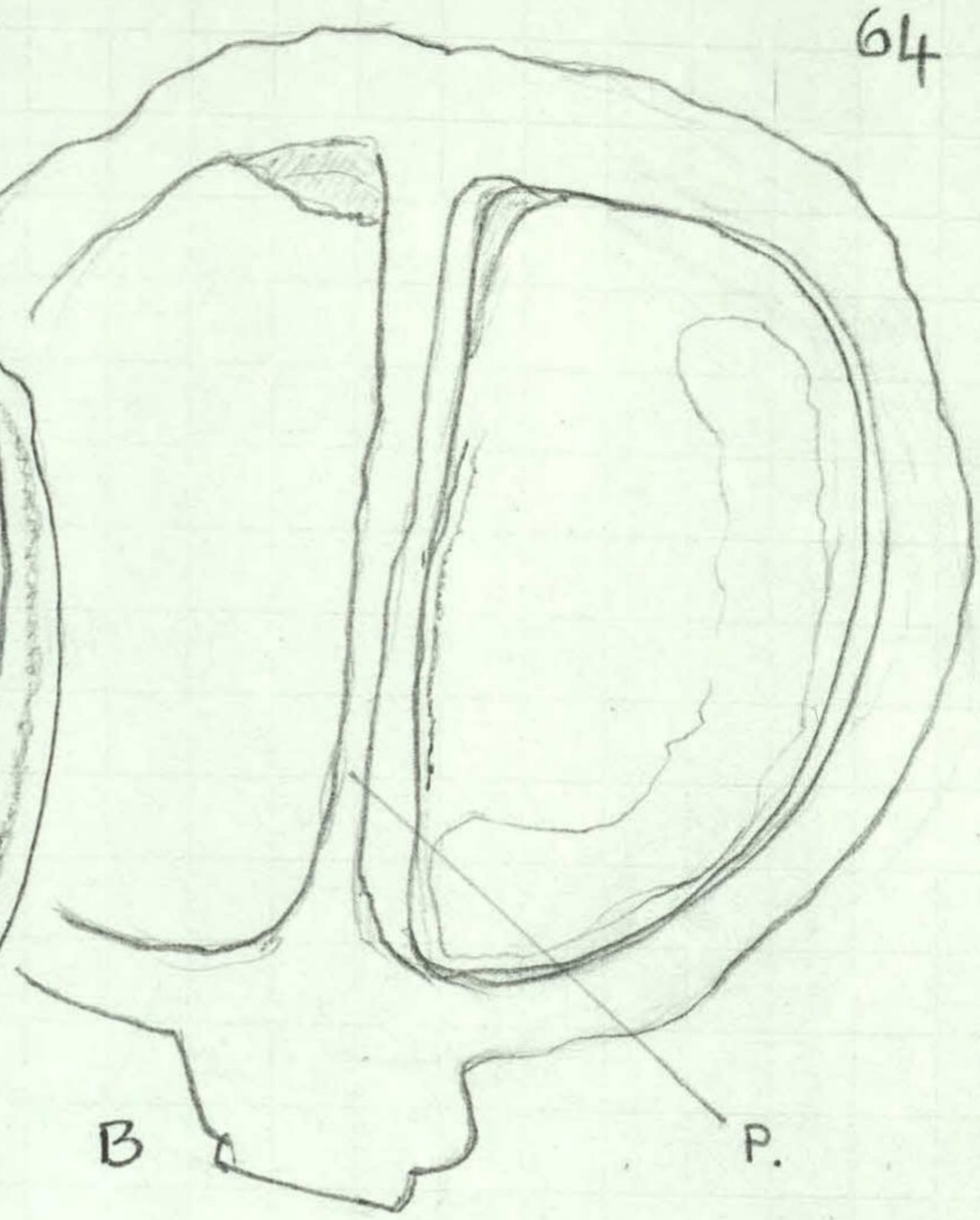
C-F SEEDS: SARCOTESTAL.

# Goarea

## (Leplaea) mayombensis



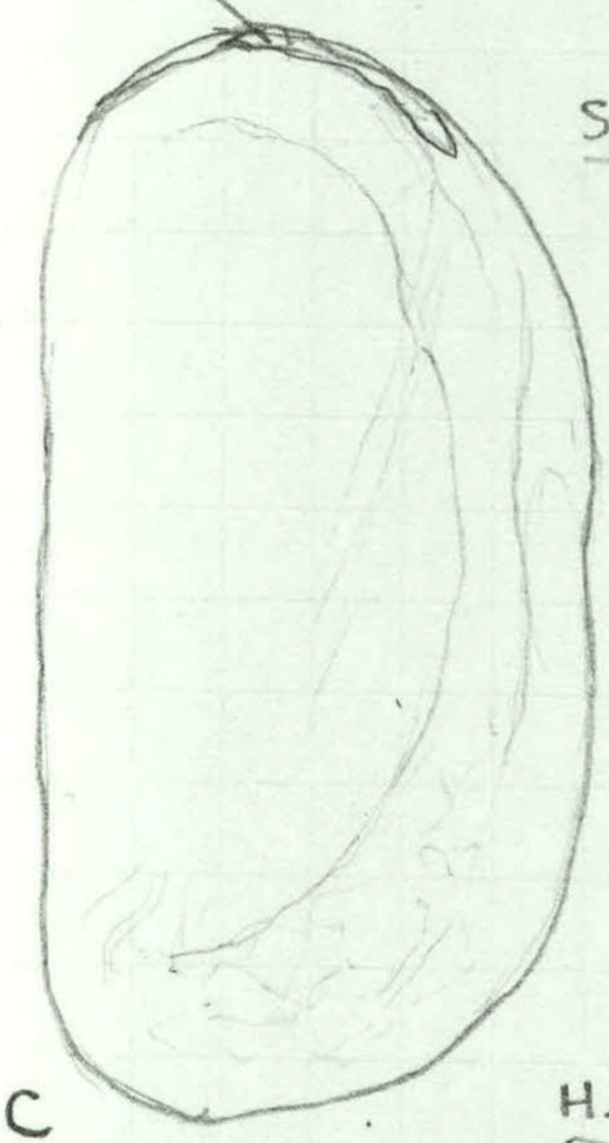
A



B

P.

H.



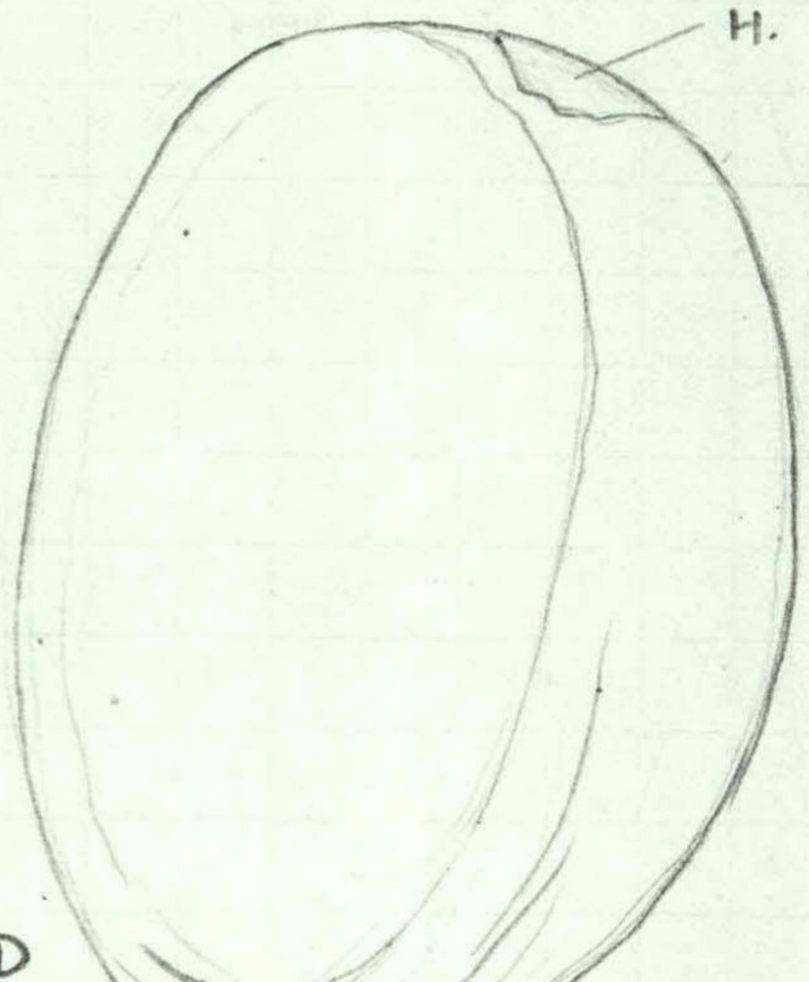
C

SEED, LATERAL VIEW

1cm

ABERRANT HEMISPHERICAL SEED. 3/4 LATERAL VIEW

H.

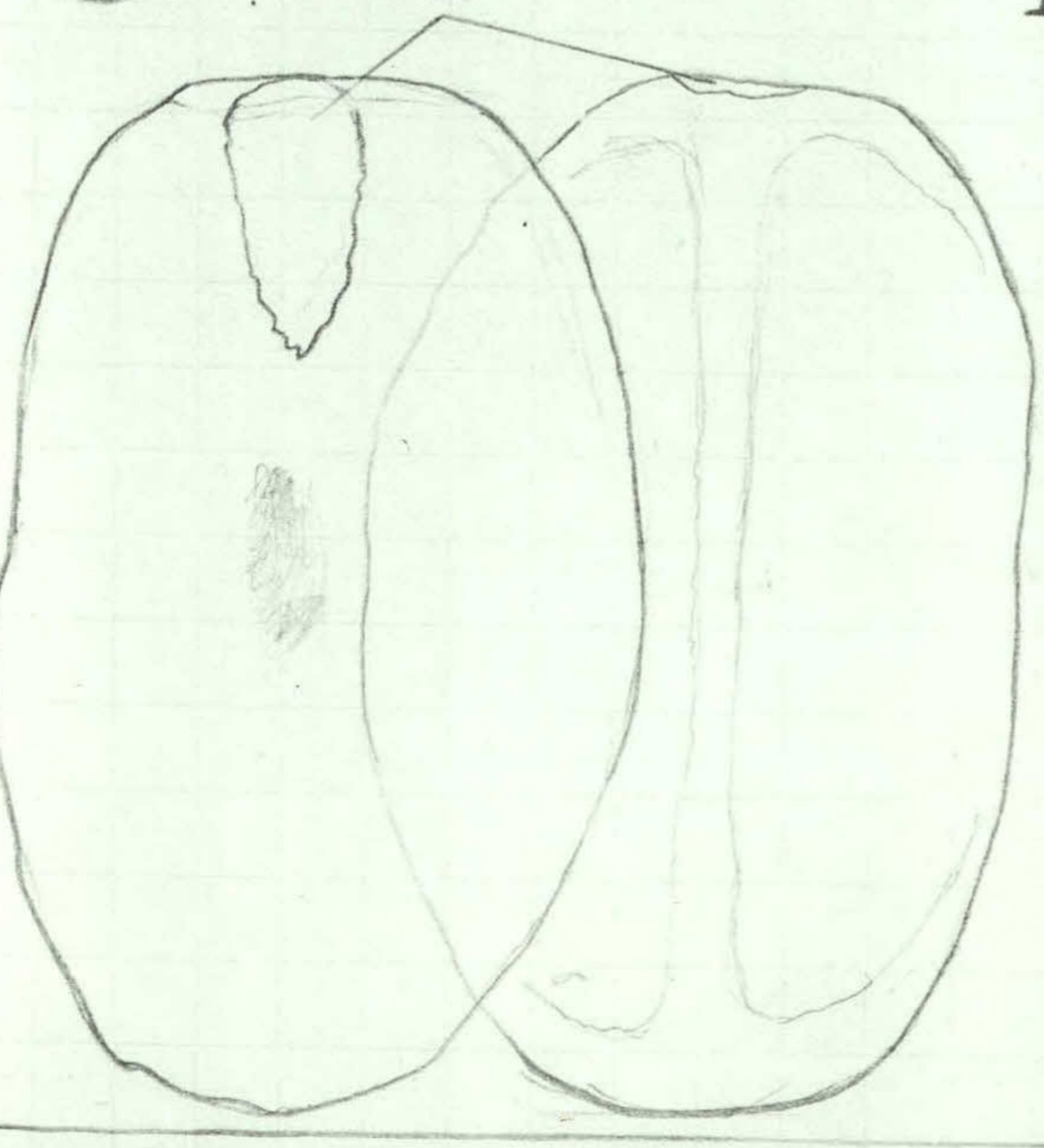


D

SECTIONS TAKEN HERE.

SEED. DORSAL & VENTRAL VIEW

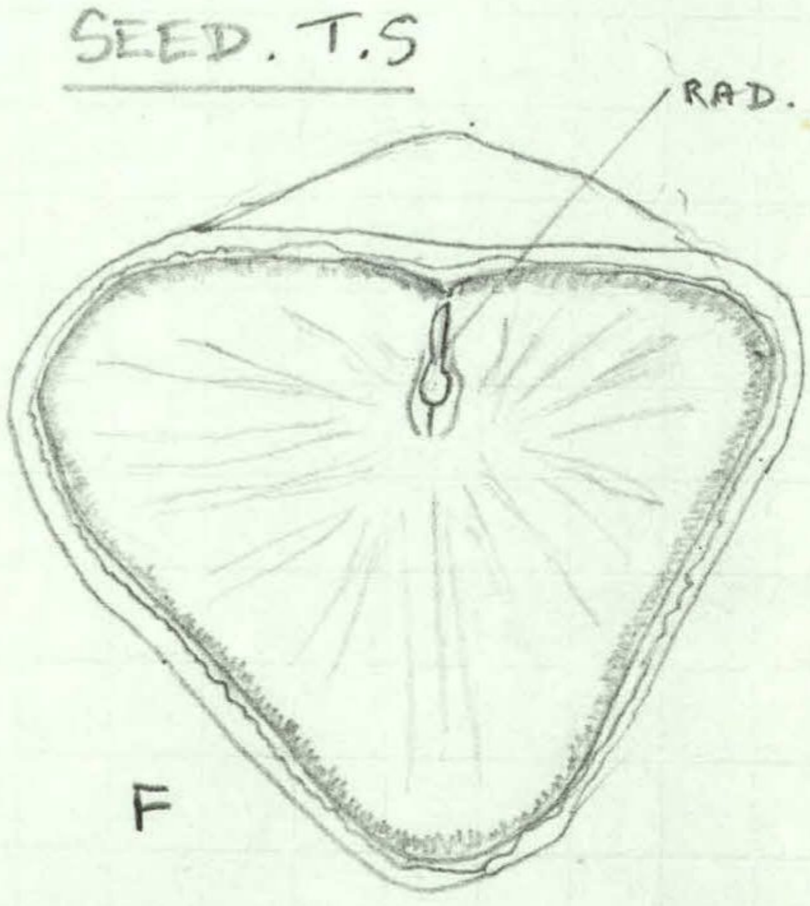
H.



E

SEED. T.S

RAD.



F

PLATE 65

GUAREA (LEPLAEA) MAYOMBENSIS

A-D SEED ANATOMY. NOTE UNITEGMIC CONSTRUCTION, THICK UPPER FLESHY ZONE OF PARENCHYMA AND LOWER ZONE OF SCLEREIDS WITH ADJACENT VASCULAR BUNDLES.

# Guarea (Leplaea) mayombensis

## L.S SEEDCOAT: TISSUE PLAN

500um

V.B.

A

SCHL.

?PERI

## O.E. SEEDCOAT: PARADERMAL VIEW

D

50um

## L.S SEEDCOAT (RECONSTRUCTED)

O.E

B

UPPER ZONE

LOWER ZONE

?PERI

C

parenchyma above, and no distinct testal I.E. exists. Probably pachychalazal.

Cuticle: very thin, barely detectable.

O.E. a single layer of prostrate, rounded rectangular cells (LS), 40-55um wide and c.25um high, the o.p.w. slightly concave, thin, c.3-4um thick.

Upper, parenchymatous zone. Very thick, from 800um to 1750um thick. Cells prostrate, ellipsoid (LS,TS), 50-85um wide and 17-35um high, walls pale brown, 1-1.5um thick, contents very diffuse, pale brown. Air spaces common but cells not notably stellate.

The above layers are easily scraped off to reveal a dense network of broad vascular bundles radiating from the hilum, these bundles also occur in the lower, sclereid zone. When seeds are desiccated, the parenchyma collapses ± irreversibly, throwing the previously concealed vascular bundles into relief.

Lower, sclereid zone. Much thinner than the fleshy zone, but up to 200um thick. Some vascular bundles included. Cells longitudinally extended, rounded polygonal sclereids: sub-isodiametric (45um long, 35um high) mingled with fibrous (175um long, 20um wide). Walls yellowish, 3-5um thick. Pits circular, to 5-6um in more fibrous (thinner-walled) cells.

Below sclereids, up to three layers of isodiametric (TS) polygonal parenchymic cells with thick (2-3um) dark brown walls and lumina empty, over an amorphous brown layer 50-60um thick of the same colour, presumably made of crushed layers of the parenchyma above.



PLATE 66

(COURTESY OF DR. D. J. MABBERLEY)

CHISOCHETON POLYANDRUS

FRUIT AND SEED PRESENTATION: SEEDS OF CHALAZAL-ARILLATE TYPE.

PLATE 66A

MICROMORPHOLOGY (S.E.M.) OF SEED SURFACE IN CHISOCHETON

A CHISOCHETON LASIOCARPUS

B CHISOCHETON GRANATUM

C CHISOCHETON LONGISTIPITATUS

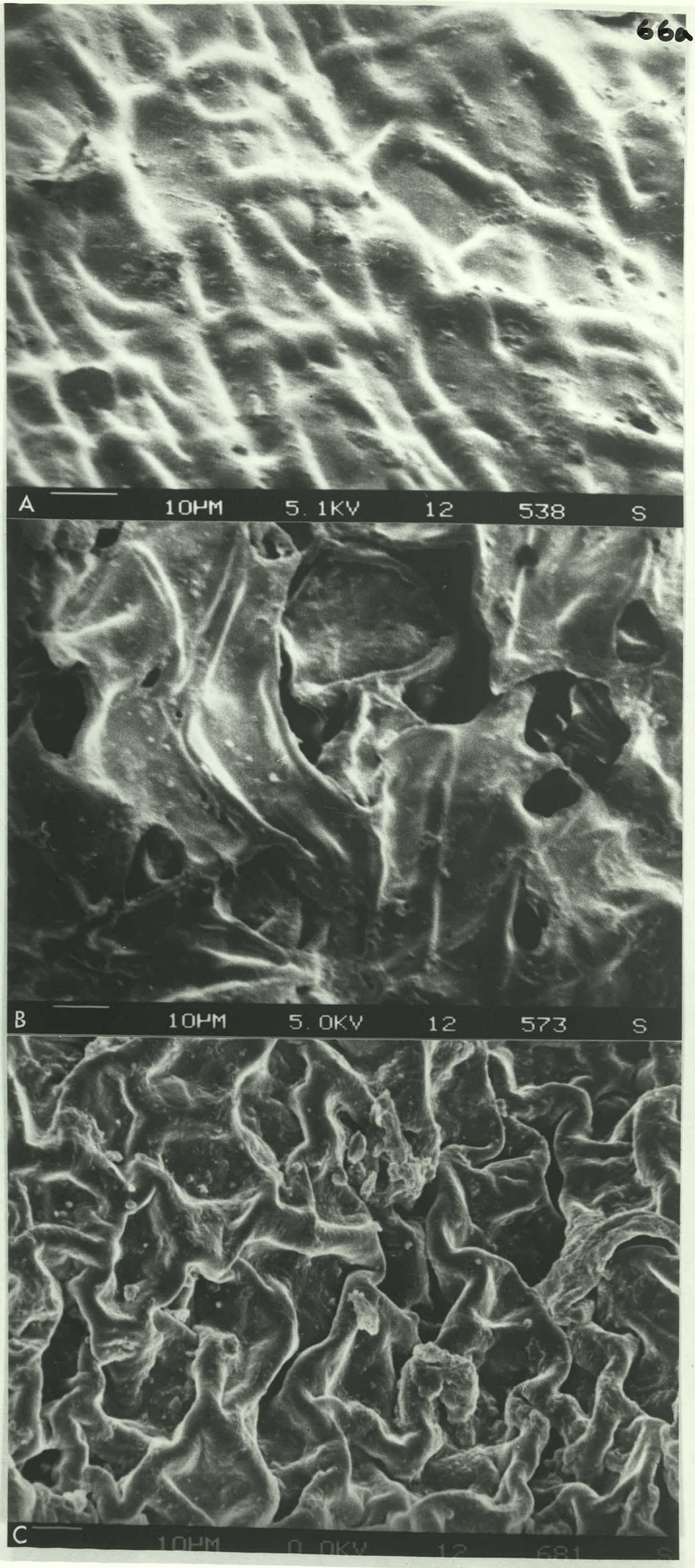

A 10μM 5.1KV 12 538 S
B 10μM 5.0KV 12 573 S
C 10μM 5.0KV 12 681 S

PLATE 66B

MICROMORPHOLOGY (S.E.M.) OF THE FRUIT SURFACE:
OUTER PERICARP.

A. CHISOCHETON MEDUSAE

B. CHISOCHETON LASIOCARPUS

C. CHISOCHETON CERAMICUS

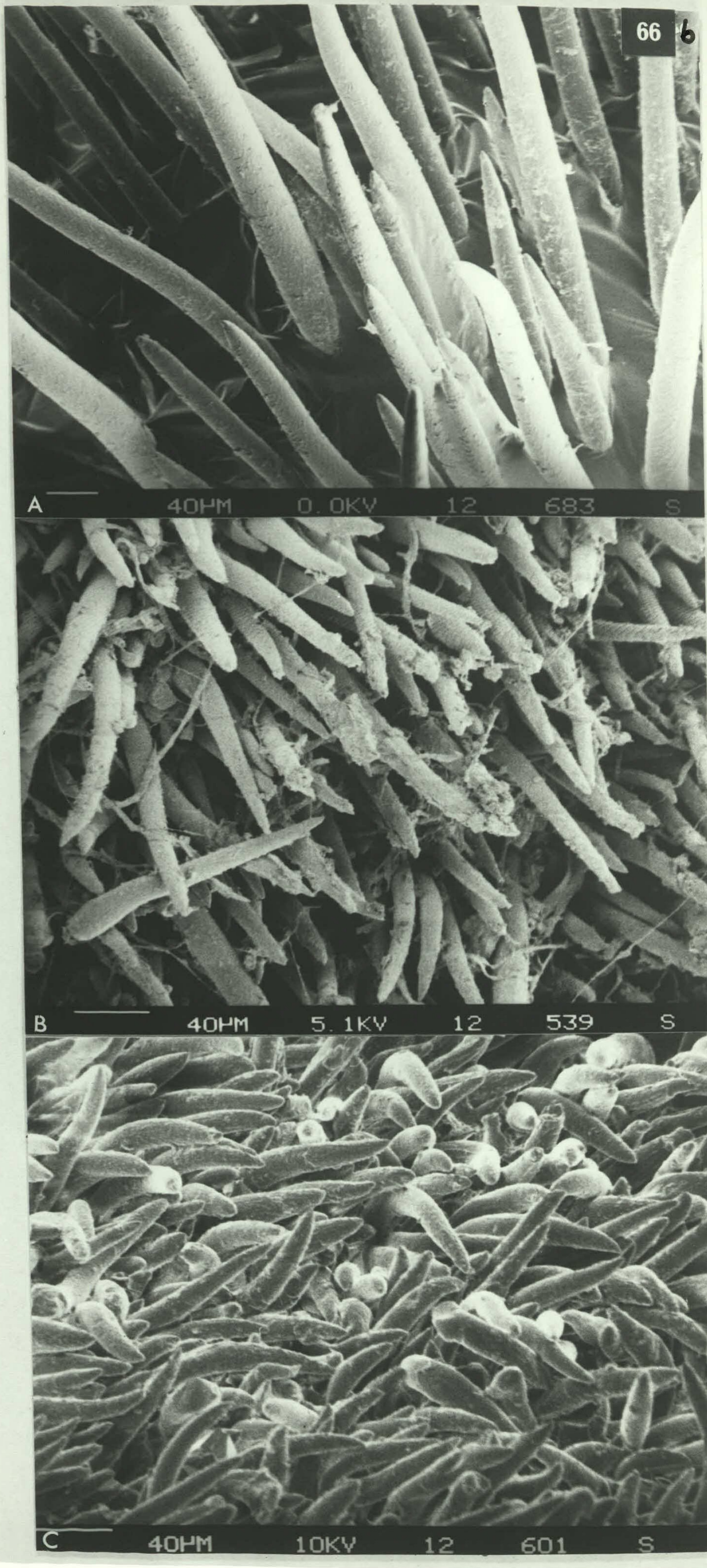

66
A 40μM 0.0KV 12 683 S
B 40μM 5.1KV 12 539 S
C 40μM 10KV 12 601 S

PLATE 67

CHISOCHETON LASIOCARPUS

A-D FRUITS: NOTE ORTHOTROPOUS SEEDS.

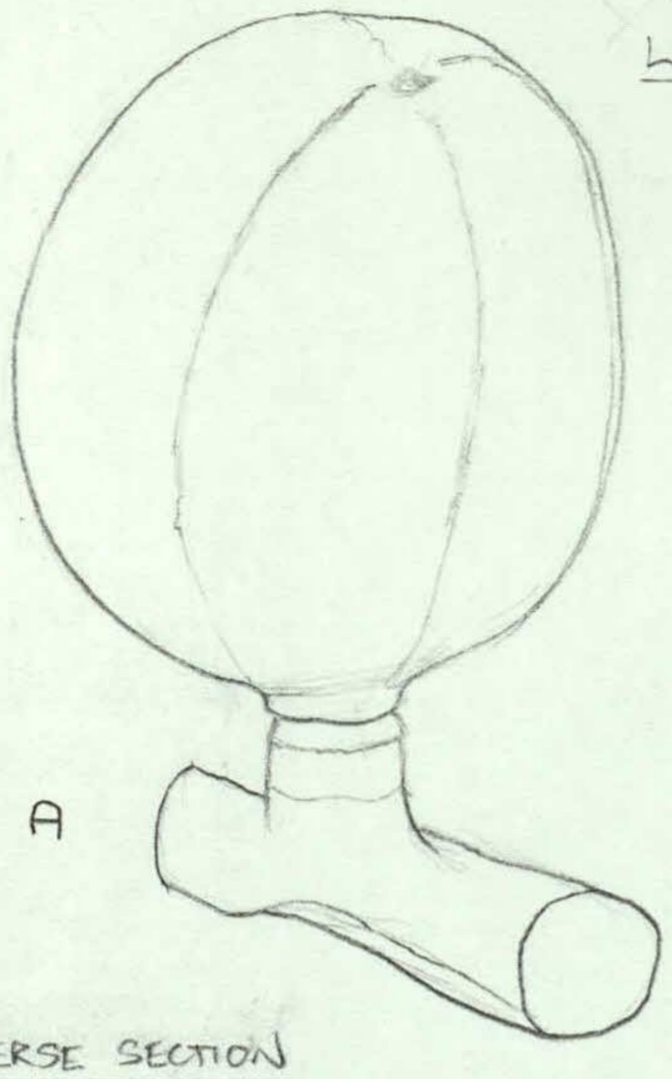
E-G SEEDS WITH CHALAZAL-ARIL.

# C. LASIOCARPUS 1754



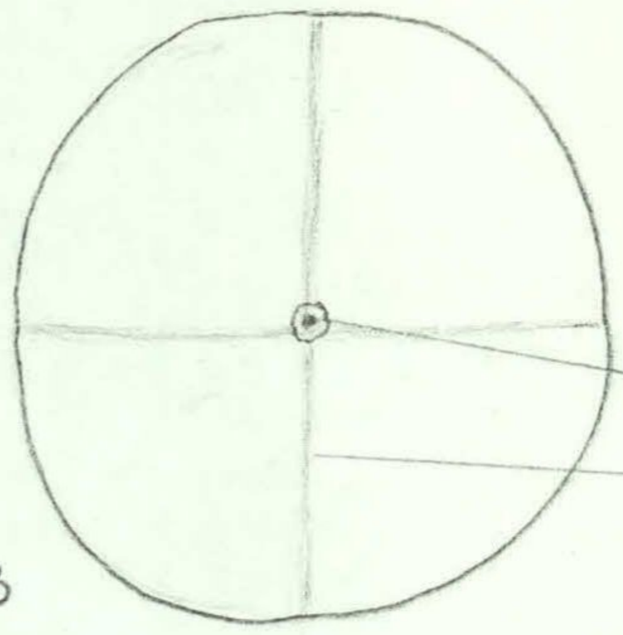
## FRUIT & SEED - MACROMORPHOLOGY

LATERAL VIEW OF FRUIT



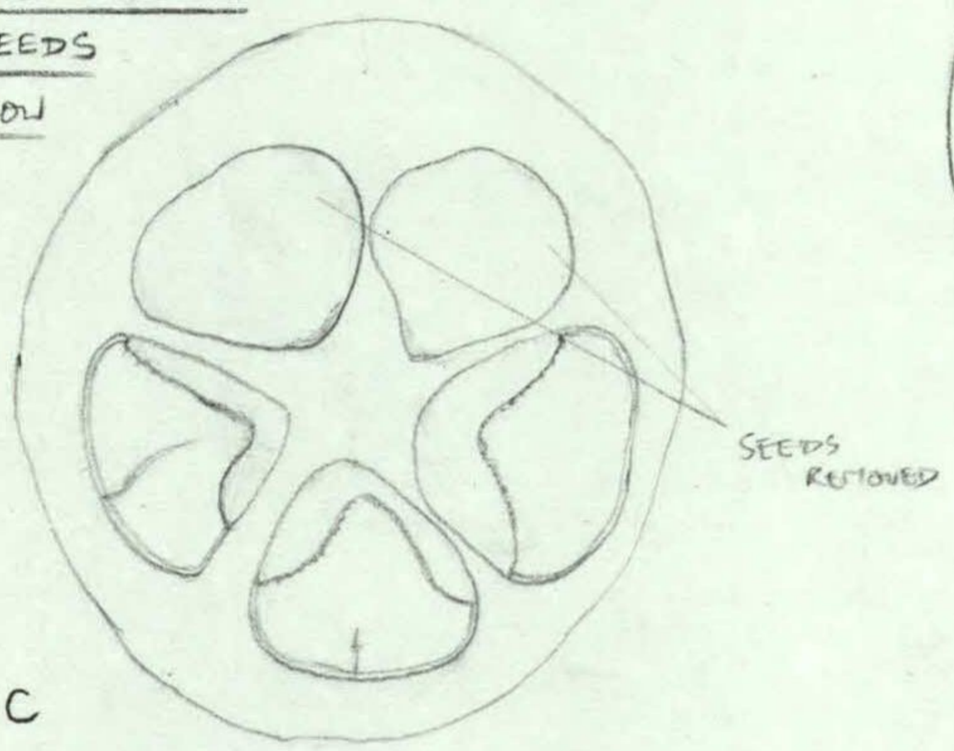
A

PLAN VIEW OF FRUIT



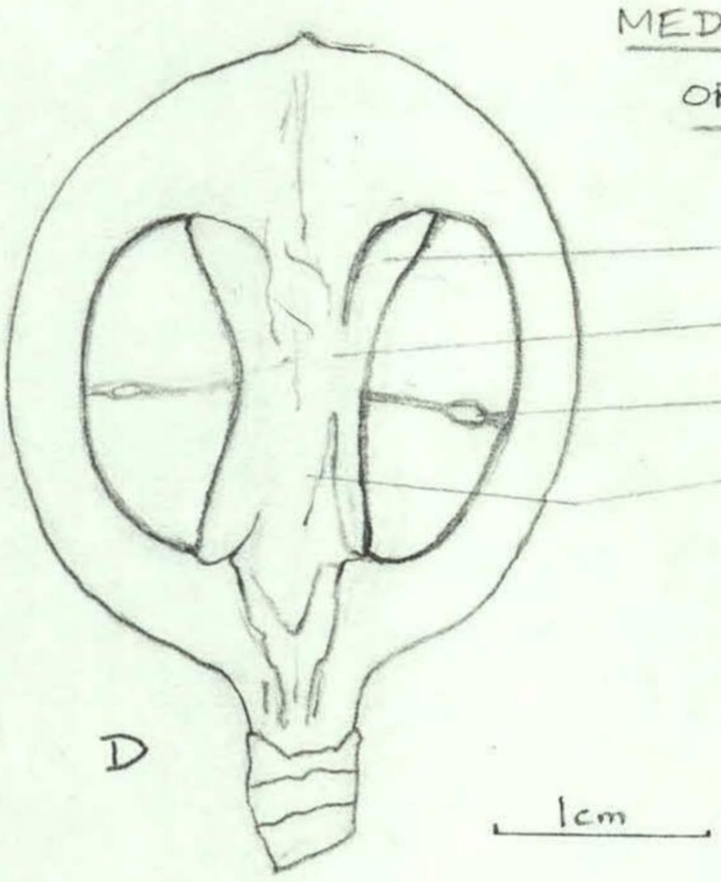

B

TRANSVERSE SECTION OF FRUIT (SEEDS N.L.S.). BELOW EQUATOR




C

MEDIAN SECTION OF FRUIT (SEEDS L.S)




D

1cm

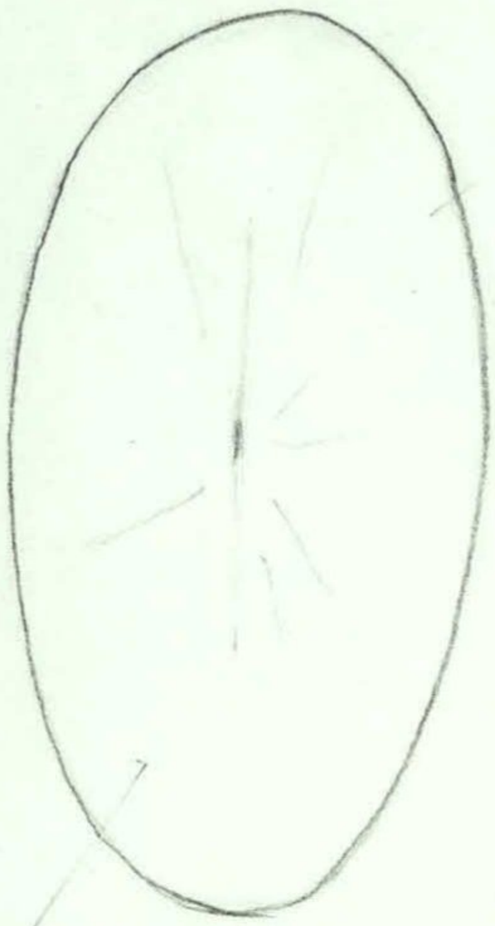
SEED:

LATERAL VIEW.



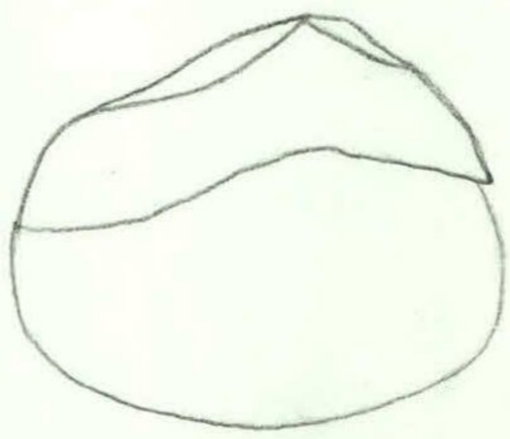

E

PLAN VIEW.



F

DORSAL VIEW



G

1cm

FLESHY CHALAZA: BROWN, V. FIRM WITHOUT LOOSE FLAPS.

INTEGUMENTS BLACK. FINE LINES RADIATE FROM THE PORELESS MICROPYLE

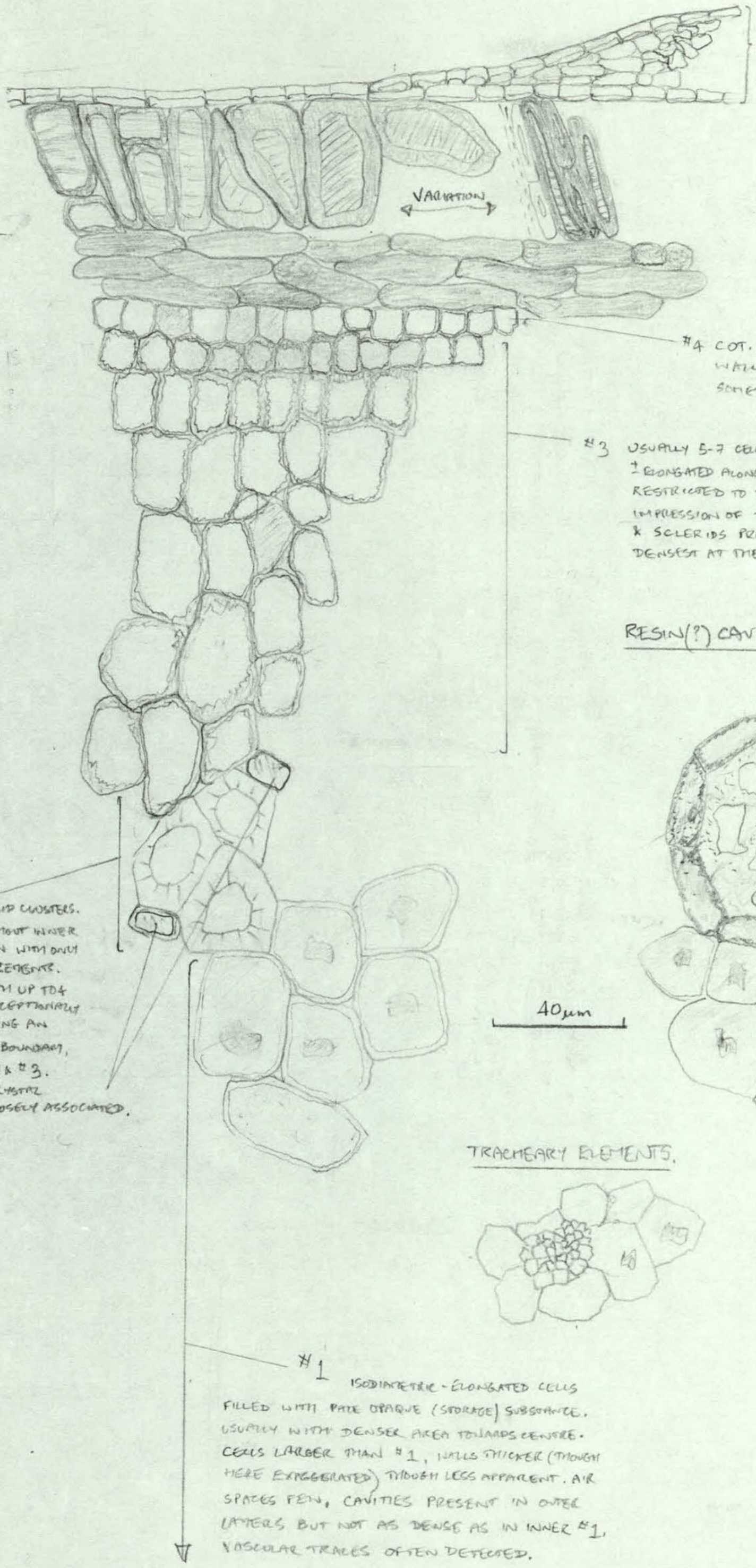
PLATE 68

CHISOCHETON LASIOCARPUS

SEED-COAT ANATOMY: NOTE TANNINIFEROUS ENDOTEGMEN,
TYPICAL OF CHISOCHETON, AND THE COLUMNAR (T.S),
COLOURED EXOTEGMIC FIBRES.
NOTE ALSO THE COTYLEDON SCLEREID CLUSTERS
WITH ACCOMPANYING TRAPEZOID CRYSTAL IDIOBLASTS.

# C. LASIOCARPUS . 1754.

## T. S. INTEGUMENTS & EMBRYO




TESTA VERY THIN (HERE 10 μ & 1 CELL THICK) PROSTRATE SHAPE & D.P. THICKENING VERY DISTINCTIVE. OFTEN LOST. MULTIPLICATION NEAR FLESHY AREA & IN (RARE) POCKETS, THE LATTER HERE. MESOPHYLL TO 5 CELLS THICK THEN I.E WITH DISTINCTIVE & THICKENED I.P.W.

} EXOTEGMEN OF PROSTRATE FIBROID CELLS. WALLS THICK, BROWN, PITTED. OBSCURELY SPIRALLY THICKENED. NOTE: HERE IN T.S.

} ENDOTEGMEN OF PROSTRATE THIN WALLED TANNIFEROUS CELLS. THIS BAND ALWAYS THINNER THAN THE EXOTEGMEN.

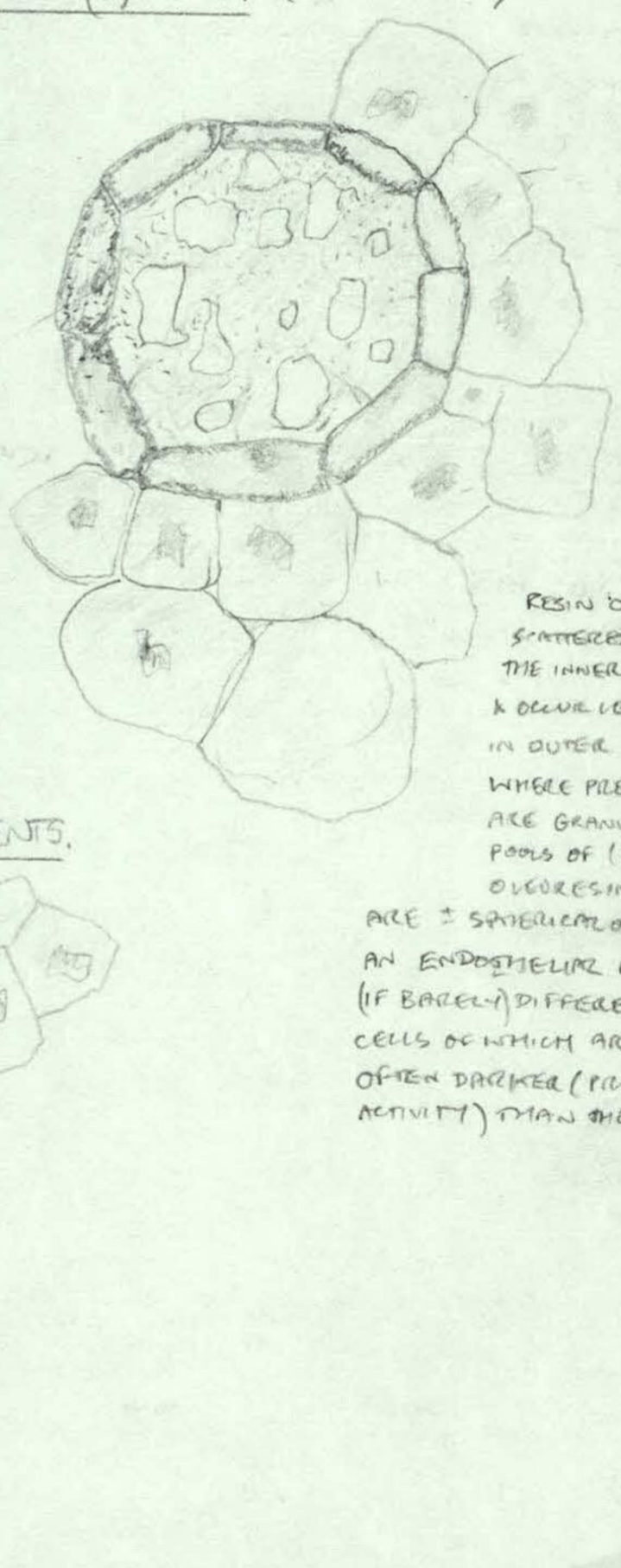
#4 COT. EPIDERMIS. CELLS CUBOIDAL, WALLS SLIGHTLY THICKER. CONTENTS SOMETIMES DARK. ONE CELL THICK

#3 USUALLY 5-7 CELL LAYERS THICK. OUTER CELLS SMALLEST. ↑ ELONGATED ALONG SEED RADIUS. THE BROWN PROTOPLASM (INACTIVE?) OFTEN RESTRICTED TO THE PERIPHERY GIVING THE FALSE IMPRESSION OF THICK CELL WALLS. SCATTERED CAVITIES & SCLEROIDS PRESENT IN THIS ZONE, THE LATTER DENSEST AT THE BORDER WITH #1

#2 BRACHYSCLEROID CLUSTERS. OCCUR THROUGHOUT INNER OF #3, OFTEN WITH ONLY ONE OR TWO ELEMENTS. DENSEST & WITH UP TO 4 SCLEREIDS (EXCEPTIONALLY TO 10), FORMING AN INTERMITTENT BOUNDARY, BETWEEN #1 & #3. TRAPEZOID CRYSTAL IDIOBLASTS CLOSELY ASSOCIATED.

#1 ISODIAMETRIC - ELONGATED CELLS FILLED WITH PALE OPAQUE (STORAGE) SUBSTANCE. USUALLY WITH DENSER AREA TOWARDS CENTRE. CELLS LARGER THAN #1, WALLS THICKER (THOUGH HERE EXAGGERATED) THOUGH LESS APPARENT. AIR SPACES FEW, CAVITIES PRESENT IN OUTER LAYERS BUT NOT AS DENSE AS IN INNER #1. VASCULAR TRACES OFTEN DETECTED.

RESIN(?) CAVITY (SAME SCALE)




RESIN CAVITIES ARE SCATTERED THROUGHOUT THE INNER PART OF #3 & OCCUR LESS FREQUENTLY IN OUTER #1 ALSO. WHERE PRESENT, CONTENTS ARE GRANULAR WITH CLEAR POOLS OF (PRESUMED) OLEORESIN. CAVITIES ARE ± SPHERICAL OR ELLIPSOID. AN ENDOTHELIAL LAYER OFTEN (IF BARELY) DIFFERENTIATED. THE CELLS OF WHICH ARE FLATTER & OFTEN DARKER (PROTOPLASMIC ACTIVITY) THAN THE CORTEX.

TRACHEARY ELEMENTS.

PLATE 69

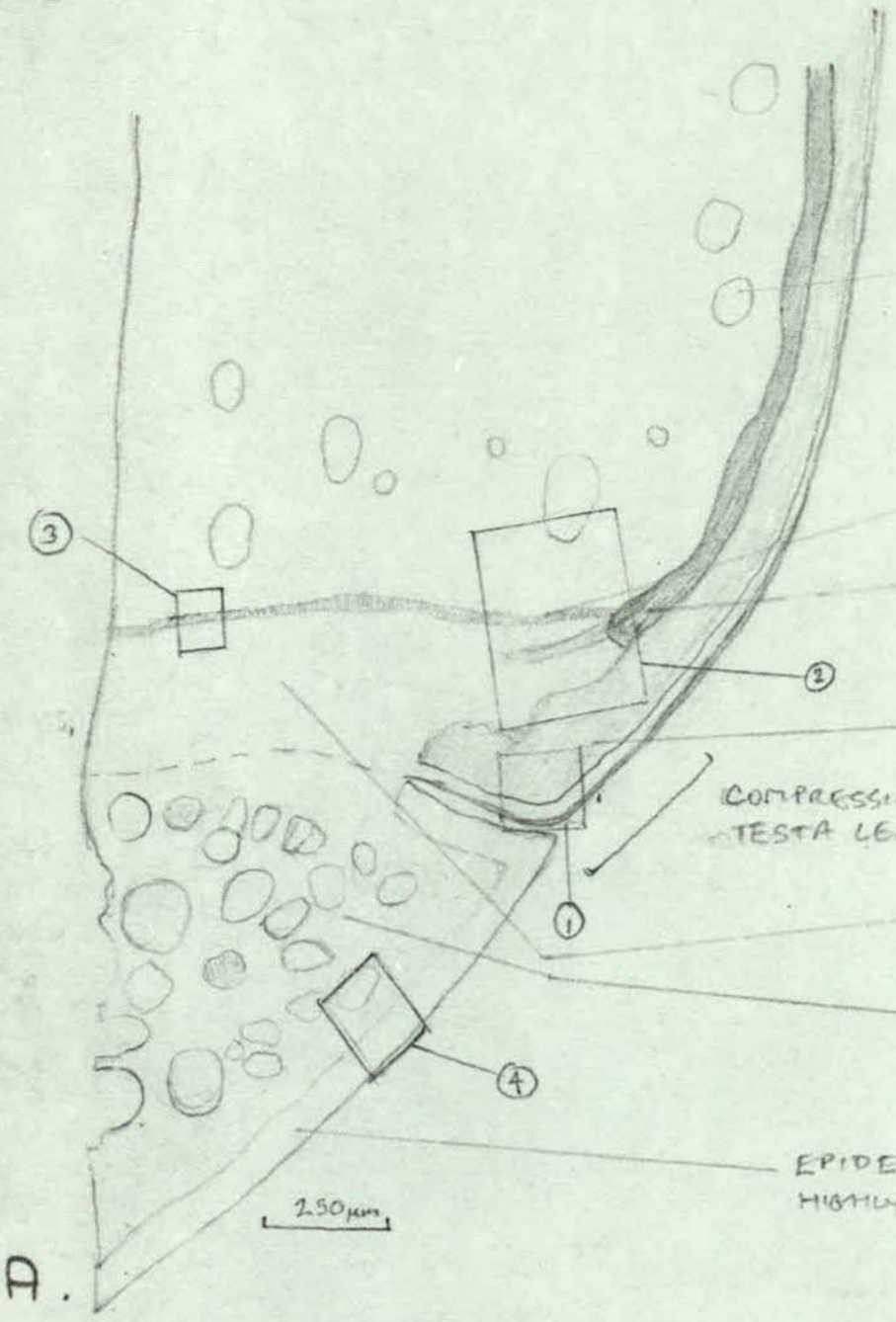
CHISOCHETON LASIOCARPUS

A SEED-COAT ANATOMY. NOTE SWITCH AT BOUNDARY OF BITEGMIC PART OF SEED-COAT WITH CHALAZAL PART: FLESHY TO NON-FLESHY SEED-SURFACE.

B TESTA- LACKING MESOPHYLL AND I.E. LACKING ENDOCRYSTALS: TYPICAL OF THE GENUS.

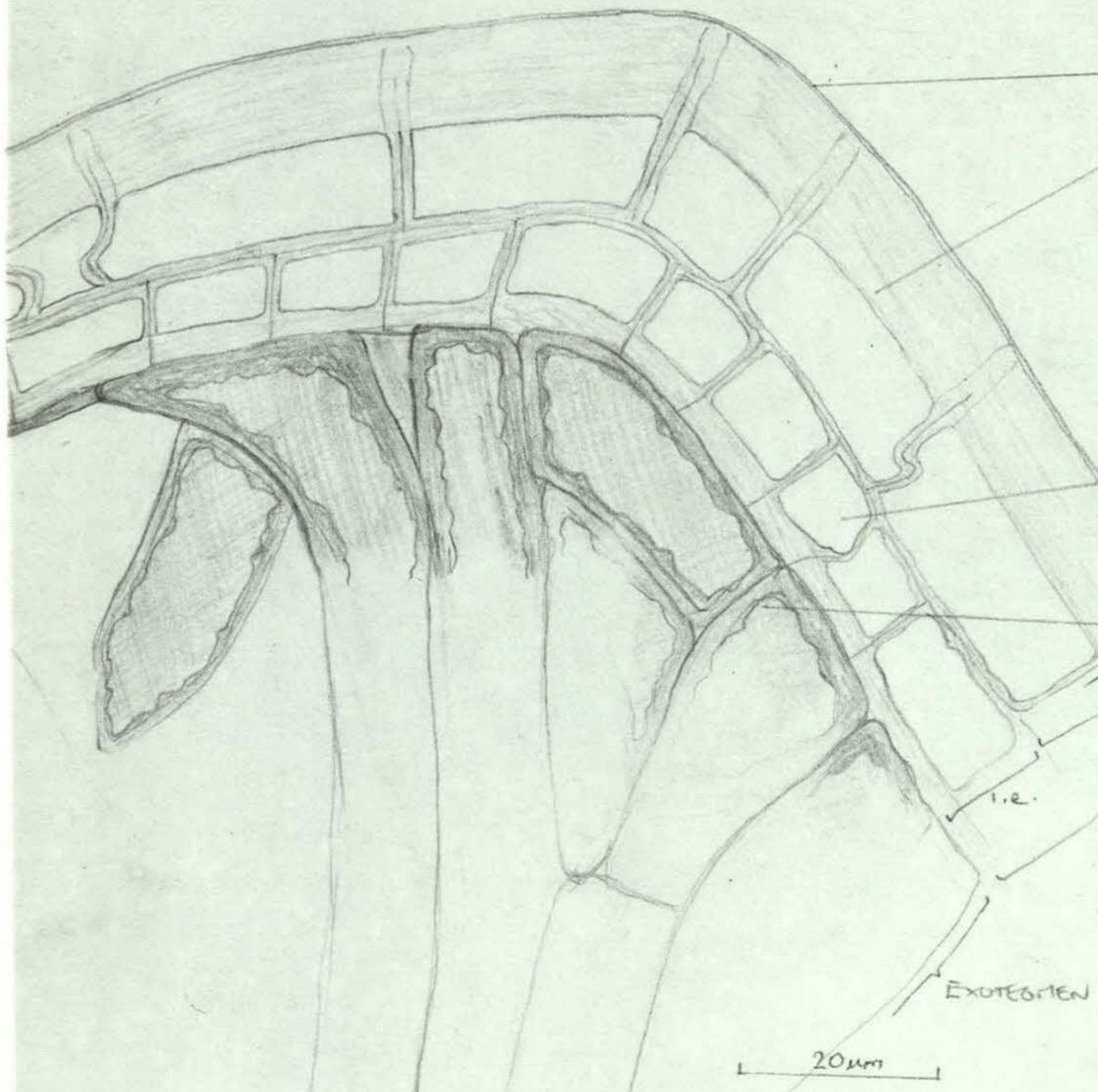
# C. LASIOCARPUS. 1754.

## L.S. TRANSITION ZONE - TISSUE PLAN




A.

## (1) TESTA & EXOTEGMEN - L.S




B.

NOTE:
EXOTEGMIC FIBROID CELLS WITH UNCHARACTERISIC ORIENTATION ERECT RATHER THAN (THE MORE USUAL) PROSTRATE.

PLATE 70

CHISOCHETON LASIOCARPUS

A-B VARIATION IN CHALAZAL AND

EMBRYO ANATOMY.

C. LASIOCARPUS, 1754.

EXOTEGMIC FIBROID CELLS

② L.S TRANSITION ZONE (ENDOTEGMENK COTS.)

ENDOTEGMEN - CELLS INCREASE IN SIZE, LAYER INCREASES IN CELL THICKNESS TANNINIZATION DECREASES. - ASSUMES CHARACTER OF LOWER CHALAZA.

CHALAZA

OUTER EPIDERMIS OF COTS. METAMORPHOSES FROM CUBOIDAL TO COLUMNAR DENSELY GRANULAR CELLS

50µm

UTENTS

A.

ESIN CANITY

-CRBID CLUSTERS

INNER CHALAZA - PROSTRATE, RECTANGULAR, COLOURLESS CELLS.

?ENDOSPERM - HIGHLY CRUSHED. STRAN COLOURED.

DIFFERENTIATED TYPE OF COTYLEDON EPIDERMIS CELLS COLUMNAR, DENSELY GRANULAR, LARGE NUCLEI

B.

③ L.S. INNER CHALAZA, ENDOSPERM & COTYLEDONS.

#3 OF EMBRYO - THIN WALLED ISODIAMETRIC IN OUTER PART. PROTOPLASM BROWN, SEEMINGLY AGGLUTINATED.

25µm

PLATE 71

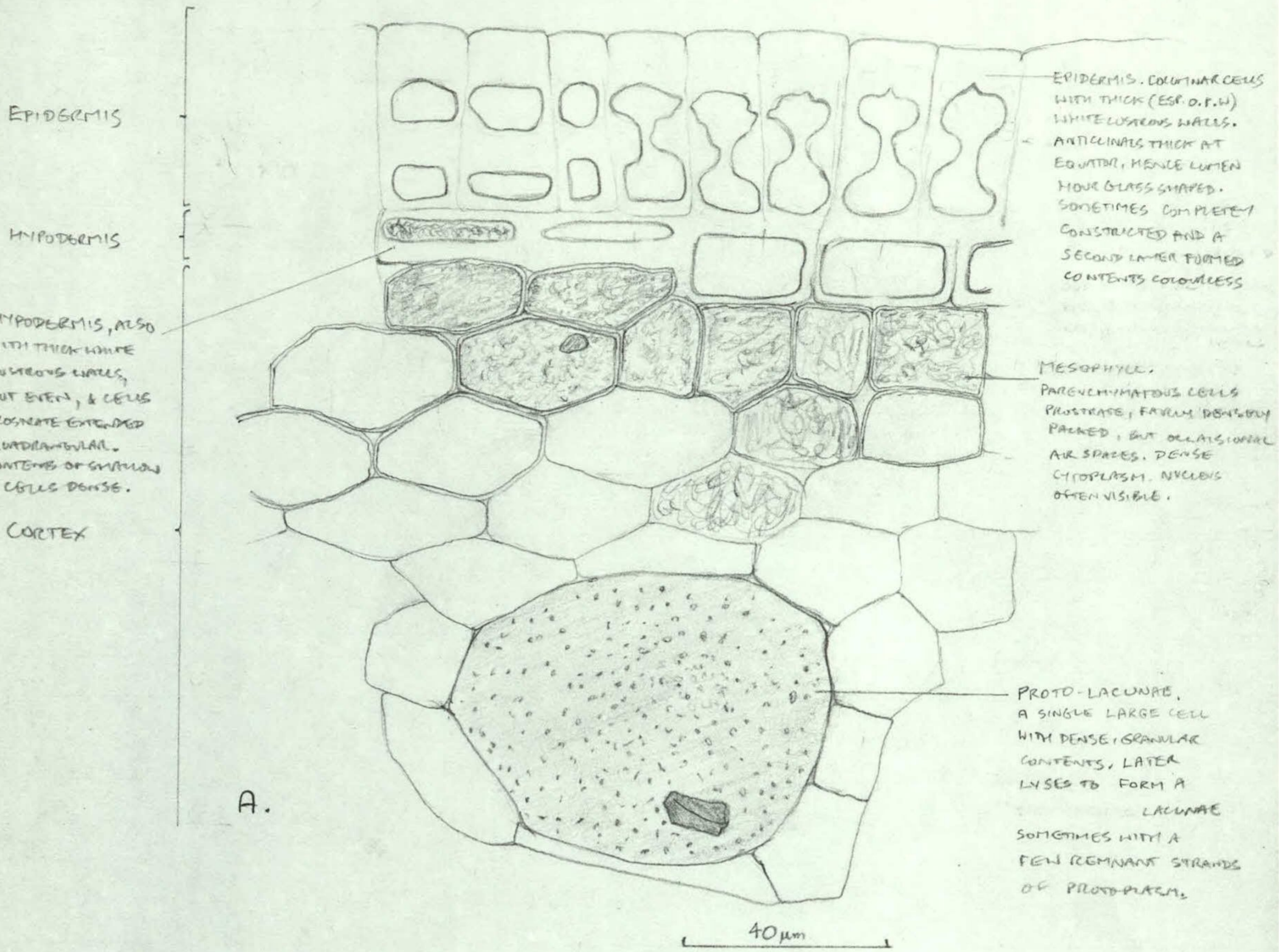
CHISOCHETON LASIOCARPUS

A. CHALAZAL ANATOMY: NOTE VERY DISTINCTIVE O.E. AND COMPARE WITH THAT OF THE TESTA (PLATE 69B)

B. EXOTEGMEN DETAIL.

# C. LASIOCARPUS. 1754

## ④. L.S. OUTER CHALAZA




## EXOTEGMEN - DETAIL

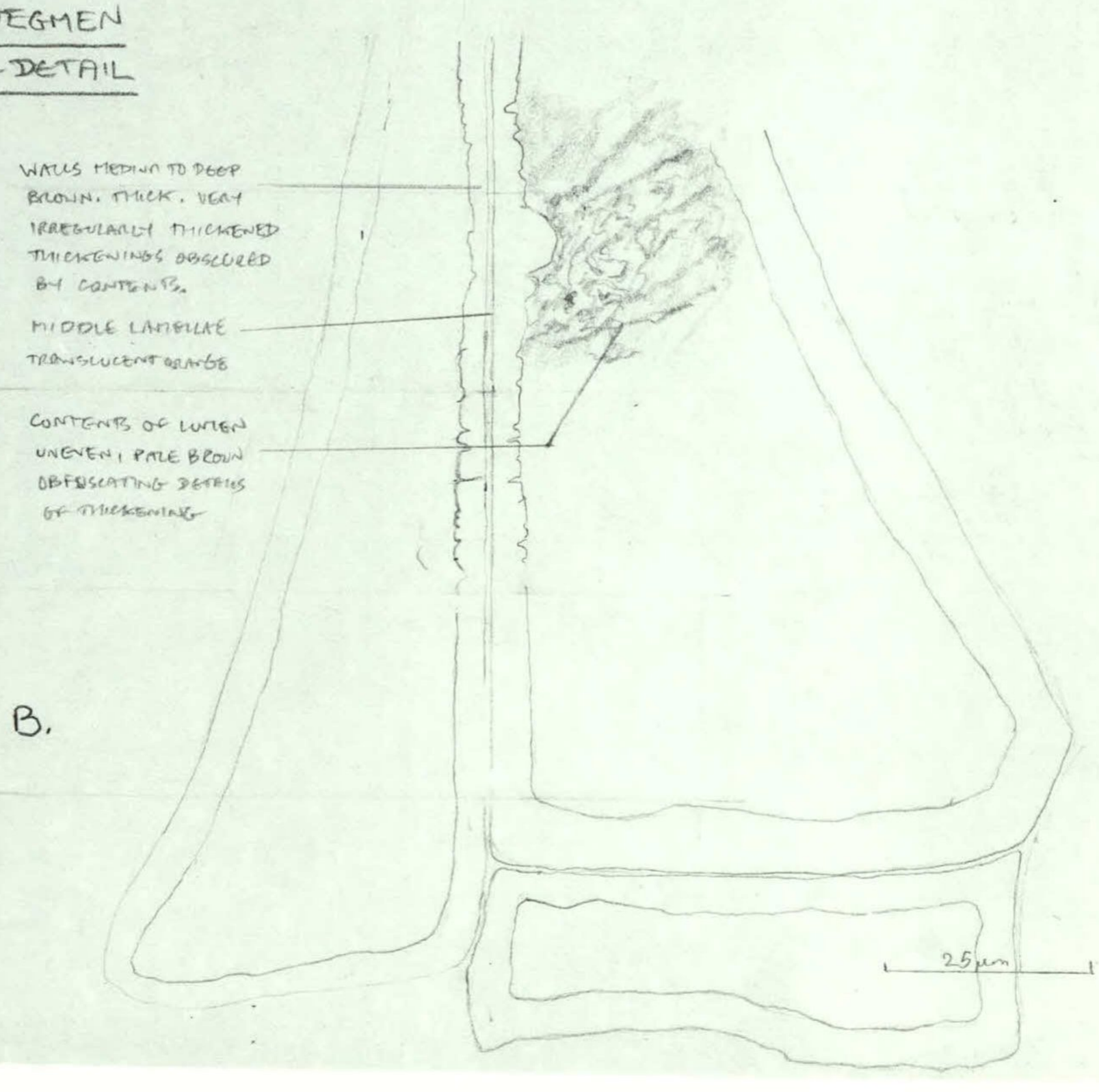


PLATE 72

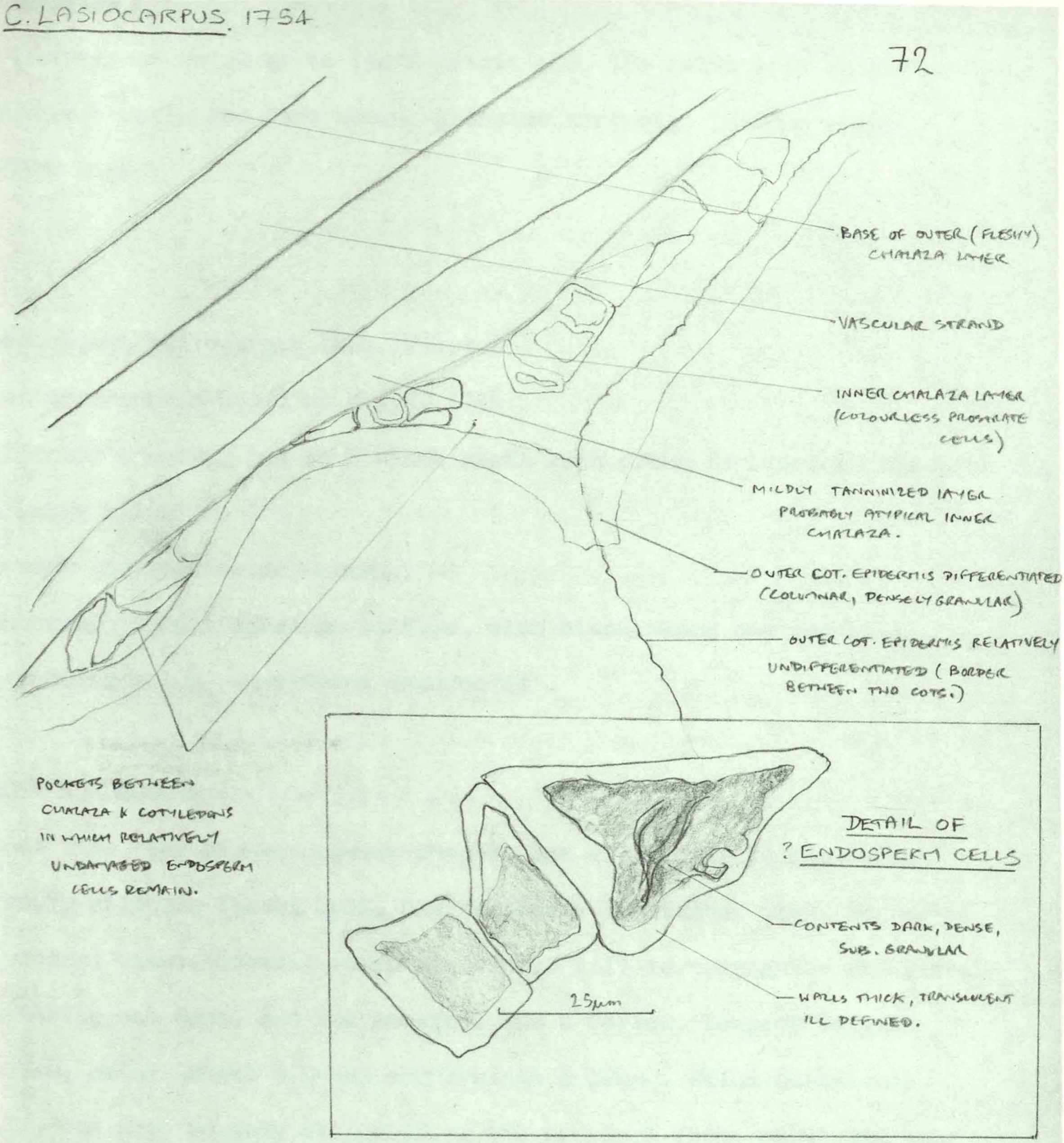
CHISOCHETON LASIOCARPUS

TISSUE MAP OF INNER SEED COAT AND OUTER COTYLEDONS

THIS FACILITATES TRACING HOMOLOGIES OF DIFFERENT CELL LAYERS.

C. LASIOCARPUS. 1754






L.S. INNER CHALAZA (UNDER HILUM),
? ENDOSPERM AND COTYLEDONS.

100µm

?PERISPERM

1-3 layers of columnar to isodiametric (LS, TS) cells with thick colourless walls and dark brown, granular contents. 10-28um wide, 18-35um high.

Chisocheton lasiocarpus (Miq.)Valeton

This description based on D.J.M. 1754.

Collector's notes: 'up to 5 black seeds with cream (unripe) to red aril and large hilum'.

Stevens (1975): 'seeds unknown'

Mabberley (1979):'seeds up to five, with black testa and red aril surrounding hilum, cotyledons superposed'.

GROSS MORPHOLOGY

Seeds five, not orange-segment-shaped, but ellipsoid. In plan view, narrowly elliptic (about 2:1), and similarly in lateral view. In dorsal or ventral views, broadly elliptic (almost 1:1) to triangular,the distal end making one face, and the proximal end a vertex. Longest length 14-17mm, axial length 6.5-9mm and breadth 8-12mm . Hilum relatively small, the scar roughly ellipsoid on the proximal face, about 7mm long and 3-4mm broad. The chalaza much larger, completely fleshy on the surface and covering about one third the surface area of the seed, some portions extending as far as the equator. No significant aperture exists at the micropyle.

ANATOMY

INTEGUMENTS

Testa

Cuticle:fairly thick, usually about 1um.

O.E.: a single layer of prostrate extended polygonal (rectangular in section) cells, 8-20um tall, 12um to 35um wide. Walls straw-coloured, the outer very thick, 9um (6-c.12um), the others much thinner, 0.5um-1um, quite often buckled. Contents colourless.

mesophyll: usually absent, but where developed, up to 5 cells thick. The cells small, prostrate extended polygonal, 11um tall, 20um wide. The walls thin c.1um thick. Contents ± colourless, sometimes with slightly grey and granular cytoplasm.

I.E.:A single layer of prostrate extended - polygonal cells, rather similar, though less developed than the O.E., the o.p.w. only a third rather than a half the height of the cell. Cells 4-12um tall, 14-26um wide. Walls up to 1um thick except the o.p.w.(5um).

Tegmen

Exotegmen: of 1-4 cells thick. The cells prostrate, fibroid and in cross section, ellipsoid to rectangular(the periclinal walls shorter than the anticlinal:thus appearing columnar). Height:(8-)13-18um(-25um). Longit. width: 95um(-200um) transverse width 11-15um. Walls thick (2.5um), dark brown. thickenings frequent but obscure (spiral?). Contents pale brown.

Endotegmen: 3 (2-6) cells thick. Cells prostrate,tanniniferous, rounded extended polygonal. Height: 9um .Width: to 40um. The endotegmen is always thinner than the exotegmen,in the ratio 1:4.

Chalaza

Outer chalaza: cuticle on average 0.75um thick, relatively uniform.

O.E. extremely distinctive. Essentially of two layers both an epidermis and a hypodermis being developed. The epidermal layer of shortly columnar cells, 35um tall, 14um wide with thick,lustrous white,unevenly thickened walls (see Plate 71A). The outer periclinal wall to 11um thick, the remainder 1-1.5um thick, except the anticlinal walls which at the equator are up to 5um thick, giving the lumen an hour-glass shape. In some instances this constriction becomes complete and a new periclinal wall is formed. The epidermis thus is intermittently multiseriate. The hypodermal cells also have thick white lustrous walls and colourless lumen, but have generally a thinner wall (1-2.5um) which is more or less evenly laid down, and are broader than long: 18um tall and 22um (12-30um) wide. The shortest cells of the hypodermis often have extremely dense dark brown contents.

The main part of the chalaza is 35-55 cells thick. The cells are cuboidal(especially at the margins) to extended polygonal. From 23um to 45um (-60um) long and 18-27um broad. THe walls are thin (c.0.75um), the contents dense and greyish brown with nuclei often present. The cells are rather closely packed, with only a few airspaces. Lacunae are scattered thickly throughout, most with contents still contained. Cells elliptic 130um (exceptionally 210um)long. Occasionally, two will occur directly adjacent to each other,appearing as a single large lacunae and enabling the very thin (c.0.25um) walls to be observed. The nuclei are brown and large up to 20um. The cells seem to increase in size with development.

Middle and lower chalaza seem undifferentiated from each other and so are treated as one here. The chalaza below the outer fleshy part is 6-12 cells thick, the cells more markedly elongate; prostrate elongate cells, 12-15um tall and 30um (exceptionally 70um)wide. Walls 1um thick, contents absent or colourless. Idioblasts and lacunae nil, but vascular bundles frequently occur. Cells are tightly packed.

TRANSITION ZONE

At the line of transition between integuments and chalaza, a furrow ± normal to the surface occurs. At the base, the cells of the highly distinctive chalazal epidermal layers. No cells intermediate in character were detected. The testal mesophyll proliferates as the furrow descends and appears to be directly continuous with the fleshy outer layer of the chalaza. The exotegmen, on the other hand, appears to terminate abruptly just before the base of the furrow in which area it is thicker than normal and somewhat disorganized.

The endotegmen merges into the lower part of the chalaza gradually. 500um before the integuments reach the furrow, this layer loses its tanniniferous nature, and proliferates, increasing from about 3 to 6 or 12 cells in thickness and also increasing slightly in size.

Sub-seed-coat

?Endosperm: a thin crushed, frequently discoloured, much interrupted layer of cells, hardly detectable at all under the integuments. Under the chalaza, usually visible as a thin yellow layer of cell walls and cuticles. Where crushing is apparently reduced, as under the hilum, the cells, in pockets of two to nine are seen to be irregularly ± isodiametric, width 36um and height 20um. The walls are almost translucent and difficult to resolve, but appear to be 3um thick. The

contents are a dense granular grey. The nucleus is large, if present.

See Plate 72.

EMBRYO

#3. 5-7 cells thick. The outer epidermis usually more or less cuboidal, 8-14um tall and 8-19um high. Walls and lumina occasionally tanniniferous. The description preceding fits the epidermis beneath the integuments and between the cotyledons and is little differentiated from the cells beneath. However, under the chalaza, these cells are notably altered (see Plate 70B): becoming columnar, with densely brownish grey contents, large nuclei and comparatively thick walls.

In contrast the lower layers of cells are comparatively large, isodiametric (outer layers) to slightly radially extended polygonal. Height 28-47um, width 15-38um. Walls thin (1um) but appear superficially thicker owing to the brown protoplast which adheres to them. Scattered (?) resin cavities throughout this layer, many with an endothelium of radially (to the cavity) flattened ,darker stained cells. Some single sclereids scattered throughout the the lower part of this layer but most at the junction with #1

#2. The sclereids in clusters of 3-4 cells (rarely to 10) are mainly distributed thinly at the border between #3 and #1. Isodiametric idioblasts, with large single trapezoid prismatic crystals are usually associated with these clusters. Sclereid dimensions: 32um to 52um in diameter (± isodiametric), wall thickness 16um.

#1. Large, thick-walled isodiametric to slightly extended cells, (40um long, 52um broad with walls 2um thick.), with pale, finely granular cell contents usually with a denser central mass. Cells fairly loosely packed and resin cavities fairly common in the outer layers.

# PLATE 73

## CHISOCHETON SCHODDEI

JUNCTION OF BITEGMIC AND CHALAZAL PORTION OF SEED-COAT.
NOTE CORRESPONDING CHANGE IN FLESHINESS OF
OUTER LAYERS.

UPPER (FLESHY) CHALAZA

MIDDLE CHALAZA

LOWER CHALAZA

INTERMITTENT BOUNDARY LAYER (FOR DETAILS SEE BELOW) BETWEEN UPPER & MIDDLE CHALAZA. NOT SEEN IN MANY SECTIONS.

OVERLAP OF THE UPPER, FLESHY PART OF THE CHALAZA, FORMING A (SHORT) THIRD INTEGUMENT

TERMINATION OF EXOTEGMEN

ENDOTEGMEN TRANSITION TO INNER CHALAZA MARKED BY INCREASE IN THICKNESS FROM 9-10 to 12-15 CELLS & FURTHER LOSS OF TANNIN

L.S. JUNCTION OF INTEGUMENTS WITH CHALAZA (TRANSITION ZONE)

300 µm

TESTA, O.E.

TESTA. I.E.

AIR SPACE BETWEEN INTEGUMENTS

BORDER BETWEEN EXO & ENDOTEGMEN

TESTA MESOPHYLL PROLIFERATES FROM NORMAL CELL THICKNESS OF TWO, TO FIFTEEN IN THE 1-2 mm RECEPTING TRANSITION.

EXOTEGMEN PROLIFERATES FROM THE NORMAL 2(-3) CELLS TO TEN CELLS THICK.

L.S. BOUNDARY BETWEEN UPPER & MIDDLE CHALAZA (INVERTED)

MIDDLE CHALAZA- CELLS LARGE, PROSTRATE, ANGULAR, EXTENDED - POLYGONAL AND THICK WALLED, NO CONTENTS.

BOUNDARY LAYER, CELLS SMALLER, VERY DENSE CONTENTS, THICKISH WALLS, ROUNDED, ELONGATE, PROSTRATE, AIR SPACES.

UPPER CHALAZA CELLS ISODIAMETRIC, MOST WITH CONTENTS (PALE GREY) & THINNER WALLS; IN CONTRAST TO MIDDLE CHALAZA.

AWAY FROM THE BOUNDARY, CELLS MORE REPRESENTATIVE: LARGER, MORE EXTENDED - POLYGONAL IN SHAPE.

PROTOPLASMIC CELL WITH PALE, COARSELY GRANULAR PROTOPLASM & LARGE NUCLEUS.

50 µm

PLATE 74

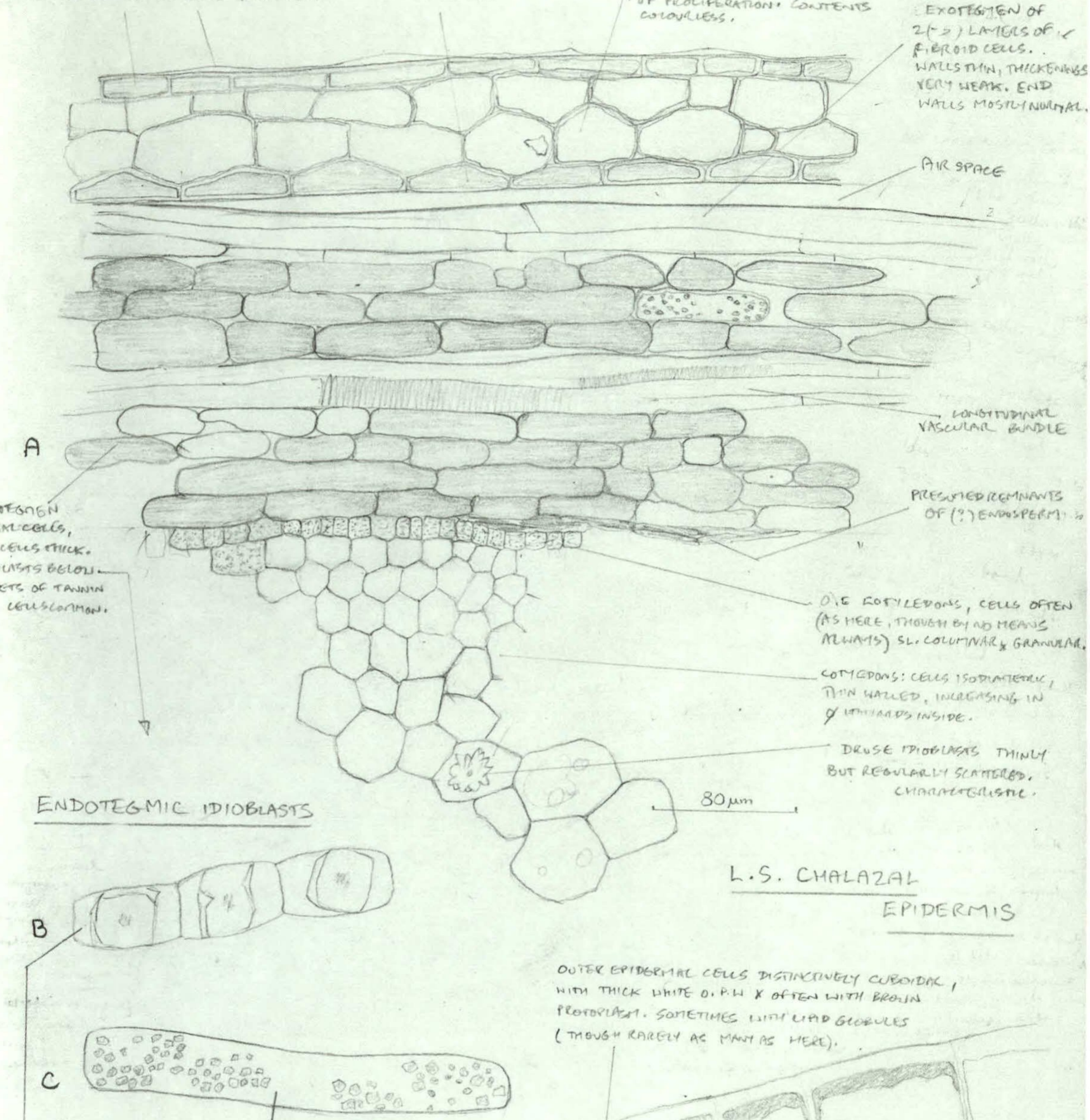
CHISOCHETON SCHODDEI

A-D SEED-COAT ANATOMY. NOTE TYPICAL CHISOCHETON CHARACTERS, THIN TESTAL MESOPHYLL, TESTAL I.E. LACKING CRYSTALS AND VERY SIMILAR TO O.E., THICK, VASCULARIZED AND TANNINIFEROUS ENDOTEGMEN.

C. SCHODDE 1. 1773

74

## L.S. INTEGUMENTS & EMBRYO (midway)




ENDOTEGMIC IDIOBLASTS







TRAPEZOID CRYSTAL CELLS. ALMOST ISODIAMETRIC, THIN WALLED. LUMEN OCCUPIED LARGELY BY A SINGLE CRYSTAL

PROSTRATE IDIOBLAST, LUMEN COLOURLESS EXCEPT FOR NUMEROUS GREY-BLACK GRANULES. DIMENSIONS AS NORMAL ENDOTEGMIC.

## L.S. CHALAZAL EPIDERMIS

OUTER EPIDERMAL CELLS DISTINCTIVELY CUBOIDAL, WITH THICK WHITE O.P.W & OFTEN WITH BROWN PROTOPLASM. SOMETIMES WITH LIPID GLOBULES (THOUGH RARELY AS MANY AS HERE).

PLATE 75

CHISOCHETON SCHODDEI

TISSUE MAP OF `AUXILIARY FLESHY ZONE': EXTENSION FROM THE CHALAZA TO THE MICROPYLE (IN A THIN BAND: SEE e.g. PLATE 76 D & E) OF FLESHY TISSUE. THIS IS PURELY TESTAL AND NOT CHALAZAL.

C. SCHODDEI
1773.

CONTENTS: GR - DENSELY, DARKLY GRANULAR
✓ - ORANGE
× - STRAW

ME. FLESHY ZONE.
CELLS SMALL THIN WALLED WITH VERY DENSE GRANULAR CONTENTS: APPEAR ± BLACK

O.E FLESHY ZONE
APPARENTLY CONTINUOUS WITH O.E TESTA, BUT CELLS MORE ISODIAMETRIC, CONTENTS ORANGE, WALLS ESPECIALLY O. PERICLINAL, AGGREGATED.

TESTA, AS ENTERS FLESHY ZONE, DEVELOPS A GRANULAR MESOPHYLL WHICH APPEARS TO PROLIFERATE TO FORM THE BULK OF FLESHY TISSUE, THIS IS METAMORPHOSED THE O.E LOSES ITS PROLIFERATE STRAW COLOURED & THIN WALLED NATURE.

THE I.E CELLS ALSO BECOME LESS EXTENDED & ASSUME GRANULAR CONTENTS, BECOMING INDISTINGUISHABLE FROM THE MESOPHYLL, BUT ALWAYS CLEARLY DISTINCT FROM THE EXOTEGMEN BELOW - THE FIBROID CELL LAYER REMAINING UNALTERED EXCEPT TOWARDS THE CHALAZA.

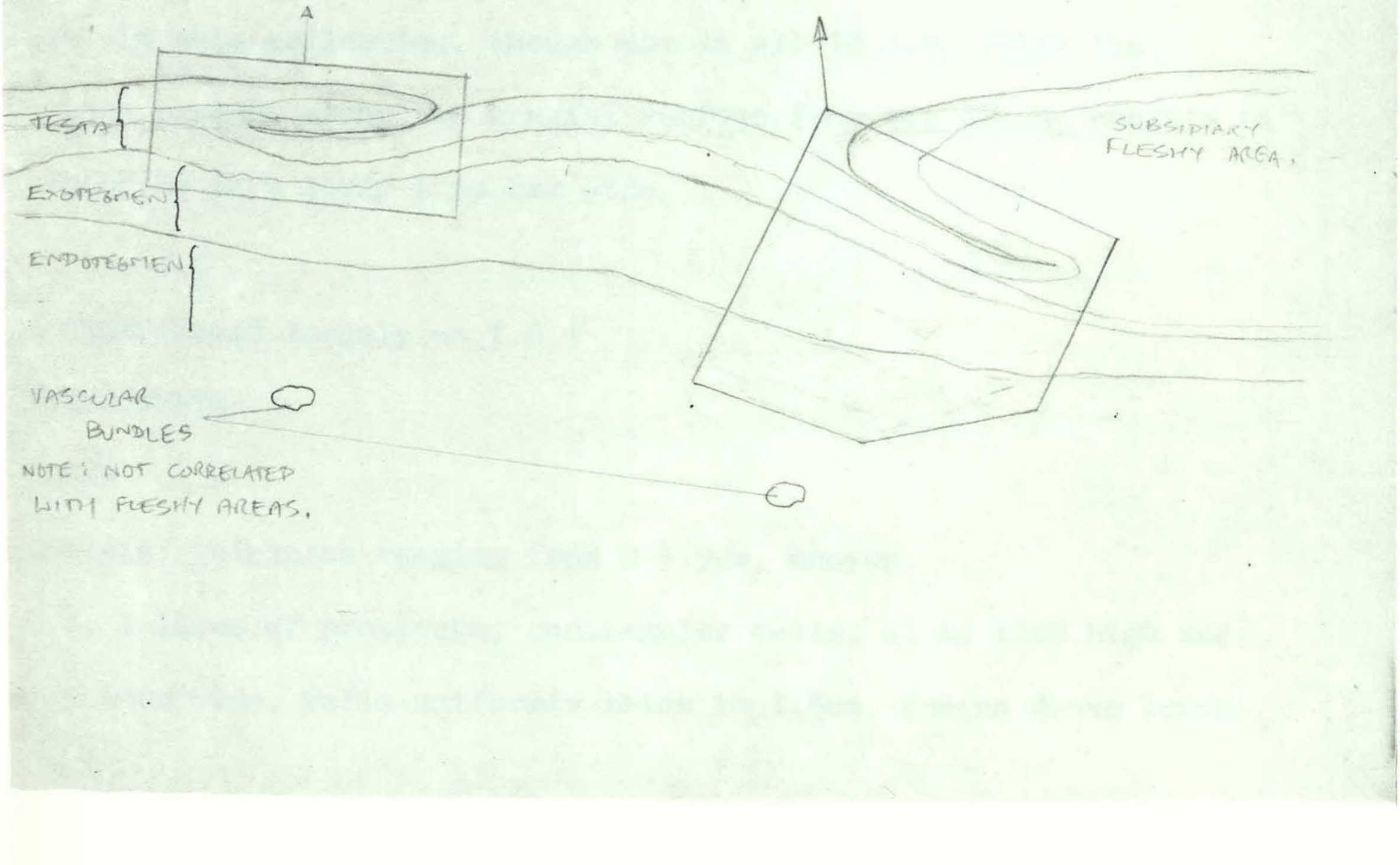
50μm

CHISOCHETON SCHODDEI 1773

T.S. AUXILIARY FLESHY ZONE.

TISSUE PLAN.

SEE NEXT PAGE.



C. schoddei P.F.Stevens

This description based on D.J.M. 1773

Collector's notes:'Fruit 6-merous with thick creamy pericarp and 6 unripe seeds with arils half covering the testa.'

Stevens (1975):'Seeds orange'

Mabberley (1979):'Seeds up to 6, with black testa and peripheral orange-red aril covering the adaxial half.'

GROSS MORPHOLOGY

Seeds six, rounded orange-segment shaped. Length 17.5mm to 25mm, length along axis 7mm, breadth 8mm. Hilum relatively small, scar narrowly ellipsoid, about 10mm to 14mm long and 2 to 3 mm broad. Chalaza fleshy extending whole of proximal length of seed and covering proximally about 1/3 to 1/4 of its surface, but seeming larger, since it overlaps the testa.

Testa forms remainder of seed surface. More or less succulent near chalaza. In this collection, though not in all (D.J.M. 1979) the succulence extends along the abaxial surface from the fleshy chalaza to the micropyle in a strip 1 to 2mm wide.

ANATOMY(Based largely on T.S.)

INTEGUMENTS

TESTA

Cuticle: thickness ranging from 0-4.9um, uneven.

O.E. 1 layer of prostrate, rectangular cells, 11 to 12um high and 20um to 68um wide. Walls uniformly thick to 1.5um. Lumina dense brown.

Mesophyll: not always developed (see Plate 75A). Generally two cells thick: cells cuboidal to prostrate rectangular, with thick walls 12-20-24um tall and 21-32-50um wide. Walls 1um thick. Lumina ± colourless. These layers proliferating 'in auxiliary fleshy zone' (see Plate 75), lacunate with modified, thinner-walled more isodiametric cells with dense contents; similar to and proximally continuous with fleshy zone of the chalaza. Limited proliferation of cells in the mesophyll also occurring for 2 to 3mm at the junction with chalaza, here mesophyll may reach 15 cells thick.

I.E. closely resembling O.E. in all respects, except in less radially compressed. Cells to 20um tall; cuticle very thin or absent.

TEGMEN

Exotegmen: 2-3(4) layered cells prostrate fibroid, 10um to 25um high to over 240um long. End walls usually square or slightly oblique. Contents absent. Thickenings appear weak and annular in transverse section (perhaps due to incomplete seed development).

Endotegmen: 8 to 10 rounded to rectangular prostrate tanniniferous cells, 31um to 150um wide and 14 to 20um high. Idioblasts of two sorts common: (i) trapezoid crystals in ± isodiametric cells, sometimes in short chains of 3-4 cells,(ii) otherwise normal endotegmic cells, solitary, containing small grey-black granules, but without tannin. Colourless cells present in scattered groups, crop up in many sections (due to seed immaturity?)

Vascular bundles, usually directed towards micropyle, frequent. With 3-4 files (rows) of vessels.

CHALAZA

Outer chalaza. Cuticle very thin or absent.

O.E.: cells ± cuboid, 25um high and 13-35um wide, in 1 layer. o.p.w. thick (2um), the other much thinner (0.75um). Protoplasm mid-brown to densely brown. Lipid globules sparse.

Upper chalaza: to 90 cells thick (though perhaps at the extremities, even deeper). The cells large, slightly extended polygonal; 35-42-47um long and 23-28-32um broad, the walls thin, 0.75um. Cells under the epidermis and towards the base of the upper chalaza tending to be smaller and more cuboidal. Contents pale and finely granular, with nuclei. Lacunae densely interspersed throughout the mesophyll, these being elliptic and with a densely granular cytoplasm and nucleus . Length 122-140-157um long.

Druse, trapezoid and (?) silica cell idioblasts are present intermittently in this tissue.

Middle chalaza: sometimes, but rarely, separated from the upper chalaza by a layer of 2-3 cells with densely granular contents, of ± intermediate dimensions, and rounded angles (see Plate 73 lower). An abnormality ? Cells large, angular, prostrate, extended-polygonal. Height: 21-25-28um, width: 37-45-53um. Walls thick, 1.5um. Lumina colourless .

Lower chalaza: usually 6-15 layered thick, exceptionally, in the vicinity of the vascular portal,3 cells thick. Cells prostrate, rounded highly extended-polygonal cells, often with tannin though frequently, large areas colourless. Width: 35um-140um, Height 16um.

TRANSITION ZONE

Integuments becoming much thicker at junction with chalaza. This increase in thickness, tapered over a distance of 1 to 2 mm and accounted for by increase in testal mesophyll from the usual 2 , to 15

layers, and the exotegmen from 2-3 cells to 10. Transition quite abrupt (see tissue diagram ), and marked by oblique cleft in the outer surface of seed between fleshy chalaza and tissue which it overlaps, forming in effect a third integument. Junction between the two epidermal types found at the base of cleft. Termination of testal mesophyll is less well marked, merges gradually with middle and to a lesser extent exotegmen continues into chalaza almost unchanged, merely increasing in thickness and decreasing in degree of tannin, to form inner chalaza.

SUB-SEED-COAT

ENDOSPERM: if at all present, this tissue is highly crushed and unrecognizable.

Embryo: comparatively undifferentiated. Outer epidermal cells usually smallest, and sometimes slightly columnar and densely granular. The rest of the cotyledon tissue of tightly packed, thin-walled (c. 0.75um), isodiametric cells the outermost small, 17um in diameter gradually increasing over a span of about eight cells inwards to up to 55um in diameter. Contents of cells pale finely granular. No resin canals or sclereids detected, but druse cells seem of frequent and characteristic occurrence in this tissue.

C.macranthus (Merr.)Airy Shaw

This description based on D.J.M.1718.

Collector's notes:'Seeds with arils half-covering them, as yet white' [Implication that this collection immature.]

Mabberley (1979):'Seeds 2.5-3.3cm long, triangular in cross section arillate, aril reddish, covering inner edges of black testa'.

PLATE 76

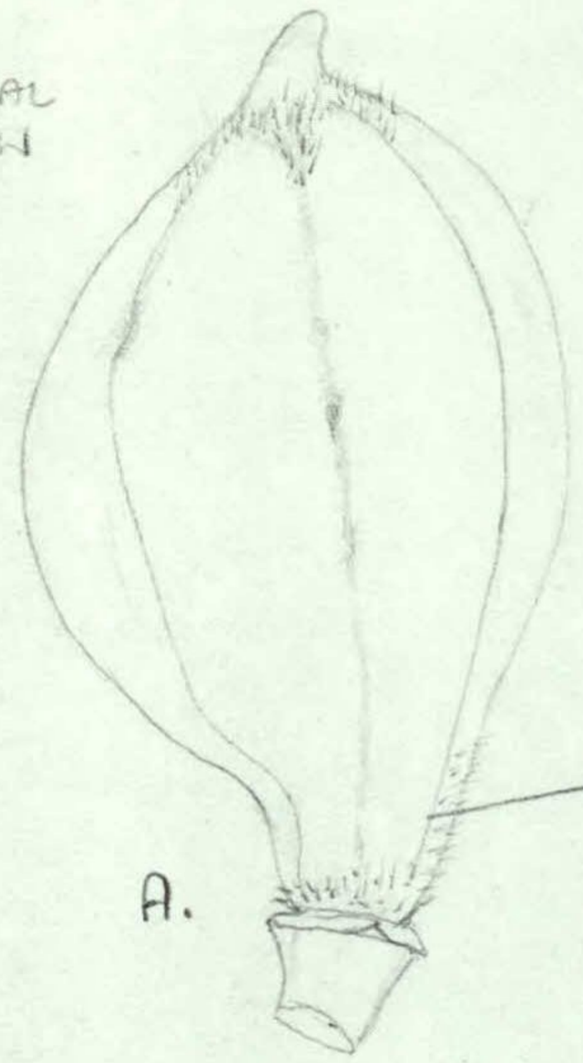
CHISOCHETON MACRANTHUS

A-F FRUITS AND SEEDS. NOTE FLESHY EXTENSION FROM THE CHALAZA TO THE MICROPYLE (D & E)- OF USE IN INFERRING PHYLOGENY.

# C. MACRANTHUS 1718c

## FRUIT (IMMATURE)

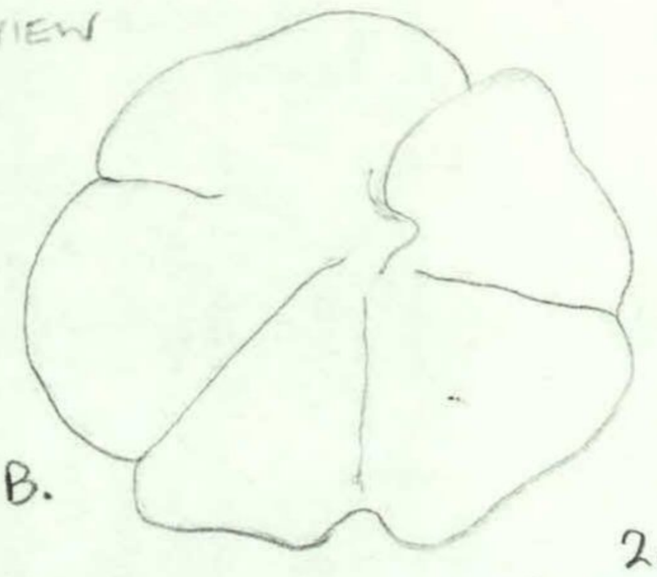
LATERAL VIEW



A.

INDUMENTUM OF TWO HAIR TYPES: THE LARGEST NUMBER OF SHORT LENGTH, BUT V. DENSE, THE OTHER LONGER, EMERGING WELL BEYOND CARPET PRODUCED BY FORMER, IRRITANT, EASILY DETACHED, THUS REMAINING AT BASE, APEX & IN SUTURES ONLY

PLAN VIEW



B.

2cm

## SEED (IMMATURE)

LATERAL, DISTAL & PROXIMAL VIEWS

MEDIAN SECTION



C.

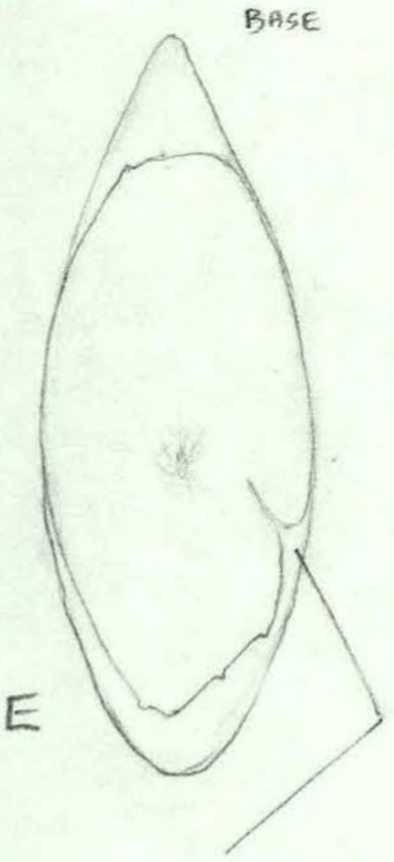


D

BASE OF FRUIT

FLANGE WHERE FLESHY 'ARIL' IS FREE FROM TESTA

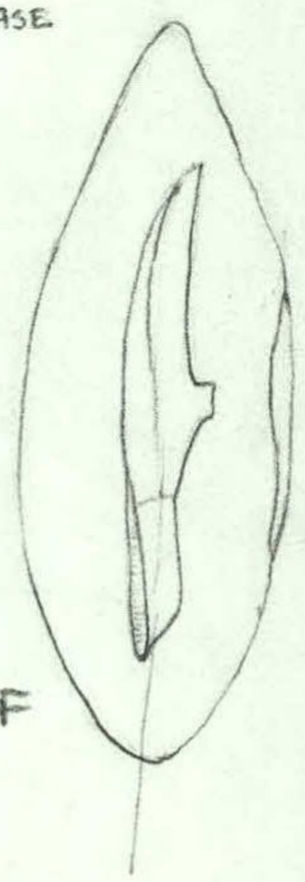
BASE



E

FLESHY LAYER WITH SUBSIDIARY PROLONGATION TOWARDS MICROPYLE. SEEN IN 3 SEEDS IN 1 CAPSULE

BASE



F

HILUM - WITH PORTION OF PLACENTA STILL ATTACHED.

2cm

PLATE 77

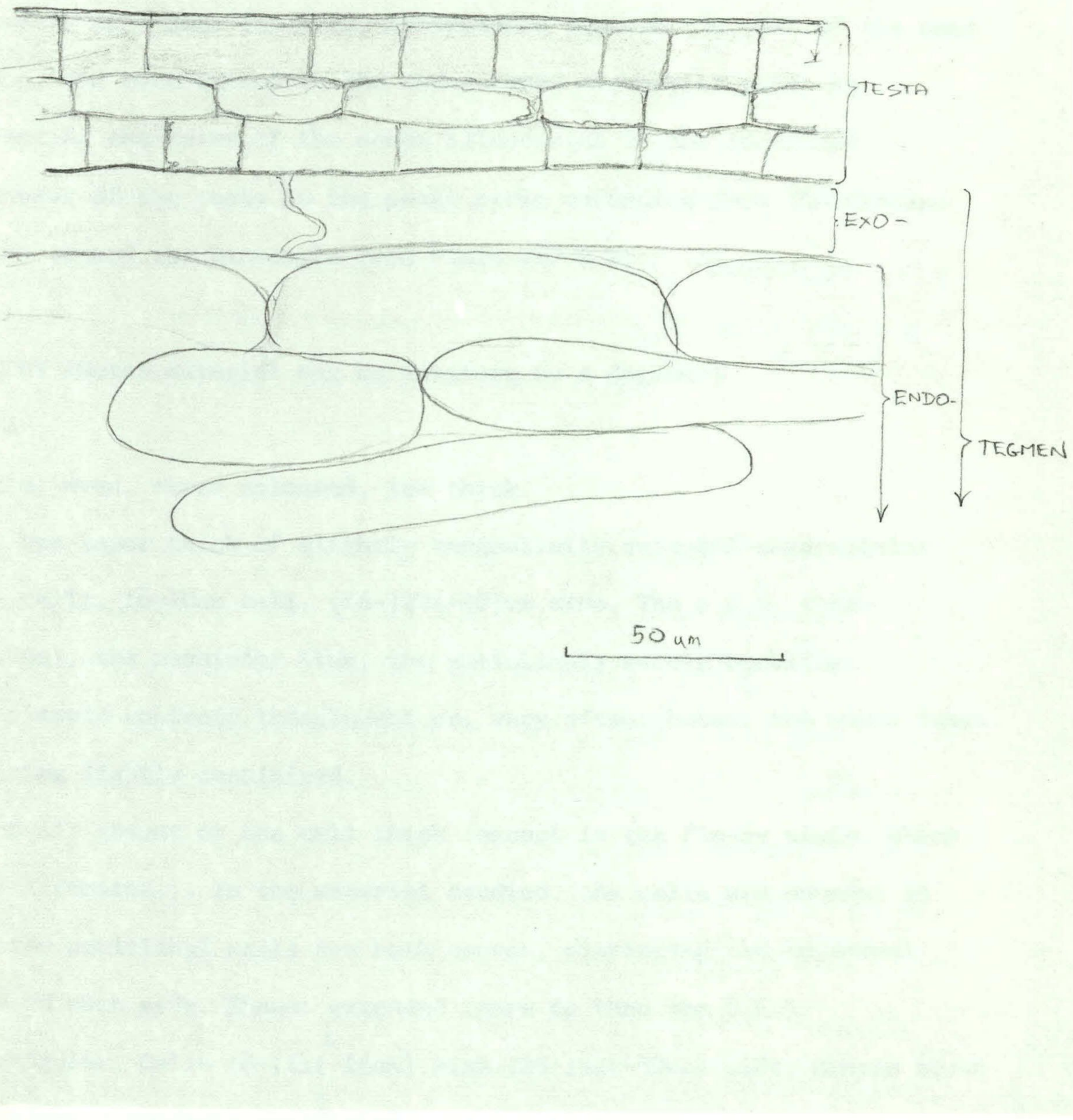
CHISOCHETON MACRANTHUS

SEED-COAT ANATOMY- NOTE THIN-WALLED EXOTEGMIC FIBRES:

DUE TO IMMATURITY OF COLLECTION.

C. MACRANTHUS 1718c

L.S. INTEGUMENTS



GROSS MORPHOLOGY

Seeds 5, modified orange-segment-shaped: basically wedge shaped in dorsal view (as an orange segment), but the distal face markedly convex and the extreme ends of the seed bluntly pointed. Longest length 25-35mm, breadth (lateral and plan views) 20mm. The chalaza much more extensive, composing 1/3 to 1/2 of the surface area of the seed, its glossy outer surface thickly succulent and overlapping the integuments proximally by 1-2mm. The shiny integuments compose the rest of the seed surface, and both extend to the undeveloped micropylar pore. An interesting character of the seeds illustrated is the localized fleshiness of the testa in the small strip extending from the chalaza overlap toward the micropyle (see Plate 76D & E).

ANATOMY (Note: material may be immature to a degree.)

TESTA

Cuticle: even, straw coloured, 1um thick.

O.E.: one layer thick of slightly tangentially extended quadrangular (n.s) cells, 16-20um tall, (16-)22(-50)um wide. The o.p.w. thick (1-1.5um), the remainder <1um, the anticlinals rarely buckling. Protoplasmic contents translucent or, very often, brown, the whole lumen appearing lightly tanninized.

Mesophyll: absent or one cell thick (except in the fleshy strip, where it proliferates.). In the material studied, the cells are unusual in that the periclinal walls are both convex, displacing the epidermal walls on each side. Shape: extended (more so than the O.E.) quadrangular. Cells (8-)11(-16um) high,(25-)32(-40um) wide. Sparse brown protoplasmic contents restricted to cell walls.

I.E. cells very similar to those of the O.E., but less usually tanninized and tending to be slightly more extended in proportion: on average 14um tall and 22um wide.

TEGMEN

Exotegmen: one cell(sometimes two.)thick, the cells 12-16um tall and 180-240um wide (narrow sample base). Unusually the walls are only 1um thick, almost transparent and without pitting. Perhaps attributable to the apparent immature state of this collection.

Endotegmen: 14-20(exceptionally 11 to 27)cells thick. The cells prostrate, rounded rectangular. Dimensions very variable: 90um (50-140um) wide and 30um(10-40um) tall. The walls 1um thick, the contents pale brown, not (unusually,possibly due to immaturity). fully tanniniferous. Air spaces frequent and comparatively large. Vascular bundles frequent in the lower part of this layer.

CHALAZA

Outer chalaza: cuticle: 1um thick, evenly distributed.

O.E.: very similar to that of the testa, only, on average more tangentially extended. 12-17um tall and 30um wide(16-50um).

Cortex: in a representative section, 50 cells(and 1120um) thick;at the tip of the seed undoubtedly thicker. The cells are mainly prostrate elliptic (though in some parts almost diametric and here usually 40um long and 30um broad.), 24um tall and 80um wide, they are thin-walled with abundant protoplasmic contents and generally each with 8-12 lipid globules of 3-4um (rarely to 6um) in diameter. Lacunae are abundantly present, up to 260um long, over a large range of sizes, the smallest with cell contents.

Lower chalaza: vascular bundles frequent. Generally the layer 10-15 cells in thickness. Can be sub-divided into two parts, the upper, 260um thick of tangentially extended quadrangular cells. 12um tall and 40um wide, the cells with pale brown fairly dense contents, the whole layer appearing brown in contrast to its nieghbours under a dissecting microscope. The walls are angular and c.1.5um thick.

The lower part is thinner, about 160um thick, the cells smaller, almost lacking contents, and uniformly cuboidal, 6um in diam..

TRANSITION ZONE

At the junction between the two parts of the seed surface marked by an inward turn of the integuments towards the hilum, metamorphosis is straightforward. Briefly: the testal O.E. metamorphoses imperceptibly (the I.E. disappearing completely) the mesophyll proliferates and appears to be partially continuous with the upper chalaza, whilst the endotegmen is confluent with the lower chalaza, the exotegmen terminating.

SUB-SEED-COAT

Endosperm. Below the integuments and above the embryo, there are two elements: the upper, a thin brown line 4-6um thick, is probably of crushed cells. The lower element is of undistinguished, sporadically occurring single cells which resemble essentially those of the embryo, but the cells smaller and radially compressed, 40um wide and 8um tall (narrow sample base). Below the chalaza a layer on average 6 cells deep of thin-walled rectangular cells occurs with fairly densely granular, slightly agglutinated contents, usually about 13um long and 4um wide

occurs. This layer gives the appearance of once being organized, but now being disrupted. At its bottom edge, disconnected cells with apparently thicker walls and denser lumina are scattered. Intermediates however, suggest that they are merely highly agglutinated and slightly distorted versions of the cells above, the thicker walls an illusion.

Below this layer occurs a thick brownish yellow band, probably derived from the walls of crushed cells.

EMBRYO.

Relatively, rather featureless, the cells isodiametric or slightly extended polygonal (non-polarized) with almost translucent protoplasmic contents, almost complete lack of ergastic materials, and very thin walls. These unusual features possibly attributable to immaturity. The cells 80um long and 50um broad. The outermost tending to be smaller and the epidermal cells regularly tangentially extended.

C. cumingianus (C.DC.)Harms ssp. cumingianus

This description based on T.D.P. 8052

Collector's notes: Seeds shining brown, surrounded by orange aril.

Stevens (1975): (As C.morobeanus Harms) 'Seed surrounded by an arillode except for the middle of the outer surface, free from the testa in outer half; cotyledons superposed'.

Mabberley (1979): 'Seeds three to four, reddish-brown, arillate, aril orange-red covering inner edges of blackish-brown testa, crenate and sometimes with extension to hilum, cotyledons superposed'.

# PLATE 78

## CHISOCHETON CUMINGIANUS

A-E DEHISCENT FRUITS AND SEEDS. NOTE THAT THE TESTA DOES NOT ALWAYS COVER THE DISTAL PART OF THE SEED-ABSENT OVER A 4cm LONG AREA IN E.

NOTE THAT TESTA ONLY PARTLY FLESHY.

C. CUMINGIANUS. 8052



FRUITS & SEEDS (WHOLE)

MATURE FRUIT IN PROCESS OF DEHISCING.

3 VALVES, SEPARATED BY BROAD SHALLOW SUTURES IN THE MEADST OF WHICH A CRACK IS ENFILADING.

3cm

DEHISCED FRUIT, THE SEEDS REMOVED.

A

VARIATION IN THE OUTER SEED COAT.

MARGIN OF HILUM

MAIN VASCULAR BUNDLE PORT.

EXTRA-HILAR CHALAZA & TESTA (THE TWO NOT DISTINGUISHABLE FROM THE EXTERIOR). SUCCULENT, CHESTNUT BROWN.

MICROPYLE. NO LARGE CENTRAL APERTURE

SEED A

DISTAL PLAN & LATERAL VIEWS.

4cm

B

2cm

SEED B.

DISTAL / LATERAL VIEW, ENTIRE SEED.

HILUM - HERE EXTENDS MORE THAN IS TYPICAL OVER THE SEED.

3cm

C

D

EXOTEGMEN. EXPOSED BY THE ABBREVIATED TESTA. DARK CHESTNUT & SLIGHTLY GLOSSY IN COLOUR. CRACKS RADIATE FROM THE MICROPYLE (MOST OF THE FIBROID CELLS ARE ORIENTATED LONGITUDINALLY, WITH FAIRLY FEW CROSS-LINKING CELLS.

THIN TESTAL MARGIN (MOST OF THE TESTA IS FLESHY) THROUGH WHICH ENDOTEGMEN CRACKS ARE VISIBLE

E

TESTA, IN THIS SEED ENCROACHES CLOSELY (FOR THIS COLLECTION) ON THE MICROPYLE.

DEMARCATION LINES BETWEEN AREAS OF DIFFERING TESTA THICKNESS.

PLATE 79

CHISOCHETON CUMINGIANUS

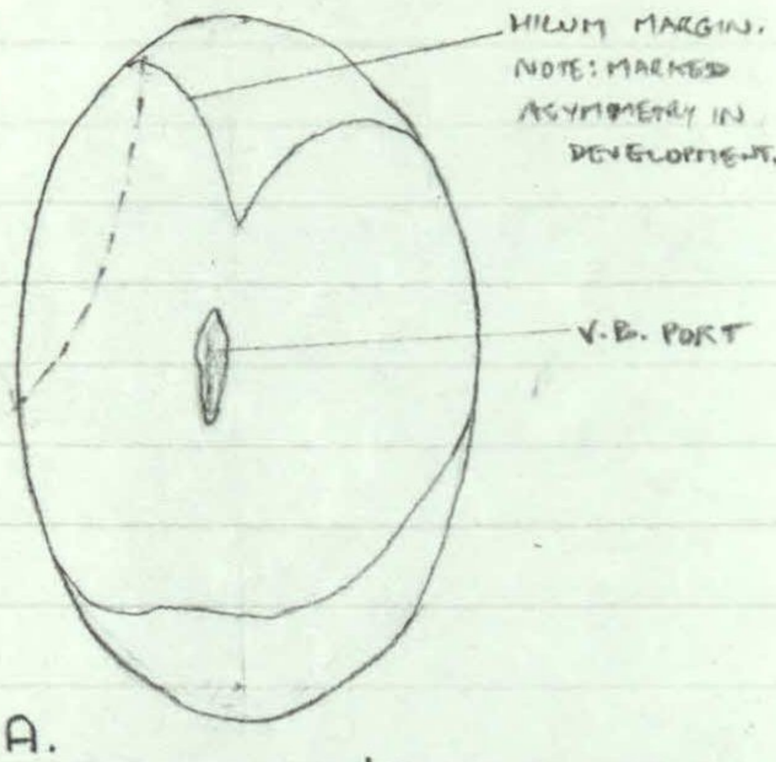
DISTRIBUTION OF FLESHY TISSUE IN RELATION TO HILUM, CHALAZA & BITEGMIC PART OF SEED.

# C. CUMINGIANUS 8052.

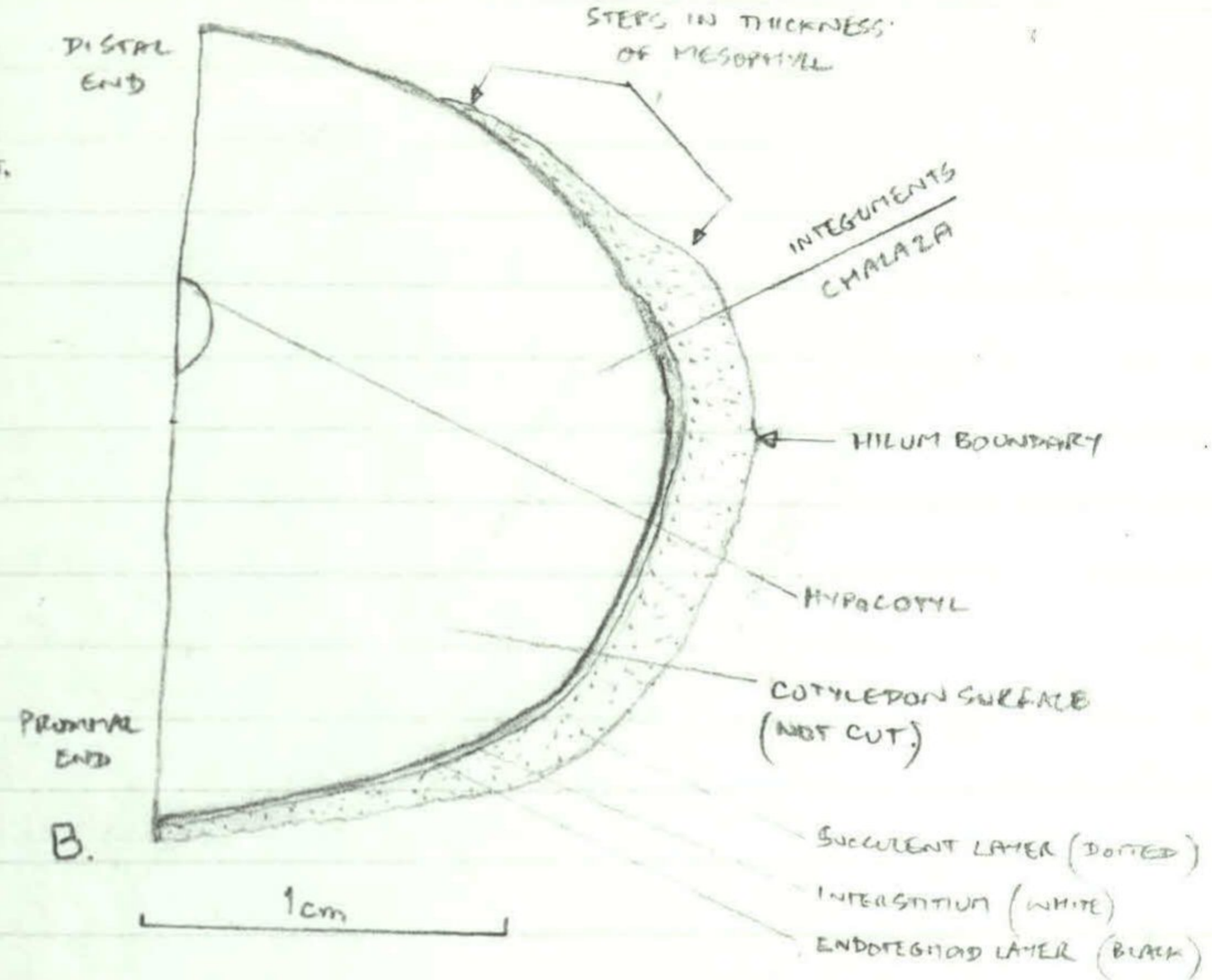


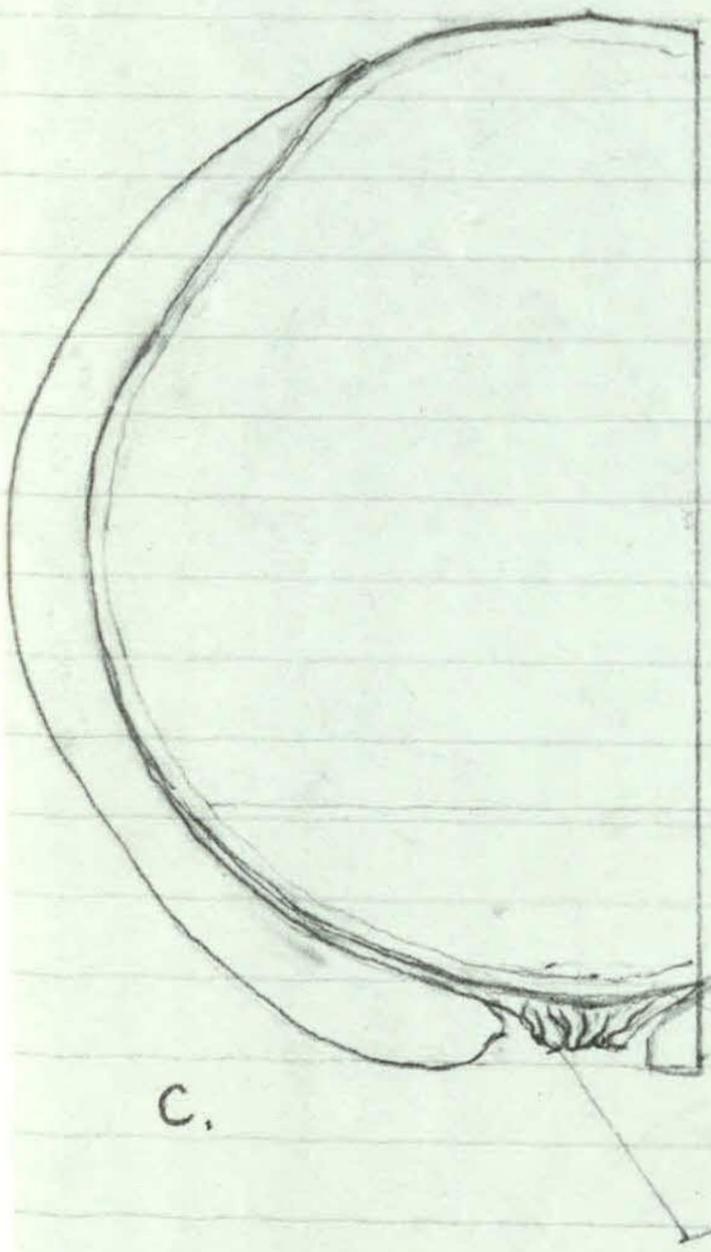
SEED C

PROXIMAL PLAN VIEW.




MACRO SECTION 'A' - ILLUSTRATING RELATION OF INTEG.: CHAL. BOUNDARY TO OTHER FEATURES.




MACRO SECTION 'B' - TRANSECTION OF VASCULAR BUNDLE PORT.

BOUNDARY BETWEEN #2 & #1 (COTYLEDON)

ENDOTEGMOID LAYER (BLACK)

VASCULAR BUNDLES. THE MAJORITY ENTER FROM THE ENDOCARP VIA THIS PORT, AT WHICH THE SUCCULENT LAYER SEEMS LACKING. FROM THIS POINT OF CONFLUENCE, THEY DIVERGE AGAIN, ENTERING FIRST THE INTERSTITIUM, THEN THE ENDOTEGMOID LAYER, IN ALL DIRECTIONS LONGITUDINALLY.

PLATE 80

CHISOCHETON CUMINGIANUS

STRUCTURE OF SEED-COAT.

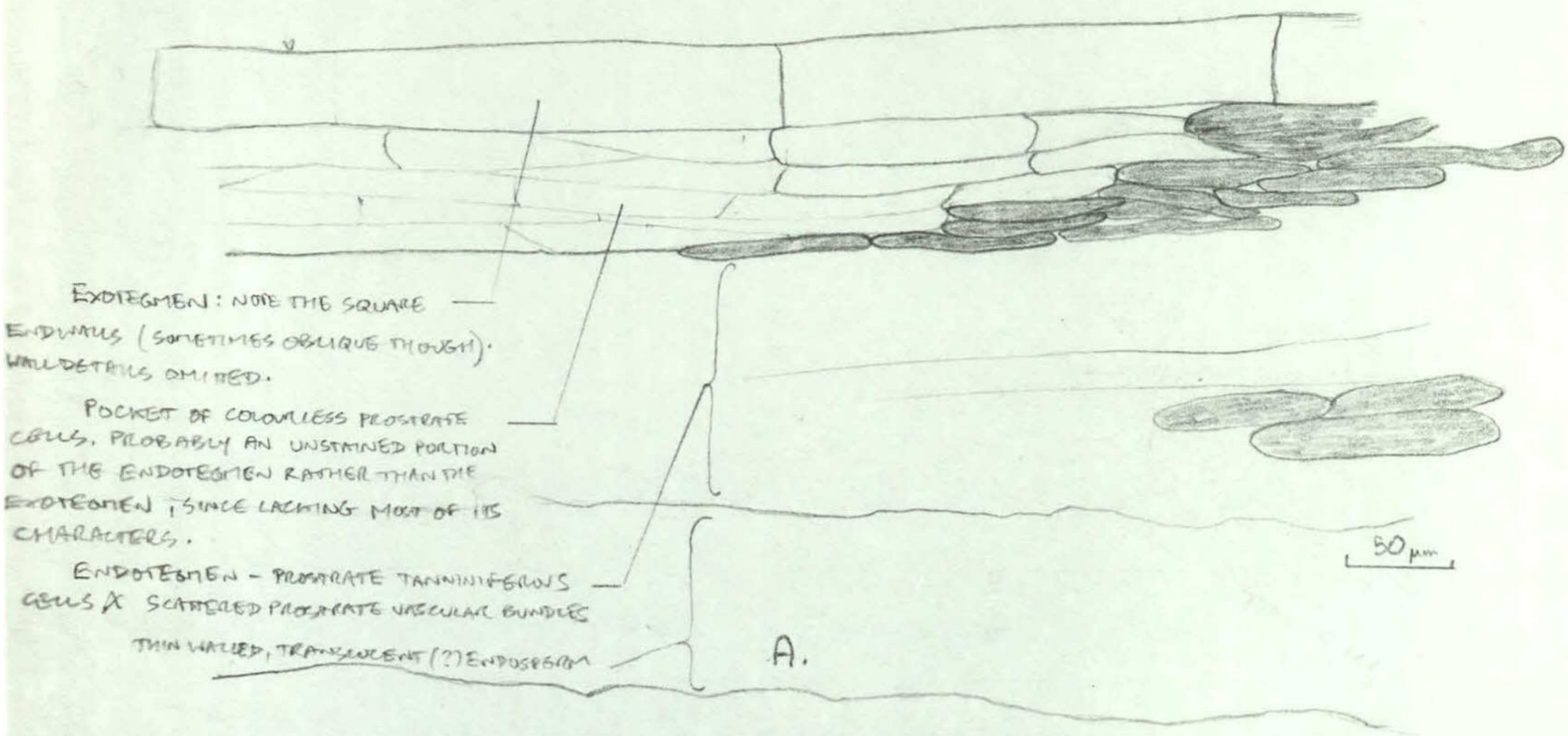
NOTE TANNINIFEROUS ENDOTEGMEN, DISTINCTIVE

& EXOTEGMIC FIBRES

C. CUMINGIANUS 8052.

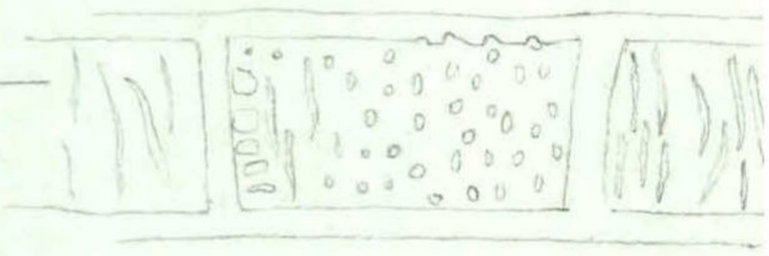


## L.S. TEGMEN (MICROPYLAR REGION)




## EXOTEGMEN - WALL PITTING.

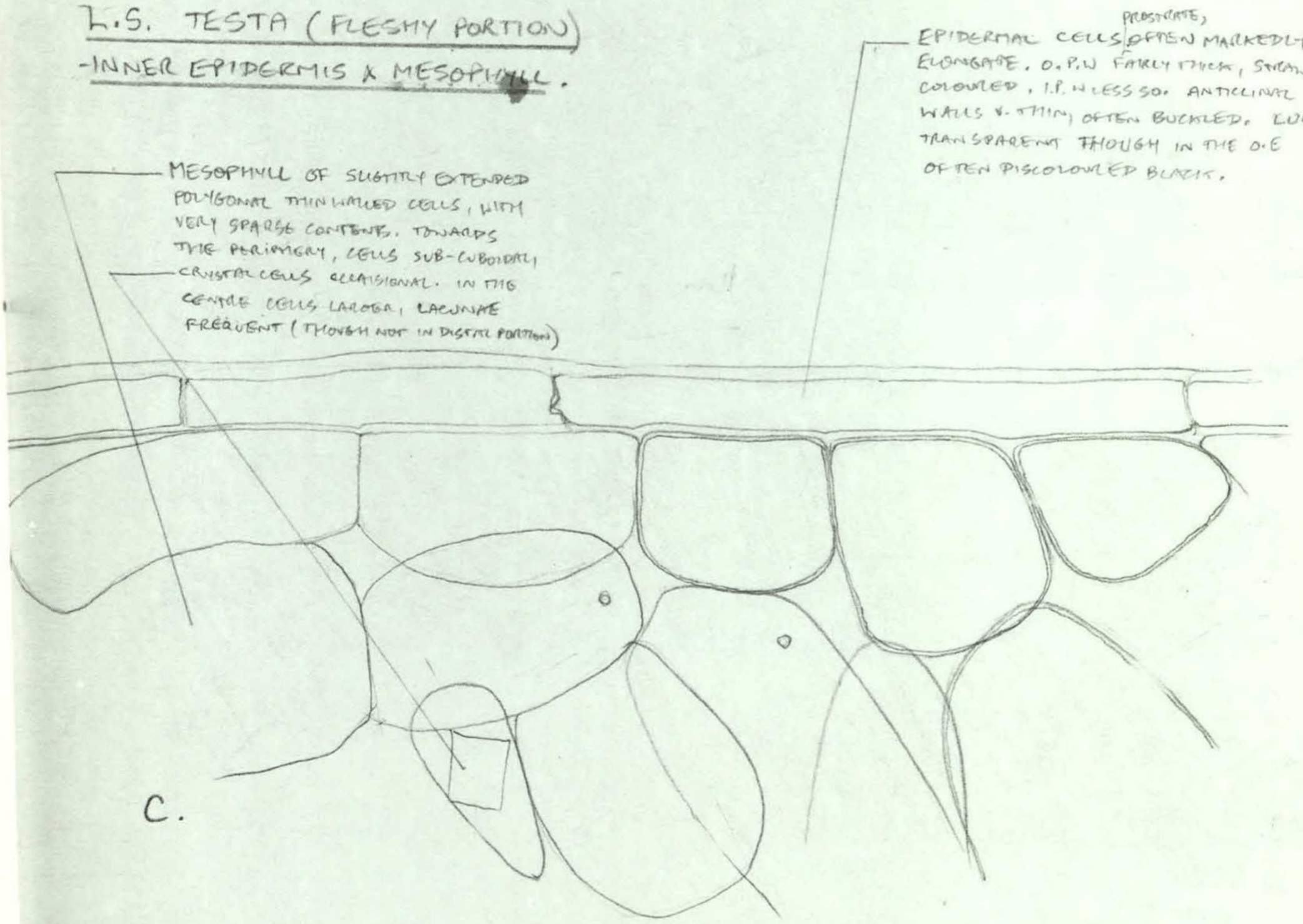
EXOTEGMEN VERY CONSPICUOUS IN SECTIONS, OWING TO THE LUSTROUS WHITE WALL. THE LARGE PITS, OF VARIED SHAPE (BOTH CIRCULAR & ELONGATE) ARE NOT OBSCURED BY THE COLOURLESS LUMEN.



B.

25µm

## L.S. TESTA (FLESHY PORTION) - INNER EPIDERMIS & MESOPHYLL.



# PLATE 81

## CHISOCHETON CUMINGIANUS

SEED-COAT AND OUTER COTYLEDON ANATOMY.

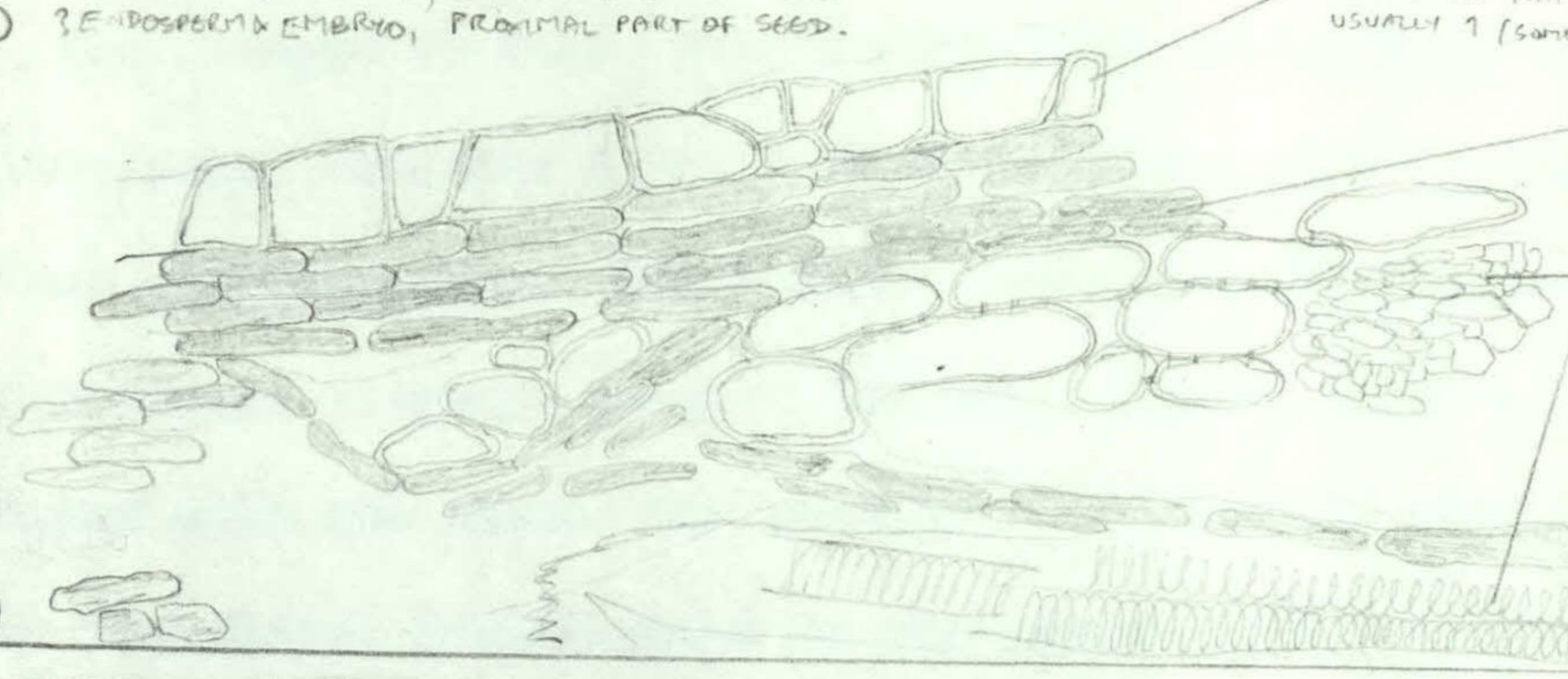
NOTE DISTINCTIVE PATTERNING AND STRUCTURE OF SCLEREIDS IN COTYLEDON (B).

# C. CUMINGIANUS. 8052



## T.S. TEGMEN & SUBTEGMEN

(A) TEGMEN
(B) ?ENDOSPERM & EMBRYO, DISTAL PORTION OF SEED
(C) ?ENDOSPERM & EMBRYO, PROXIMAL PART OF SEED.

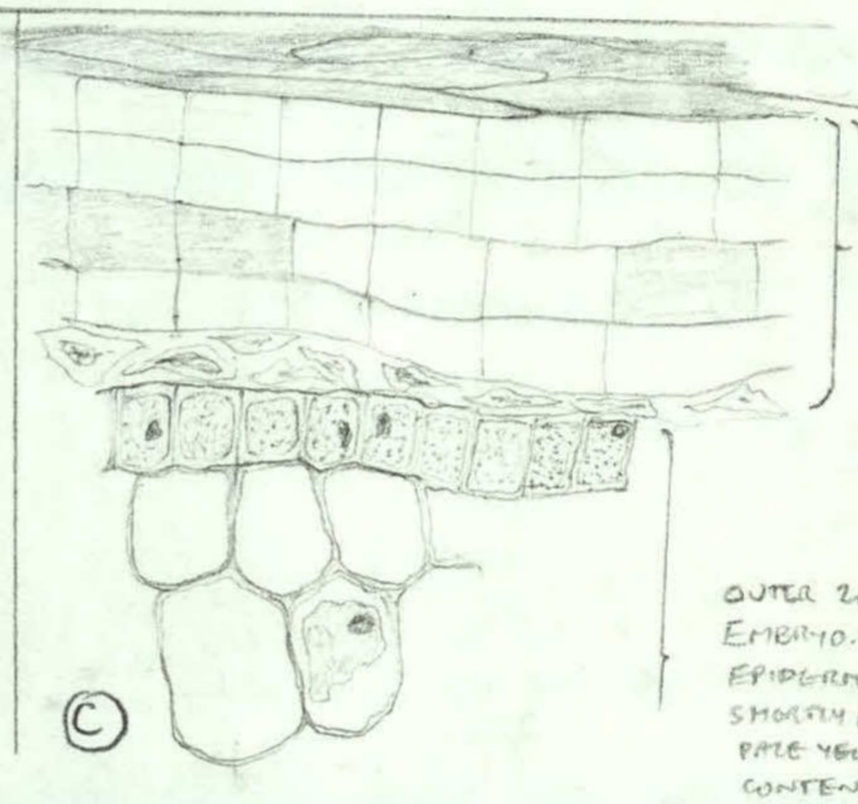


EXOTEGMEN. WALLS VERY DISTINCTIVE: IN CROSS SECTION, ± SQUARE, GLISTENING WHITE, PROMINENTLY PITTED. USUALLY 1 (SOMETIMES 2) CELLS THICK.

ENDOTEGMEN - OF PROSTRATE, TANNINIFEROUS CELLS, 9-12 CELLS THICK. HERE PENETRATED BY TWO LARGE VASCULAR BUNDLES, RUNNING NORMALLY TO EACH OTHER.

35 µm

(A)



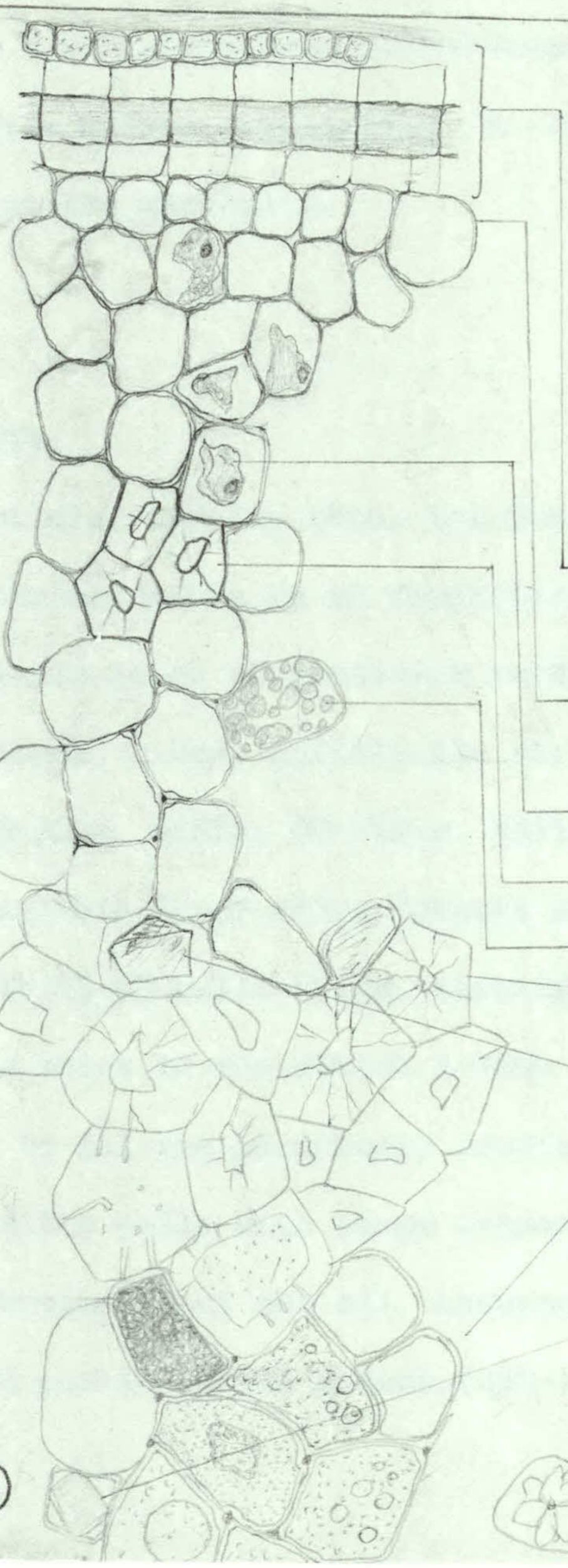
LOWER PORTION OF ENDOTEGMEN

?ENDOSPERM. HERE, THE UPPER LAYER NOT DIFFERENTIATED, THE TANNINIFERED LAYER INTERRUPTED OR ABSENT.

THE LOWER LAYER OF RADIALLY CRUSHED CELLS.

OUTER ZONE (#3) OF THE EMBRYO. HERE, THE EPIDERMAL CELLS DIFFERENTIATED: SHORTLY COLUMNAR, THICKER, PALE YELLOW WALLS, GRANULAR CONTENTS, NUCLEI VERY EVIDENT.

(C)



#3

ENDOSPERM (?) THE UPPER LAYER OF CELLS DIFFERENTIATED FROM THE LOWER.

OUTER EPIDERMIS OF EMBRYO, SCARCELY DISTINCT (MERELY SMALLER & ROUNDER) FROM THE CELLS BELOW.

EMBRYO, #3. PROTOPLASM USUALLY BROWN, CONGEALED. NUCLEI OFTEN VISIBLE. WALL THICKNESS & CELL SIZE INCREASES TOWARDS #2. SCLEREIDS IN SMALL NUMBERS SCATTERED THINLY THROUGHOUT THE ZONE.

IDIOBLAST WITH TANNINIFEROUS GLOBULES

#2 SCLEREIDS IN CLUSTERS OF 10-20 AT JUNCTION OF #3 & #1, OFTEN SO DENSE AS TO FORM A ± CONTINUOUS BAND, PITS ANASTOMOSING.
TRAPEZOID CRYSTAL CELLS OFTEN ACCOMPANY AS IDIOBLASTS

#2

#1 INNERMOST REGION OF EMBRYO. CELLS SLIGHTLY LARGER, WITH THICKER WALLS, COLLENCHYMATOUS THICKENINGS. CONTENTS PALE & FINELY GRANULAR, OIL GLOBULES FREQUENT.

#1

OCCASIONAL IDIOBLASTS

(B)

18 µm

GROSS MORPHOLOGY

Seeds three, not orange-segment-shaped, but ellipsoid. In plan view, very broadly elliptic (sub-circular), in side views more narrowly elliptic. Max. length 45-55mm. Axis length 23mm, breadth 33mm of a small seed. Hilum large, covering 2/5-1/2 of the surface area of the seed usually, but sometimes more. The chalaza usually of about the same extent, but always slightly larger. The outer fleshy layer of the latter is continuous with the testa, the mesophyll of which is also fleshy except for the distal 3-10mm which is only about 5 cells thick and extends as a thin sometimes translucent pellicle to within 4-12 mm of the micropyle before terminating. No significant aperture exists in the exotegmen at the micropyle.

ANATOMY

INTEGUMENTS

Testa. Cuticle: usually thin, 1-1.5um. 4um thick over the proximal part of the outer epidermis as an aberration.

O.E.:a single layer of prostrate rectangular cells, o.p.w. 3(-4)um, i.p.w. thinner, c.2um, anticlinals very thin, 0.75um, often buckled. Height: 15-20um, width: 40-160um. Walls brown, contents absent. In this collection, this layer often damaged and discoloured.

Mesophyll: 45-55 cells thick, tapering somewhat abruptly at intervals to 5 cells thick in the distal 3-10mm of the testa. Cells extended polygonal to (at the periphery) isodiametric. 63um in length, 39um broad. Smaller cells with large trapezoid crystals common as idioblasts in some sections, but not all. Lacunae frequent except in the extreme of the distal portion where absent.(240-)320(-400um).

I.E.: more or less identical to the O.E., excepting the thinner o.p.w., lowered incidence of anticlinal buckling and better preservation.

Tegmen.

Cuticle: well developed but very irregular over the exposed portion, often forming beads. Frequently 2.5um thick.

Exotegmen:one(to two) cells thick, of prostrate, thick walled, fibroid cells. Height 21um, width 275um, wall thickness 3(-4)um. Usually square in transverse section, and often with square end walls. Walls very distinctive since conspicuously pitted and lustrous white in colour although occasionally stained pale brown. Lumina colourless.

Endotegmen: 9-12 cells thick, of prostrate, tanniniferous, rounded, extended polygonal cells. Height (15-)21.5(-39um), width (55-)80(-100um), walls yellowish brown, 2um thick. Some cells lacking tannin, and with colourless lumina. These occasionally in large groups, especially where the testa is fleshy. Heavily vascularized, especially in the lower layers.

Chalaza

Cuticle: usually thin, c.1um, but towards the junction with the endocarp, at the hilum edge, may increase to 32um (aberration?).

Outer chalaza: practically identical and continuous with the fleshy testa. The outer epidermal cells on average wider, the mesophyll deeper (c.55-70 cells thick).

Middle chalaza: usually 15-20 cells thick, prostrate almost brick like cells with colourless lumina. Width (47-)62(-90um), height

(14-)15.5(-17.5um). Walls 0.8um thick. Often invaded by horizontal and very thick vascular bundles.

Lower chalaza: cells continuous with the endotegmen of the integuments, and only slightly modified: lumina usually lacking tannin and colourless, dimensions slightly larger in width and height. This layer also is invaded by the vascular bundles. Usually 5-20 cells thick.

TRANSITION ZONE

The change in the tissues between integuments and chalaza is relatively small. Where the integuments fuse with the chalaza, the most noticeable feature is the abrupt termination of the exotegmen. It may proliferate for a little way into the chalaza, but this is abnormal. As noted under the heading 'chalaza', the testa is altered remarkably little. The endotegmen tends to become thicker and colourless, the upper part, perhaps due to compression, becoming more angular and regular, to form an interstitium (referred to above as the 'middle chalaza'.)

SUB-SEED-COAT

Endosperm

The (putative) endosperm is both well developed and distinctive. It is between 3 and 6 layers thick. The upper part is usually differentiated as a single layer of small (5-6um in diameter), comparatively thick walled (c.1um) cuboidal cells.

The middle part is of two to four layers of thin walled, prostrate, extended-quadrangular cells. These usually give the appearance of being derived from a common initial layer, since their anticlinal walls coincide. They are thin-walled with colourless contents, about 12um wide

and 6um tall. Often, one of the middle of these layers is tanninized. Such cells are usually taller, 8(-12um) and slightly wider, on average 16um.

The innermost part is a less well-defined layer of 0-3(-4) cells thickness of radially compressed quadrangular cells. The cell shape often greatly distorted by compression,but, where discernible with fairly thick, colurless walls and dark, dense cytoplasm.

Variation in the endosperm is marked. The upper layer seems most strongly differentiated from the middle at the equatorial zone of the seed (taking the micropyle and centre of hilum as poles) and is especially developed at the transition zone. However, under the majority of the chalazal region, it is not well defined. Conversely, the lower part does not occur beneath the chalaza and not, or at least only fragmentarily, under the integuments.

The degree of tanninization also varies. In some areas of the seed a well defined layer of the seeds is coloured by their tanniniferous contents. In other areas, the colour may be only intermittent, or even absent, and only the thin walls, rectangular shape and multiseriate nature of this layer serve to differentiate it from the embryo below.

EMBRYO

#3 of 9-12 layers. Cell shape slightly extended polygonal. c.20um wide, c.24um tall. Walls 0.7um thick in average, becoming noticeably thicker toward the inside of the zone. Protoplasm dense, usually appears congealed in centre of lumen together with the large nucleus. Cells with similar dimensions and large numbers of tanniniferous globules occur as idioblasts. The outer epidermal cells are smallest, and approach the isodiametric, but otherwise are are not, under the integuments, markedly different from the cotyledon cells beneath. Under the

larger portion of the chalaza however, these cells are more differentiated, being shortly columnar, with conspicuous protoplasts and nuclei, and thick yellowish walls.

#2. The sclereids nearly all in clusters of 10-20 cells situated at junction between #1 and #3, with cells of #3 between the clusters. Very often, the clusters are so frequent here that they coalesce and form an almost continuous band, though of very irregular thickness. A few smaller clusters or single sclereids occur in the middle of #3 and even up to within 4 cells (though usually rather more) of the other epidermal layer.

Isodiametric idioblasts containing large trapezoid crystals are closely associated with the sclereid clusters. Frequently 2 or 3 occur on their outer edge. Very rarely, these crystal cells congregate in groups in zone #3.

#1 Cells slightly extended-polygonal, tightly packed with few air spaces. Cells larger than those of #3, on average 36um long and 30um broad. Walls thicker than the average of #3, about 2um, with noticeable corner thickenings. Protoplasm markedly different, being pale and finely granular, occasionally with denser areas in the centre of the lumen, and quite often with lipid globules of of varying sizes. Idioblasts, especially trapezoid and druse crystal cells are sometimes found in this zone, especially the outer part.

INFRA-SPECIFIC VARIATION

C.cumingianus (C.DC.) Harms

This description based on T.D.P. 8084

Collector's notes:'Seed dark brown and shining, surrounded by a yellow(immature) aril'.

GROSS MORPHOLOGY

Seed in fragments (one fruit) so measurements difficult. Those made, and the distribution of the superficial tissues, match the ranges given in the description of T.D.P. 8052, excepting in the greater amplitude of the micropylar pore (not developed in the other) through which the embryo protrudes visibly and in the raised nature of the exotegmen where it occurs at the surface.

ANATOMY (Cursory description)

Testa (measurements from extreme distal portion)

Cuticle: to 1.5um.

O.E.: a single layer of tangentially extended quadrangular cells, 8um high and 21um (16-31um) wide, o.p.w. thickest.

Mesophyll: 5 (transparent distal flange) to 21 (fleshy portion) cells thick, the latter with lacunae to 280um. The cells ± isodiametric with brown living protoplast, 22um in diameter. Dimensions uniform.

I.E.: similar to O.E.

Tegmen

Cuticle: on the exposed portion to 4um. Beaded and uneven.

Exotegmen: 1(-2) cells thick, the cells 21um high and 290um wide. End walls oblique. Walls (and contents) amber yellow, 3um thick. Pitting very distinctive, the pits elongated consistently. 4um long and 0.75um wide.

Endotegmen: 12-15 cells thick, the upper 2-4 cells partly tanninized, the lower not at all. 22um (rarely 14um to 30um) tall and 63um (28-100um) wide. The cells prostrate rounded rectangular in shape. Vascular bundles plentiful in the middle part. A few of the upper cells sometimes more angular and elongated in appearance (exotegmic characters).

Chalaza

Upper chalaza: 50-60 cells thick, the cells thin walled, ± isodiametric, 58um in diameter. Lumina filled with protoplasm and comparatively large numbers of lipid globules up to 10um and even 16um in diameter. Lacunae plentiful, elliptic, nearly always empty. 280(-490um) long.

Lower chalaza: 23 to 26 cells thick. The cells extended (tangentially) quadrangular, 22um tall (14um to 40um) and 77um wide. Lumina with contents sparse, so as to appear transparent. Heavily vascularized.

SUB-SEED-COAT

Endosperm

Fairly uniform in structure (so far as this can be seen) under both parts of the seed-coat. The outer part apparently a layer of heavily tanninized cells forming a brown layer 8um thick, the anticlinal walls difficult to determine, due to crushing.

The lower part of apparently thick-walled cells. The contents deep dense brown, the walls ± transparent. Height 5-16um, depending on extent of crushing; width 21um.

Whilst the upper part is usually continuous, the lower is interrupted.

Embryo

#3. The epidermal layer under the integuments merely of slightly smaller, more isodiametric cells than the underlying cortex, but, under the chalaza, strongly differentiated from the cortex, the cells cuboidal to extended (tangentially) polygonal. 15um tall and 19um wide. The contents densely granular with dark contents.

The cortex proper 8-12 cells thick over the sclereids, deeper between. The shortly extended polygonal cells 45um broad and 62um long. Walls irregularly thickened, to 1.5um, thickest in the lowest part.

#2. Sclereids in clusters (but a few idioblasts seen) of about 5 cells in diameter, i.e. 15 to 25 cells per cluster. The sclereids radially extended, 74um tall and 57um broad. The walls 8um thick with ramiform pitting. Trapezoid-crystal cells found in association with about 40% of clusters.

#1. The cells large, extended polygonal, 68um long and 50um broad. The walls thick, 1.5-2um and corners often collenchymatous, the thickening 7um (to 10um) in diam.

The contents pale, finely granular, sometimes agglutinated. Without the nuclei seen in #1.

C.ceramicus(Miq.)C.DC.

This description based on T.D.P. 7917

Collector's notes:'..two large yellow seeds'.

Stevens.(1975): 'seed with a sarcotesta perforated by a small hole on the outside; cotyledons collateral'.

Corner (1976): 'C. sandoricocarpus K.et V. <A synonym of C. ceramicus(Miq.) C.D.C.> (Java,Koorders 28607; Herb. Bogor., fruits in alcohol.) Fig. 383.

PLATE 82

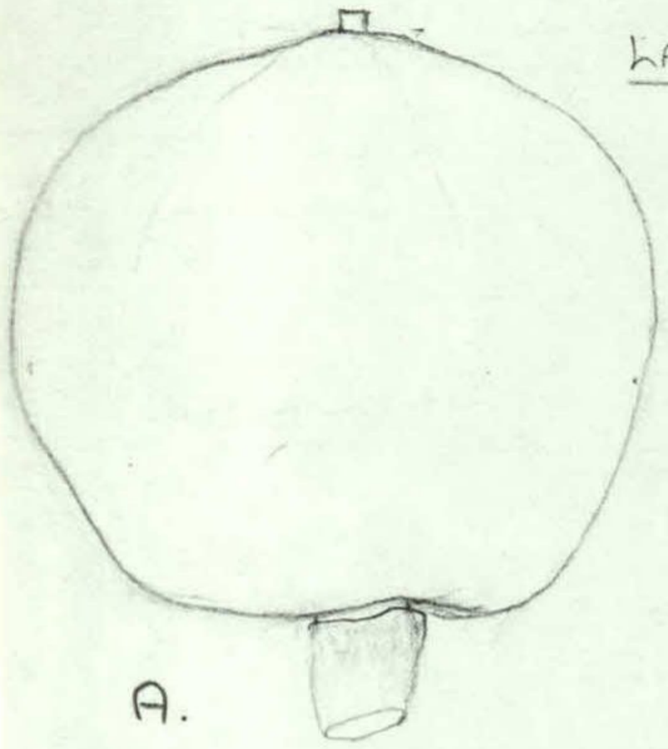
CHISOCHETON CERAMICUS

A-H FRUITS AND SEEDS. NOTE THAT SEEDS ARE SARCOTESTAL.

C. CERAMICUS 7917

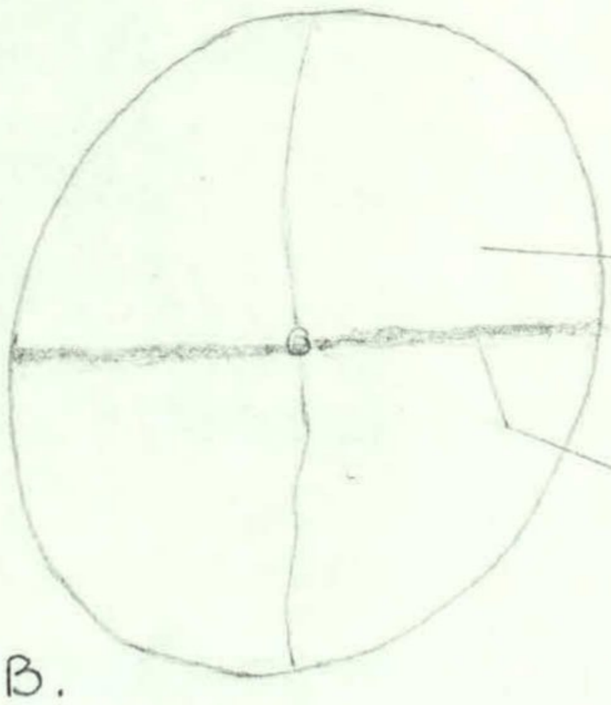


# GROSS MORPHOLOGY - FRUITS & SEEDS



A.

LATERAL VIEW

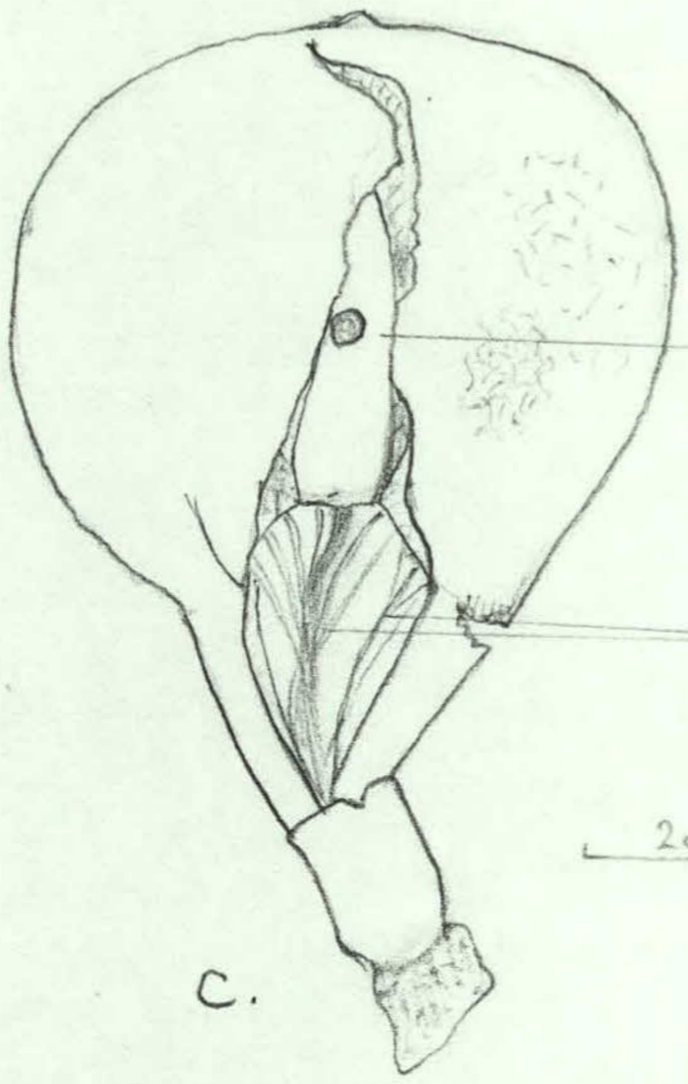


B.

PLAN VIEW

SURFACE SMOOTH MAINLY (THESE EASILY REMOVED EASILY BY ABRASION).

SUTURE LINE OF DEHISCENCE



C.

LATERAL VIEW - DEHISCENCE

SEED: MICROPYLE EXPOSED

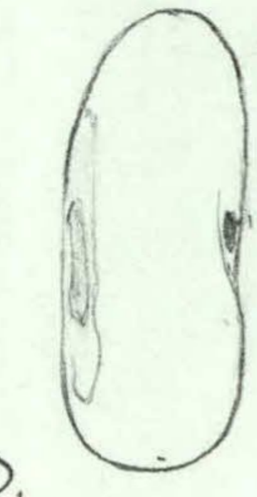
VASCULAR SUPPLY

2cm

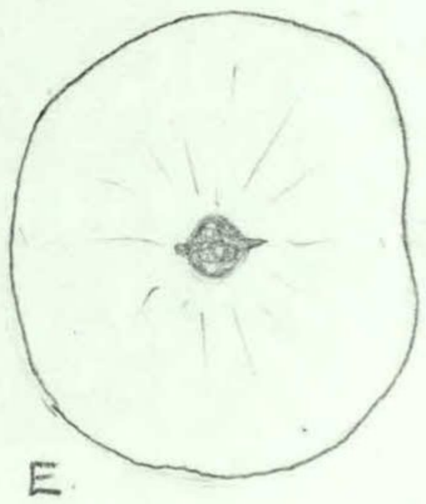
SEEDS: LATERAL VIEW

DISTAL PLAN VIEW, VARIATION IN TESTA AT MICROPYLE

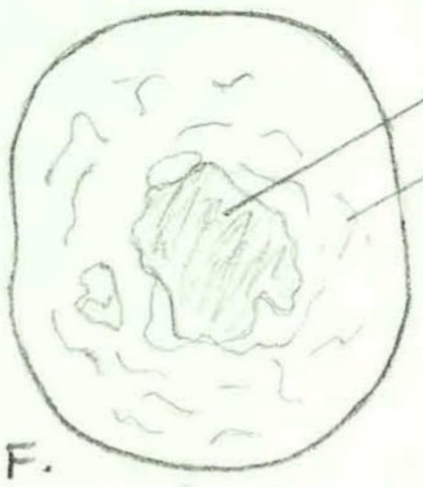
PROXIMAL PLAN VIEW



D.



E.



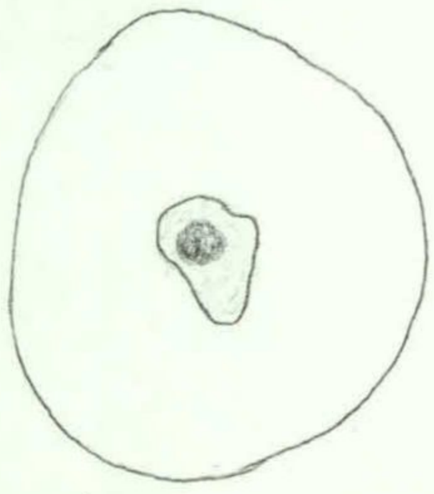
F.

CIRCULAR HILUM

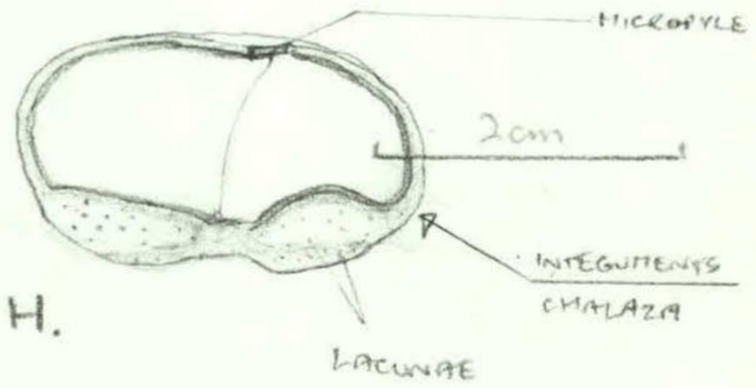
WRINKLES IN CHALAZA

MEDIAN SECTION

2cm



G.



H.

MICROPYLE

2cm

INTEGUMENTS

CHALAZA

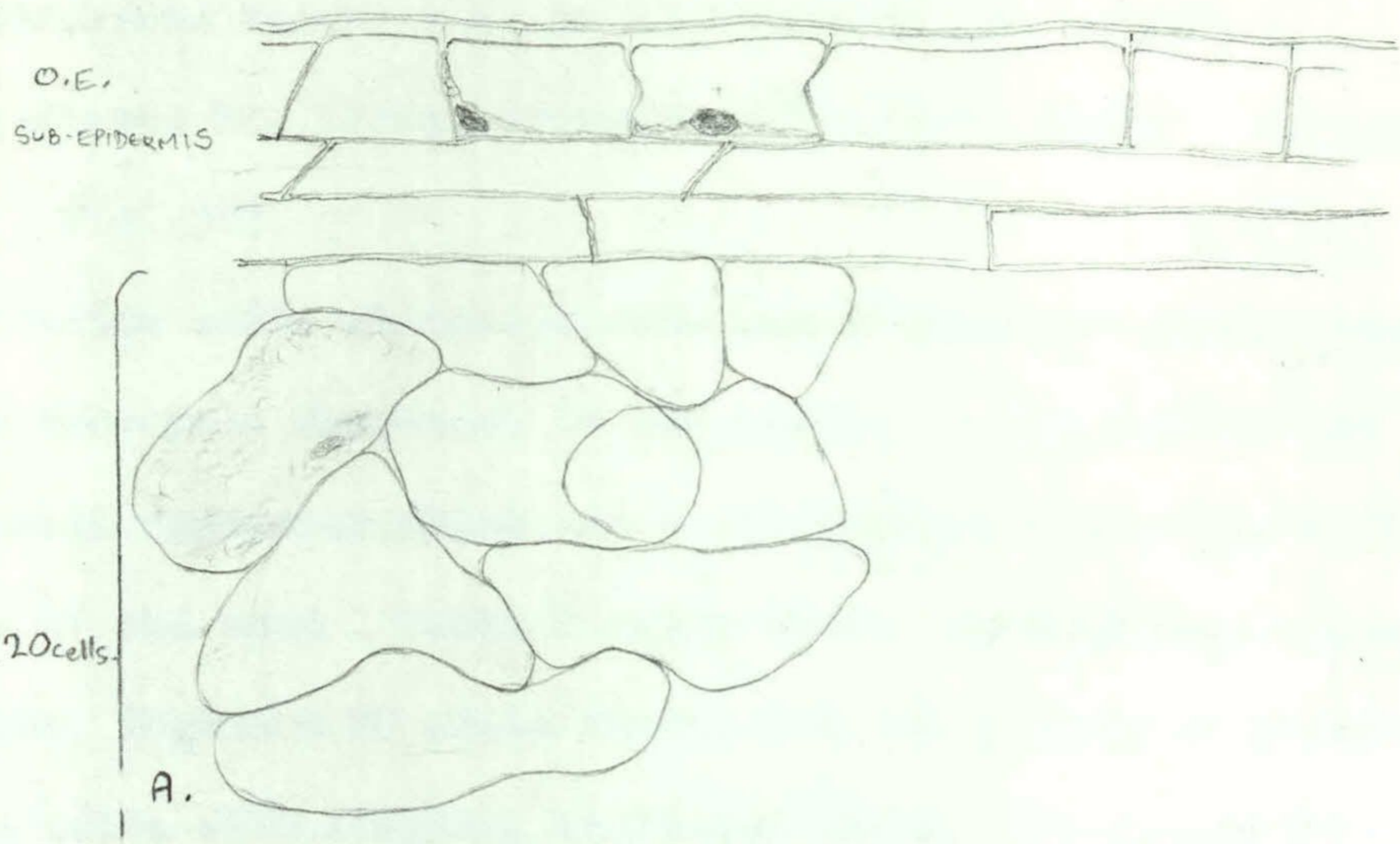
LACUNAE

PLATE 83

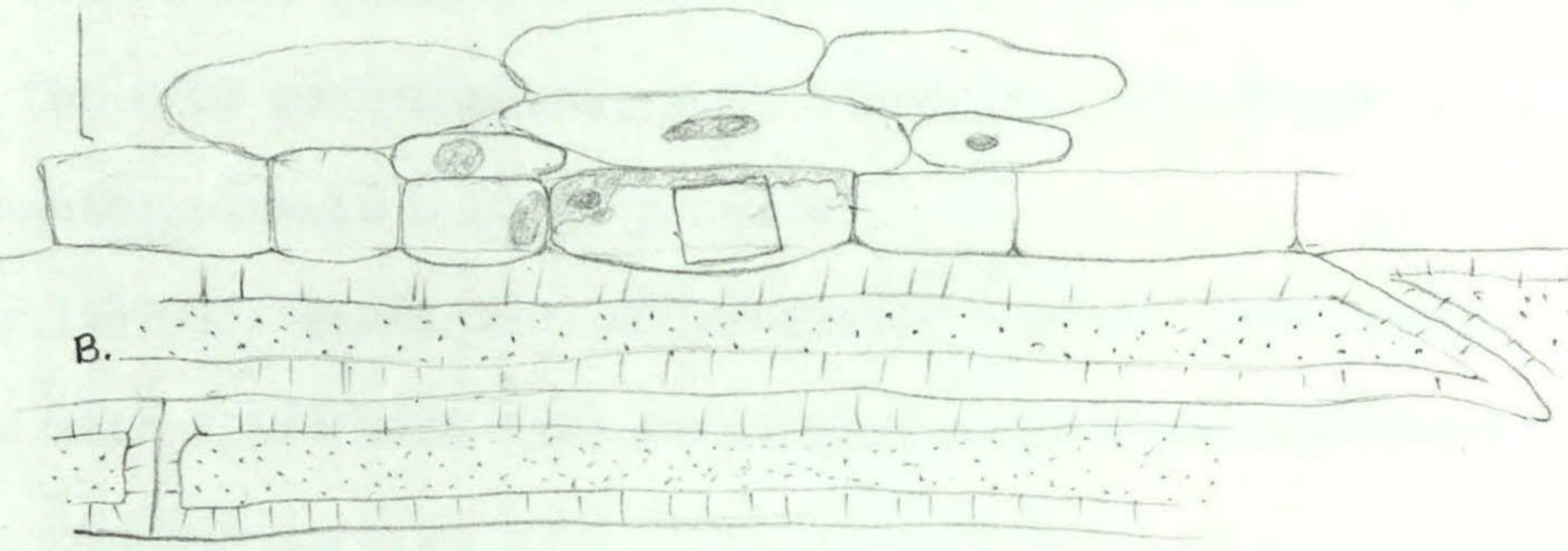
CHISOCHETON CERAMICUS

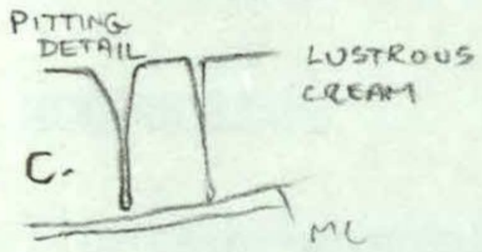
A-C SEED-COAT ANATOMY. NOTE TESTAL O.E. HYPODERMIS,
VERY THICK (MANY CELL LAYERS) TESTAL
MESOPHYLL, I.E. WITH CRYSTALS & UNITED TO TEGMEN.
TEGMEN WITH TEN LAYERS OF FIBRES.

TESTA. UPPER PART. L.S.

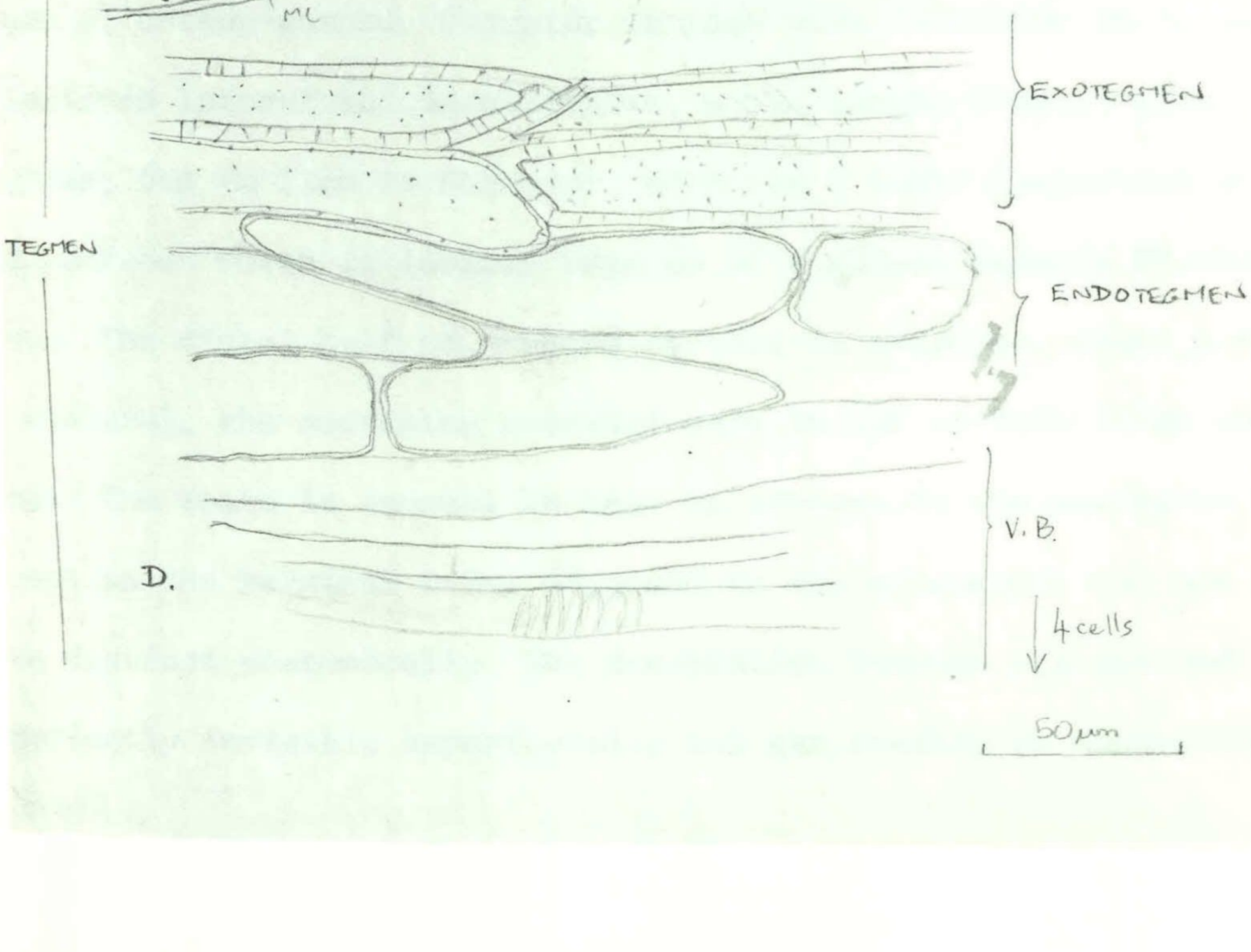



LOWER TESTA & UPPER EXOTEGMEN L.S.




LOWER EXOTEGMEN X UPPER ENDOTEGMEN



Seeds as in C. divergens <A synonym of C. patens Blume; E.J.H.C description below> but subglobose with less dilated chalaza, exarillate. Testa and tegmen thick; v.b. as a network in the tegmen.

C .divergens Bl. (Java, Koorders 4885; Herb. Bogor., mature fruits in alcohol.) Fig. 383.

Seeds 12-15mm wide, ellipsoid-compressed, blackish brown, orthotropous with the micropyle depressed in the middle of the convex free surface;aril funicular,thick, as a red cushion with a short flange round the base of the seed . Testa 2 cells thick, thin-walled, unspecialized, pellicular. Tegmen c.20 cells thick; O.E. as a layer of longitudinally elongate cells with slightly thickened walls, not or scarcely lignified, not truly fibriform; mesophyll thin-walled, pervaded with a network of v.b. from the wide pachychalaza; I.E. unspecialized. Embryo straight; radicle minute; plumule with long hairs'.

Mabberley (1979): 'seeds 1-2, shining pale orange , sarcotesta perforated with 1.5mm hole near micropyle; cotyledons collateral'.

GROSS MORPHOLOGY

Seeds 2, button-shaped. Circular in plan view (diameter 25-35 mm), elliptic in lateral and dorsal views, axial length 10mm to 15mm. Hilum circular, 6mm to 11mm in diameter, covering a small proportion of the seed surface which is largely made up of a glossy expanse of fleshy tissue. The distal half to a third of this is thickest, about 3-4mm deep and chalazal, the remaining proximal part is 1mm or less thick and testal. The testa is unusual in that it adheres to the exotegmen below (except in the terminal 1-2mm adjacent to the micropyle) but the two are quite distinct anatomically. The demarcation between chalaza and testa is perfectly invisible superficially but can readily be identified by

peeling back the testa from the micropyle towards the hilum. At the transition zone, the tissue ceases to peel smoothly, and tears instead, exposing a layer of torn cells. If these are scraped away, the vascular bundles which run longitudinally throughout the middle chalaza are visible (to the naked eye) entering the indurate lower chalaza which other wise superficially resembles (and might be confused with) the exotegmen. The micropylar pore is c. 2mm in diameter. The testa does not always extend to it, but may terminate up to 5mm away.

ANATOMY

TESTA

Cuticle: 0.5-0.75um, evenly distributed.

O.E.: one(-three?) cell layers deep. The outermost sharply cuboidal to tangentially extended, quadrangular in section. In paradermal section five or six sided, isodiametric sometimes slightly extended polygonal. 14-20um tall, 24um to 28um (rarely to 40um) wide.

O.p.w.:3um thick, anticlinals 1um, sometimes very slightly buckled. Protoplasmic contents very sparse, usually restricted to one edge with the large nucleus. The lumen otherwise quite transparent.

A hypodermis two cells thick appears in the distal parts of the testa but is apparently absent from other regions. It is not highly differentiated from the mesophyll and may be an artefact of compression. Where it does appear, its cells are quite highly tangentially extended quadrangular, 6-10um high and 20-40um wide. The walls are c.1um thick and protoplasmic contents are brown, minimal.

Mesophyll: 15-20 cells thick. Relatively uniform in thickness, even to the terminus at the distal end of the seed. Near the transition zone, the layer increases to c.25 cells thickness and lacunae (not otherwise detected in the testa) appear. The cells are large, extended polygonal, 29um broad, 40um long (those toward the margin tending to be more isodiametric and slightly smaller) The walls thin (1um),the contents grey and coarsely granular, not very dense, with large nuclei. Druse and trapezoid crystals occur singly in sparse idioblasts.

I.E. a single layer (no hypodermis detected) of cells of similar dimensions to the O.E.: 15-18um tall, 20-50um wide, protoplasmic contents brown, nuclei large , distinct from the O.E. in the higher frequency of large trapezoid crystals (which seem characteristic) and the o.p.w., which are often bowed outside and mostly fused with the wall of the exotegmen. However, the two tissues never intermingle and indeed, the testa can be peeled from the tegmen without tearing any cells: the two are quite distinct.

TEGMEN

Exotegmen: 9-12 cells thick, the fibroid cells with thick (5um), lustrous, cream walls, frequently pitted. The lumina colourless or slightly yellow. Near the micropyle the contents, especially of the outer cells, become deep brown. Around the micropyle, cell orientation alters from longitudinal to latitudinal.Cells 70-200um (-400um) wide, 20um to 25um tall.

Endotegmen: 4-6 cells thick. The cells prostrate , but not tanniniferous, otherwise as normal endotegmic cells: rounded and with vascular bundles pervading. Some of the cells nearest the exotegmen are distinguished by weak pitting. Width: 30um-120um, Height 18-30um.

CHALAZA

Upper chalaza.

Cuticle: c.1um thick, even.

O.E. cells practically identical to those of the testa.

Cortex: up to 65 cells thick in the deepest part, 25 to 30 cells near the junction with the testa. Shape and character very similar to that of the testal mesophyll (thin-walled, extended polygonal cells etc.) but tending to be still larger, commonly 50um broad and 65um long. Lacunae, usually lacking cell contents, 240um long. Trapezoid crystals and druses occur singly in cells as idioblasts. Raphides were detected in one section, toward the hilum boundary.

Middle chalaza: up to 25 cells thickness the cells somewhat smaller than those of the upper chalaza , and more uniform in size and polarization: consistently tangentially extended quadrangular, 30um wide and 19um tall. Walls 1um thick, protoplasmic contents very sparse, though a nucleus often discernible. Longitudinal vascular bundles frequent in this layer.

Lower chalaza: 25-50 cells thick (tending to increase in thickness toward the proximal part). The cells, though tangentially extended polygonal are unusual in lacking tannin and most notable for their comparatively thick and pitted walls. Whilst their shape is often rounded, in some parts , where packing is close the cells are distinctly angular and resemble those of the exotegmen. However, they are easily distinguished by their shorter width and consistently thinner walls. Cells 50-70um wide , 20-26um tall, and walls 2.5um thick. Protoplasmic contents are detectable in most cells.

TRANSITION ZONE

The transition from testa to chalaza is marked by relatively little anatomical change. The epidermis is virtually unaltered, whilst the mesophyll becomes progressively thicker, with more lacunae. The epidermis is virtually unaltered, whilst the mesophyll becomes progressively thicker, with more lacunae. The most significant change is the loss of the highly characteristic crystalline endotestal epidermis.

Changes in the tegmen are, in contrast, marked. At the point of transition, the outer exotegmic cell layers cease. The lower ones, at first sight, seem to continue and even proliferate from 12 cells thick (tegmen) to 25 cells thick (chalaza). Closer examination reveals that the inner exotegmic together with the endotegmic cells are actually metamorphosed into a different cell type: less extended, and with thinner walls and, and more protoplasmic contents than exotegmic cells . This is an unusual state of affairs since, usually, the lower chalaza, which these cells compose , is tanniniferous and without pitted cells. However, the lower chalaza often seems to have an affinity with the endotegmen and in this species ,this too is without tannin and near the exotegmen, pitted. The connection between cells of the middle chalaza with the testa is not really apparent.

SUB-SEED-COAT

?Endosperm. Between the tegmen and embryo, a variety of structures occur which here will be treated as three layers; the first occurs below the integuments and is particularly well developed at the distal end. It appears to consist of an upper part of one to two cells thickness of angular, cuboidal cells 10-14um in diameter with thick (2um) red walls

and clear lumina. The lower part is of columnar to cuboidal cells , 10um tall and 6-10um wide, which are deep red in colour (walls and contents together). Much irregularity occurs.

The second ( Description of the second layer is based on tissue from collection D.J.M. 1720. This is more immature, therefore less decomposed and has better sectioning characteristics.) is also best seen below the integuments where it reaches 230um in thickness. It is composed largely of a single chain of large 'lacunae' cells with cell contents usually present, similar to those of the outer chalaza .The ?endospermal lacunae are large, usually elliptic, non-polarized and 220um long, 160um broad. They are surrounded by a matrix of thin-walled cells with dense grey granular contents, 16um in diameter where isodiametric. However, the shape rather variable. Around the margins of the lacunae, the cells highly elongated. The proportion of volume of matrix cells to volume of lacunae is low . The matrix between, above and below the matrix may be composed of as little as two cells thickness. Below the chalaza, this layer appears to be crushed, the lacunae lost though the matrix cells remain intact, if disorganized. The layer here is a mere 34um thick.

The third layer was not detected below the integuments, and only seen below the chalaza. The uppermost part a distinct yellowish layer 20-30um thick, possibly derived from crushed cell walls. Below it occur, in pockets of isolated individuals or small clusters, cells of irregular, but approximately isodiametric shape, 12um in diameter with thick, almost translucent walls and dense brown protoplasmic contents.

Embryo. The epidermal cells are quite distinct from those of the cortex below, being isodiametric or tangentially extended, with dense brown protoplasmic contents and nuclei partly filling the lumina. Cells 10um tall and 10-20um(-35um) wide . Walls 1um thick. Stomata occasionally

detected. Under part of the chalaza, especially near the hilum, the epidermal cells become columnar, with contents granular. The layer of cells (about two cells deep) below the epidermis are intermediate between the main cortical cells below and the epidermis. They are 14-24um(-35um) tall and 24um wide. Their contents largely consist of large numbers of small granules.

Cells of the main cortex are extended polygonal, usually rounded and non-polarized, but much larger, 60um long and 50um broad (walls 1um) with little variation. They are packed solid with granules, though these are much larger (each up to 14um) and of distinctive character, being translucent, (ellipsoid) or 3 lobed round bodies, with divisions between the lobes.

INFRA-SPECIFIC VARIATION

Collection T.D.P. 7917 was made in the Sepilok forest reserve near Sandakan (former B.N.B.) . To investigate the extent of variation in the species, another collection, D.J.M. 1720, derived from Morobe Dist. (Papua New Guinea) was also anatomically investigated. Unfortunately the seeds were immature to an extent, a fact evident from the smaller size and lack of dehiscence in the fruits and anatomically in the reduced wall thickenings and presence of smaller, denser proto-lacunae. Proportions of cells and thicknesses of tissues however, compared well with those seen in collection 7917. For example, the mean exotegmen thickness was 10 cells (within the range described for collection 7917), the endotestal epidermis was crystalline. The only difference of any significance was seen in the testal O.E., the cells here more strictly cuboidal in L.S.; on average 16um long and 15um wide.

C.longistipitatus (F.M.Bailey) L.S.Smith

This description based on T.D.P.8077

Collector's notes: 'inside of pericarp a soft spongy mass with one or more seeds embedded in it. No white sap'.

Stevens (1975): 'Fruit ± spherical, 3-3.5cm long, stipe 1-2cm, hairs of one length; pericarp spongy. Seed with a sarcotesta perforated by a hole in the middle of the outer surface; cotyledons collateral'.

Mabberley (1979): 'Seeds 3, sarcotestal, with hole at the micropyle, cotyledons collateral'.

GROSS MORPHOLOGY.

Fruits to 26um long (incl. stipe) thus probably immature. Seeds two, spherical, diameter to 11mm. Hilum small, circular, 3mm to 4.5mm. The surface of the seed entirely fleshy, the proximal third being the upper chalaza, the remainder the testa. The two fleshy parts are continuous, and not distinguishable by superficial observation. However, if the testa is pulled back from the micropyle towards the hilum, the point at which it ceases to peel,but tears, can be shown to be the transition zone. At the distal end of the seed, both integuments form the wall of a small micropylar pore.

ANATOMY(Immature material)

TESTA

Cuticle: 0.5um thick, even.

O.E.: a single layer of tangentially extended rectangular cells, 10.5um tall and 23um (less usually to 40um) wide. The o.p.w. thickest, 2um thick.

Protoplasmic contents very sparse and translucent.

Mesophyll: 10-12 cells thick (110-120um) thick, without lacunae in the distal part, but gradually increasing to 20 cells, near the transition zone, and with lacunae in at least the proximal third. The cells with plentiful brown protoplasmic contents (mostly tangentially) polygonal, 33um long and 16um broad.

Druse idioblasts frequent in the middle part, the clusters large up to 24um.

I.E.: a single layer of cells which, beyond being rectangular in L.S., are not otherwise differentiated from the mesophyll.

This integument, apart from the 1-2mm around the micropyle, adheres (weakly) to the exotegmen.

TEGMEN

Exotegmen: 5-12 cells thick. In the micropylar portion packed tightly and forming a brown layer 20um thick. An isolated fibre being 4um tall and 35um long. Toward the transition zone, development is more advanced, the cells are 14um tall and 40-70um in width, the end walls normal, the contents a slightly reddish brown. No pitting detected.

Endotegmen: very sparse, often just isolated cells, and these often not clearly distinguishable from vascular support. Usually prostrate rounded rectangular, without tannin, 18um tall and 37um wide (narrow sample base). Sometimes with druses.

Chalaza

Upper chalaza: cuticle 0.5um, even.

Epidermal layer one cell thick, the cells almost cuboidal in L.S., 19.5um tall and 20um wide, the o.p.w. thickest, 2-3um. The protoplasmic contents very pale, practically translucent.

Cortex below 20-35 cells thick. Forming a layer 720um thick. Thickness comparatively uniform around the seed. Lacunae plentiful, 185um long, tending to be circular in the lower chalaza. The cells tightly packed, elongated, polygonal, with dense protoplamic contents, mostly contracted. No evidence of lipid globules. The cells predominantly tangentially extended, 46um long and 27um broad. A few druse idioblasts in the lowermost portion.

The lower chalaza not well demarcated from the upper, about half the thickness; 410-450um, with vascular bundles quite frequent. The cells extended quadrangular with nuclei and protoplasmic contents of little diversity. Not tanniniferous. The cells 11um tall and 28um wide. Druse idioblasts, the crystals 16um in diam. are frequently found. More rarely, trapezoid-crystal cells also occur.

SUB-SEED-COAT

Endosperm: forms a thick and distinctive layer, 255-310um thick. The major part occupied by a single chain of large spherical lacunae, 95-100um in diam., still occupied by densely granular cell contents. The lacunae are embedded in a matrix of extended polygonal cells with fairly granular contents, large nuclei and thin walls, 20um long and 12um broad. This layer extends uninterrupted around the inner seed-coat apart from an area under the chalaza. Towards the micropyle, the layer

decreases to 120um in thickness, the lacunae are also smaller, (40-)65(-105um) in diam.

EMBRYO.

The outer 18-20 cells of small size, slightly extended polygonal in section, non-polarized, tightly packed, with thin walls, less than 0.5um and dense cytoplasmic contents. The longest dimension 9um, the cells uniform in size throughout.

The innermost cells are much larger, also extended polygonal and non-polarized. The contents are sparse and ± translucent.

C.pentandrus(Bl.)Merr. ssp.paucijugus(Miq.)Mabberley

This description based on T.D.P. 7865

Collector's notes: 'According to the guide, it (the fruit) splits at maturity. seed-coat whitish green.'

Stevens (1975) '...Fruits of C.pentandrus (i.e. Sub sp. pentandrus) are smaller, being less than 2cm in diameter'

Mabberley (1979)'...fruit to 21mm diameter...; seeds 2, flattened, to 1.5cm diameter, sarcotestal'.

GROSS MORPHOLOGY

Fruits to 30mm broad. Thus though fruit intact, seeds probably practically mature. Seeds: 2 (to 3) large and 2 (to 4) small. Seeds button-or lens-shaped, sometimes with lateral facets by mutual compression. Basically circular in plan view, distal surface convex, proximal surface planar. Maximum diameter to 34mm, axial length to

11mm. Hilum irregularly circular to elliptic, well defined. Maximum length to 20 mm, hilum covering one sixth to one seventh of the seed surface. Rest of seed surface shiny, with large veins plainly visible radiating and forking at and from hilum. Distal hemisphere almost always testal, integuments sometimes extending to outer rim of proximal hemisphere. Transition zone usually well defined, chalazal surface being duller in contrast. Testa not fleshy. Chalaza upper surface perhaps slightly fleshy. Micropylar pore often well developed sometimes in a slight depression, occasionally colpate. Testa often abbreviated, leaving a rounded or irregular aperture up to 3.5mm in diameter, micropyle then endostomal.

ANATOMY (Based largely on L.S.).

INTEGUMENTS

TESTA

Cuticle: to 1um thick, even, except near chalazal boundary where beaded, then to 10um.

O.E. One layer thick. Cells generally tangentially extended, quadrangular, significantly more so away from the chalaza where less radially crushed and organization more easily observed. 10-12-14um tall, but frequently 7um in main part of testa. 12-23-40um wide. Walls yellowish, o.p.w. 2um, remainder 1um. Sparse protoplasmic contents, colourless.

Mesophyll usually 0 to 1 cell thick but near transition zone increasing to 3 cells, where cells are 12um tall and 50um wide. In main part of testa, height is reduced (due to a greater radial compression, presumably) to as little as 4um, periclinal walls bowed outwards,

tending to alternate with epidermal cells. Contents sometimes yellowish in main part of testa, in contrast to epidermal cells above and below with colourless lumina.

I.E. very similar to O.E., but tends to be shorter in height and more tangentially extended.

TEGMEN

Exotegmen: 1(-2) cells thick, increasing to 3 cells at transition zone. 85um to 170um wide , 20um high. Walls 2um thick , walls and contents deep brown. Pitting scarce.

Endotegmen: 18 to 22 cells thick. Cells prostrate, rounded, rectangular, air spaces frequent, lumina colourless. Dimensions relatively constant. Width 93um , height 30um . Walls 1um thick. Protoplasmic contents present. Some cells showing presence of tannin occur irregularly in the middle part of the layer. Vascular bundles frequent.

CHALAZA

Outer chalaza : cuticle 0.5um (to 1um) thick.

Outer epidermis very similar to that of testa, but in as far as it extends, shorter and wider: 10um high and 56um wide. Cortex of 20 (near transition zone) to 9 cells (main part) thick. Cortex of 20 (near transition zone) to 9 cells (main part) thick. Cells prostrate, elliptic, often with short arms. Contents a pale brown protoplast.No lacunae seen. A few large oil droplets in most cells, up to 16um wide. Cells 42um high, 28um wide. Walls 0.75um .

Middle chalaza: 10 to 12 cells thick. Cells extended quadrangular with rounded angles and ± colourless contents. 24um tall and 70um wide.

Prismatic crystal cell idioblasts scattered thinly in this layer. Vascular bundles large and very frequent.

Lower chalaza: 8 cells thick. The cells with tannin so that layer appears black in macro-section. Cells prostrate, shortly elliptic 31um tall and 60um wide, walls thin, 0.75um.

TRANSITION ZONE

Somewhat unusually, there is no declivity in integument bedding plane at this point, and although the outer chalaza proliferates, no flap occurs. The O.E. testa is completely continuous with that of chalaza and very little modified (see chalaza). Testal mesophyll, which increases in thickness towards transition zone seems ± continuous with upper chalaza. I.E. testa and exotegmen cease abruptly, latter after increasing to 3 cells in thickness and becoming disorganized, some cells becoming latitudinally orientated. Endotegmen invades into chalaza to a small extent, before metamorphosing, whilst red brown tannin cells of lower chalaza invade tegmen to a variable extent, usually at least 200 to 300um tapering gradually to 2 cells in thickness, remaining inside endotegmen.

SUB-SEED-COAT

ENDOSPERM:

Usually restricted to a layer of crushed cells. One, sometimes two, cells thick. Tangentially elongate. Cell limits difficult to detect. occasionally, pockets of large colourless cells of 2 to 3 cells thickness and several hundred um length (especially prevalent near hilum) occur. These are tangentially extended, and somewhat less

crushed, 40um wide and 16um tall, walls extremely thin ( < 0.5mm), contents transparent.

EMBRYO

=3 Under integuments epidermal layer is one cell thick, cells isodiametric , cubic or slightly rounded. Protoplasmic contents fairly dense, but not granular. 12um in diameter.

Under most of chalaza, epidermal layer is thicker, about four cells thick, outermost cells smallest, cuboidal to tangentially extended, 11um tall and 16um wide, walls 1um thick with few airspaces. Outer two layers of cells with densely granular contents.

Cortex. 5 to 9 cells above sclereid clusters (deeper between), shallowest between cotyledons. Cells nearly all isodiametric, five (to 6)-angular, cells tightly packed with few airspaces, on average 42um in diameter, upper cells smallest (diameter 19um), lower larger (50um diameter). Walls 1um to 1.5um thick, brown. Protoplasmic contents sparse, lipid globules occuring regularly though sparsely, these large, but few per cell. A very few sclereids, apparently isolated occur in lower part, but are possibly connected with clusters.

#2.Sclereids in clusters of 18 to 23 cells, where these are isolated, but more often one or a short series coalescing with neighbours to form an intermittently continuous layer 3 to 4 cells thick. Component cells slightly radially extended, 55um tall and 42um wide. Walls 3um thick. Pits simple.

#1 Large isodiametric or extended polygonal cells, 70um in diameter or 40um broad and 160um long. The walls up to 1.5um thick, unevenly within a cell, but the corners not collenchymatous. The contents distinctive in

being packed with spherical or elliptic translucent lipid globules of all sizes up to 16um in length.

C.sarawakanus (C.DC.) Harms

This description based on T.D.P. 7882

Collector's notes: 'seed-coat dark shining brown, surrounded by a mealy white ?aril'.

Mabberley (1979): 'Seeds 2 with shiny dark brown testa, partly covered in aril'.

GROSS MORPHOLOGY

Seeds two to three per fruit, irregularly oblate-spheroidal. Sometimes with equatorial facets due to mutual compression of seeds in the fruit. Axial length of the seeds 17-26mm, breadth 27-32mm(to 22mm where faceted.). Hilum very large, usually covering 2/3 to 3/4 of the seed surface, this range found even within one fruit capsule (see Plate 84) The chalazal margin usually extends, irregularly, a little further than the hilum; usually for only 1-2mm (a maximum of 8mm) and sometimes not extending at all. The outer layer of the chalaza proper is entirely fleshy; the hilar portion matt (described as mealy by the collector) with vascular bundles often visible on the surface. The short and irregular extra-hilar rim is a glossy medium brown.

The dark brown integuments cover the remaining distal part of the seed. The thin pellicular testa does not extend entirely to the micropyle, but falls short by 1-5mm. The micropyle, a small pore filled by embryonic tissue, is situated at the flatter, sometimes depressed, distal pole of the seed.

PLATE 84

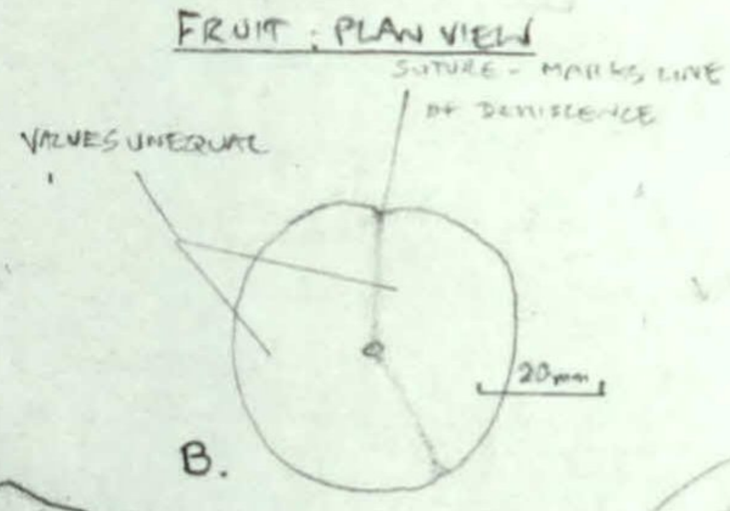
CHISOCHETON SARAWAKANUS

SEEDS: VARIATION IN SIZE OF HILUM AND FLESHY AREA.

C. SARAWAKANUS 7882

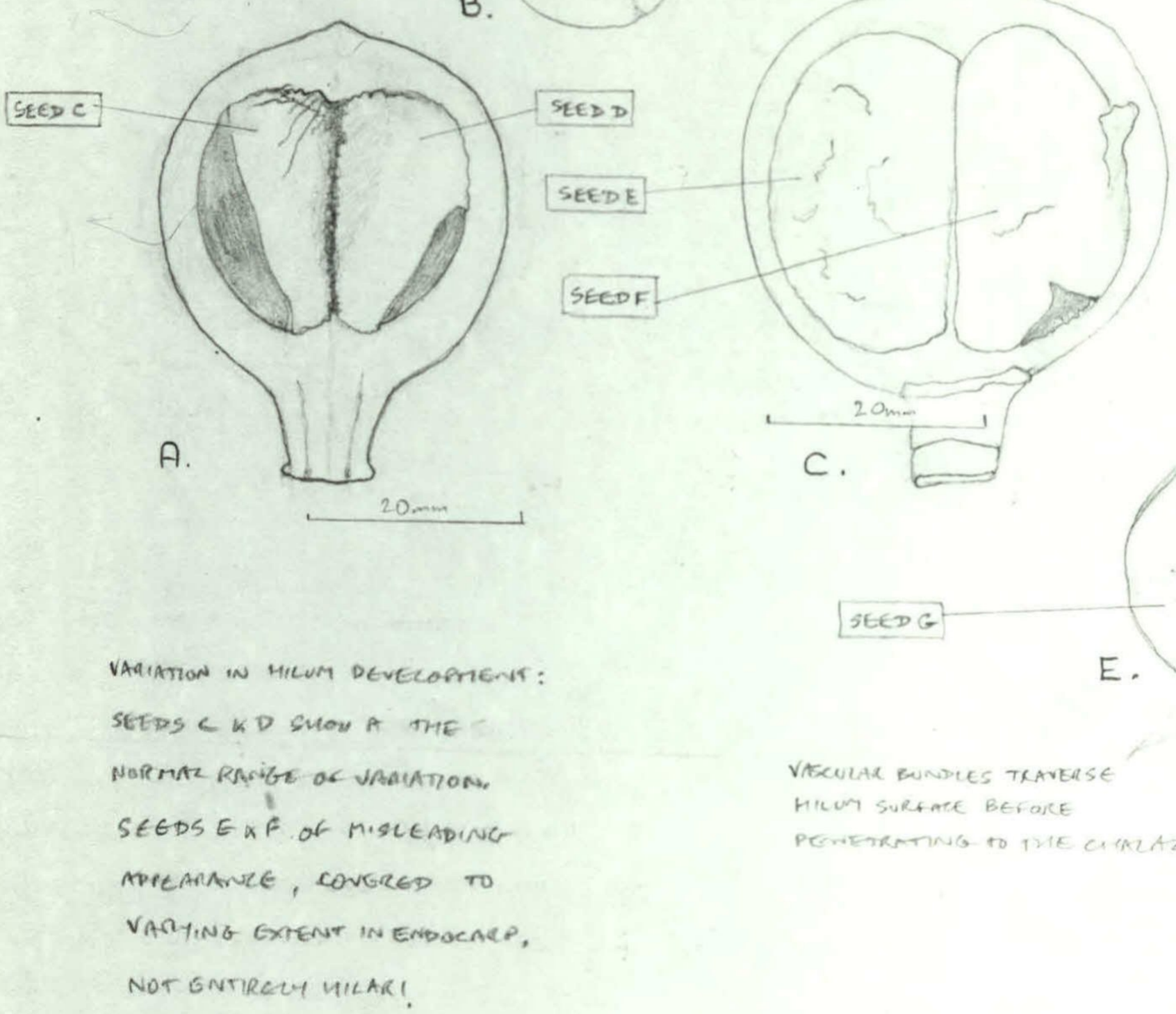
FRUITS & SEEDS - GROSS MORPHOLOGY (CONT.)

FRUIT : PLAN VIEW

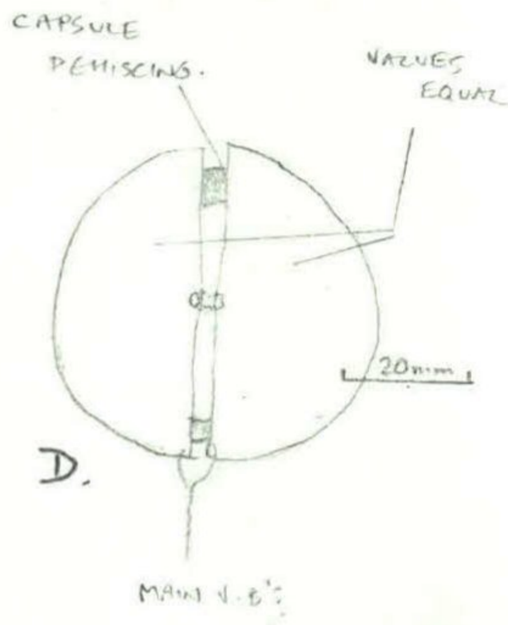



FRUIT & SEED
- VALVE REMOVED.

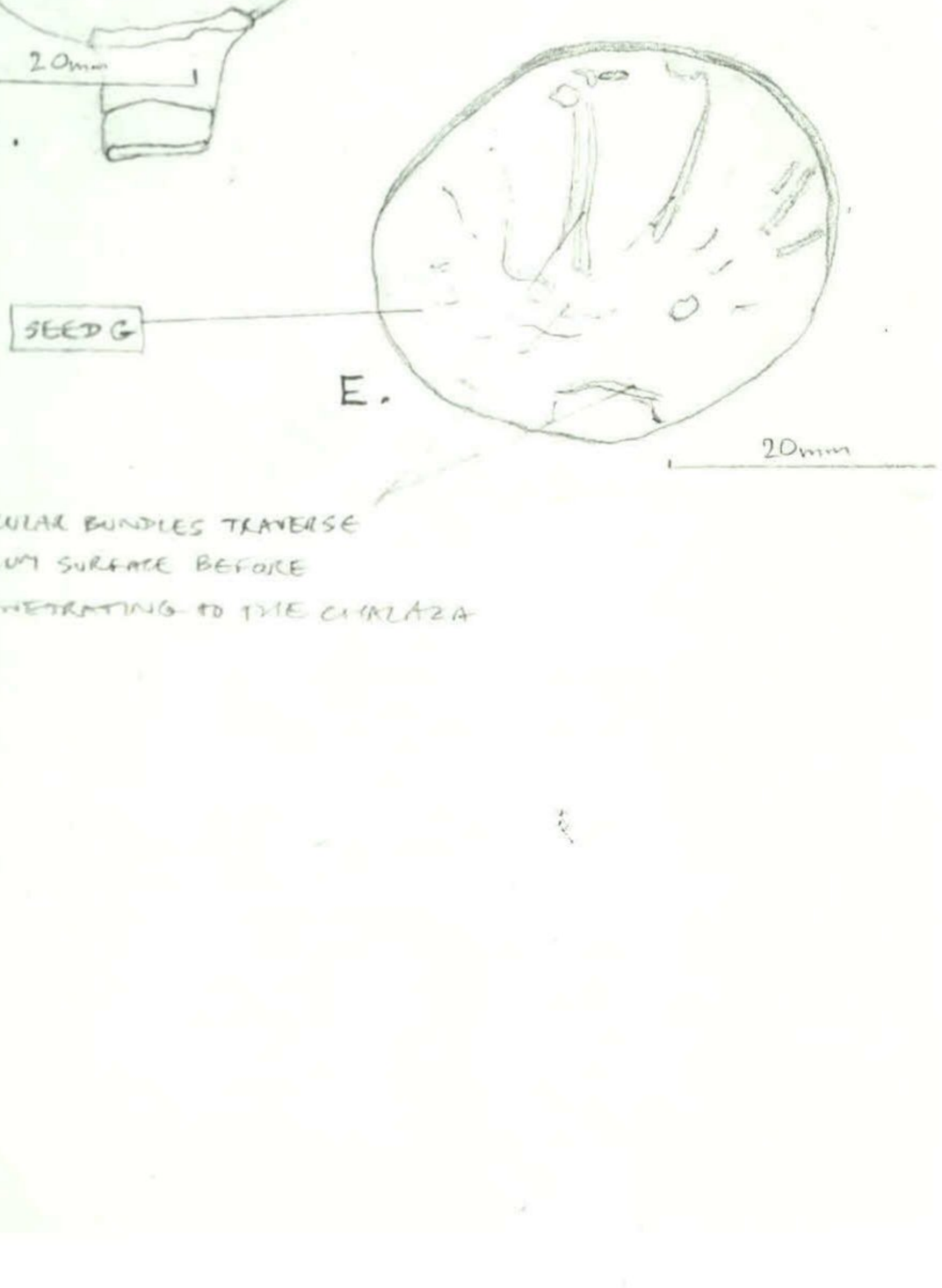
FRUIT & SEED
- VALVE REMOVED




FRUIT - PLAN VIEW




SEED - PROXIMAL PLAN VIEW




VARIATION IN HILUM DEVELOPMENT:
SEEDS C & D SHOW A THE NORMAL RANGE OF VARIATION.
SEEDS E & F OF MISLEADING APPEARANCE, CONFINED TO VARYING EXTENT IN ENDOCARP, NOT ENTIRELY HILAR!

VASCULAR BUNDLES TRAVERSE HILUM SURFACE BEFORE PENETRATING TO THE CHALAZA

PLATE 85

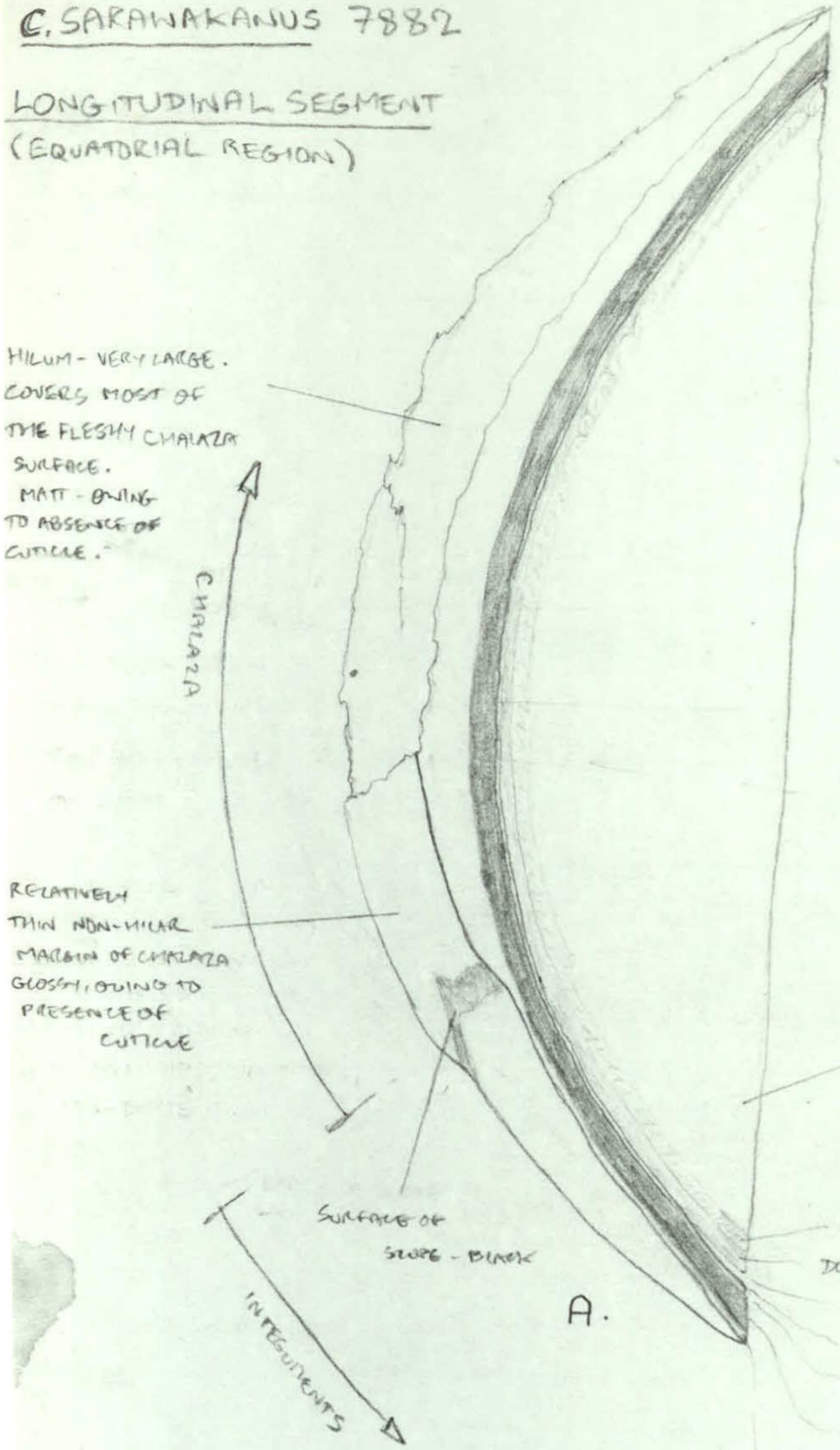
CHISOCHETON SARAWAKANUS

A TISSUE PLAN, SHOWING THE DISTRIBUTION & RELATIONSHIPS OF HILUM, CHALAZA, BITEGMIC PART OF SEED-COAT AND FLESHY TISSUE.

B-D SEEDS, SHOWING THE LARGE HILUM AND ENDOSTOMAL MICROPYLE.

C. SARAWAKANUS 7882

LONGITUDINAL SEGMENT
(EQUATORIAL REGION)




FRUITS & SEEDS - GROSS MORPHOLOGY

MICROPYLE - SITUATED IN DEPRESSION
RADICLE EMERGES THROUGH THE APERTURE.

PLAN VIEW

PROXIMAL/LATERAL VIEW

LATERAL VIEW

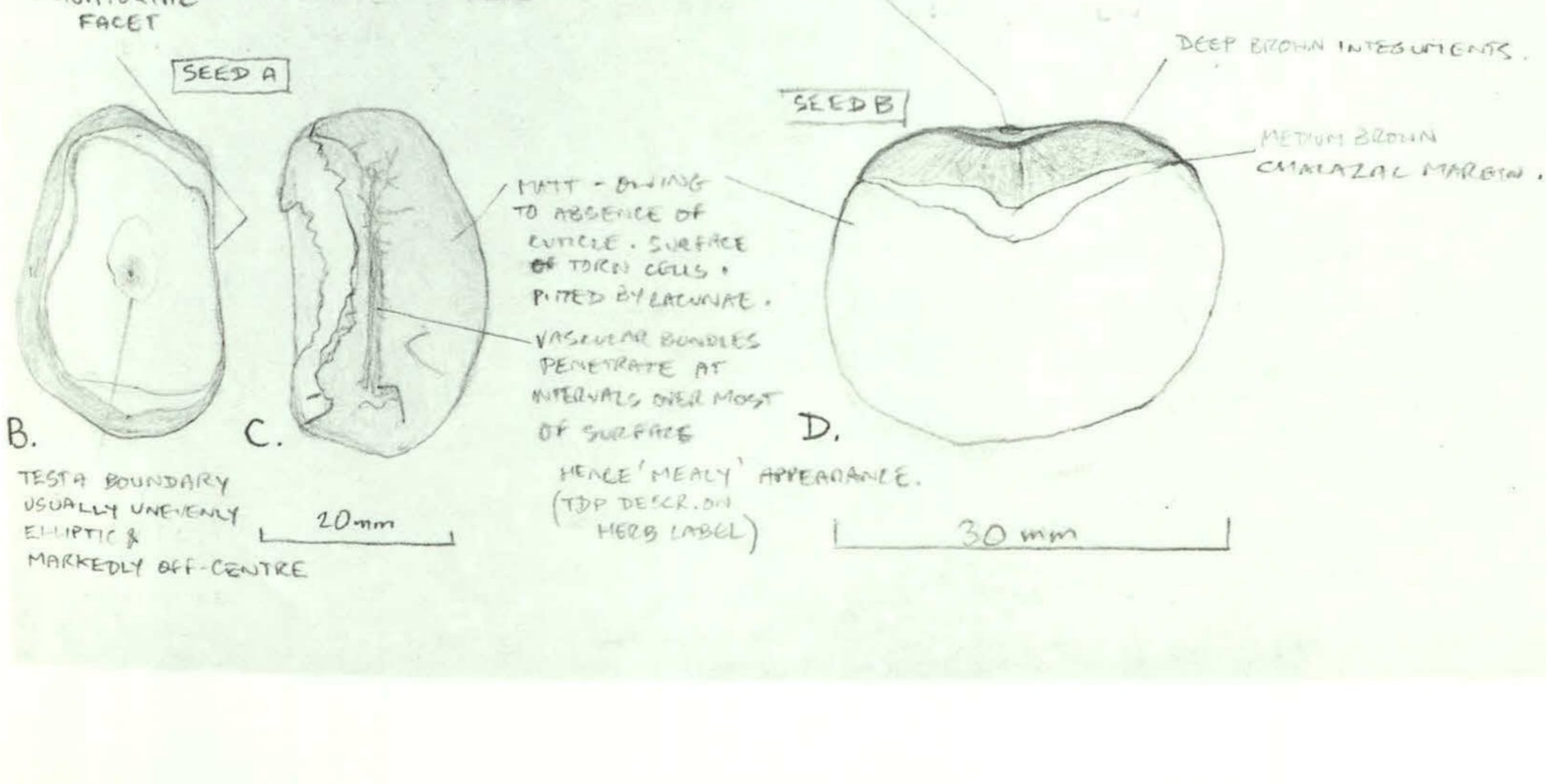


PLATE 86

CHISOCHETON SARAWAKANUS

SEED-COAT ANATOMY, SHOWING THE UNION OF INTEGUMENTS AT THE CHALAZA. A. TISSUE PLAN.

B. CELL DETAILS.

# TRANSITION ZONE L.S. - TISSUE PLAN

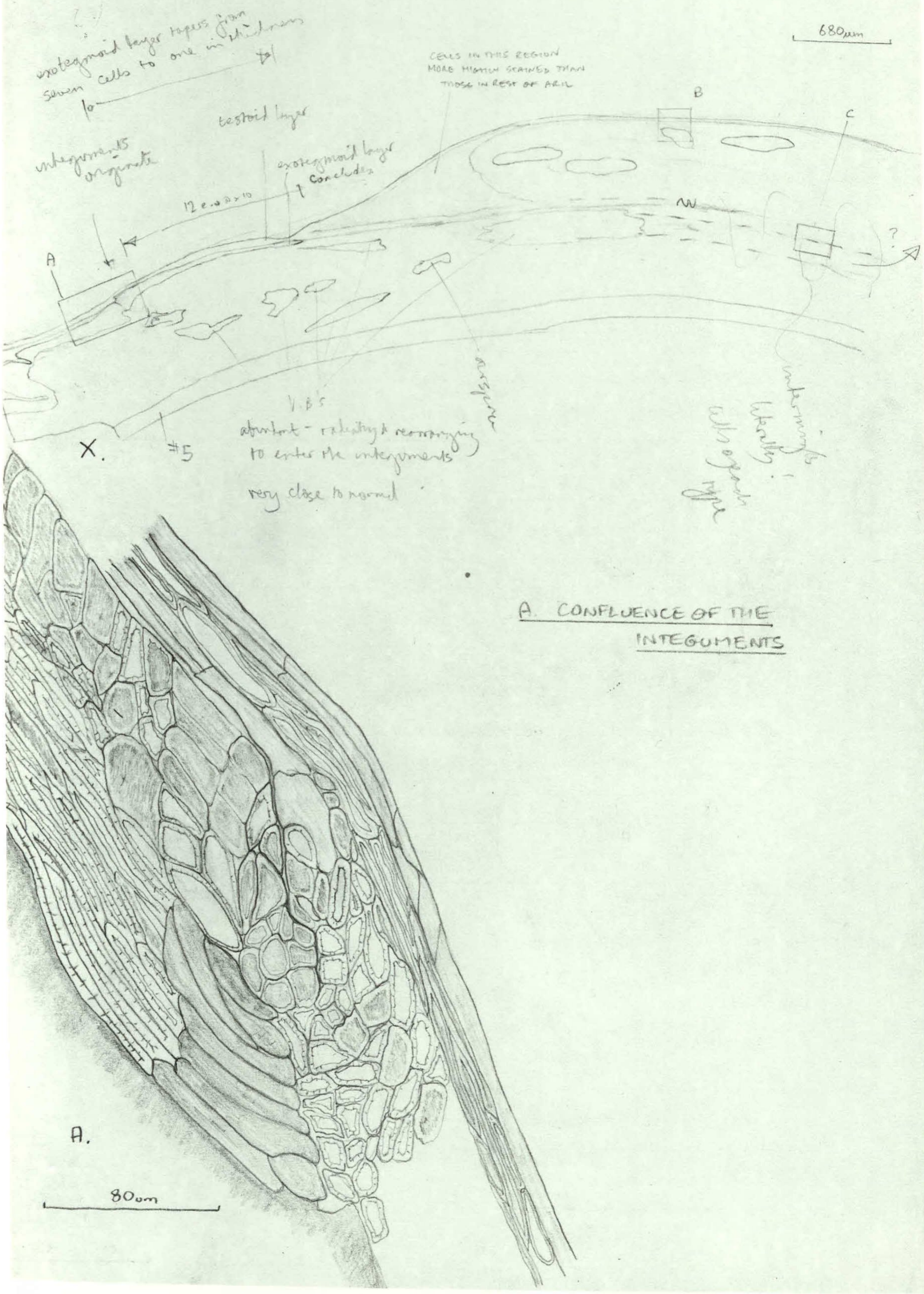


PLATE 87

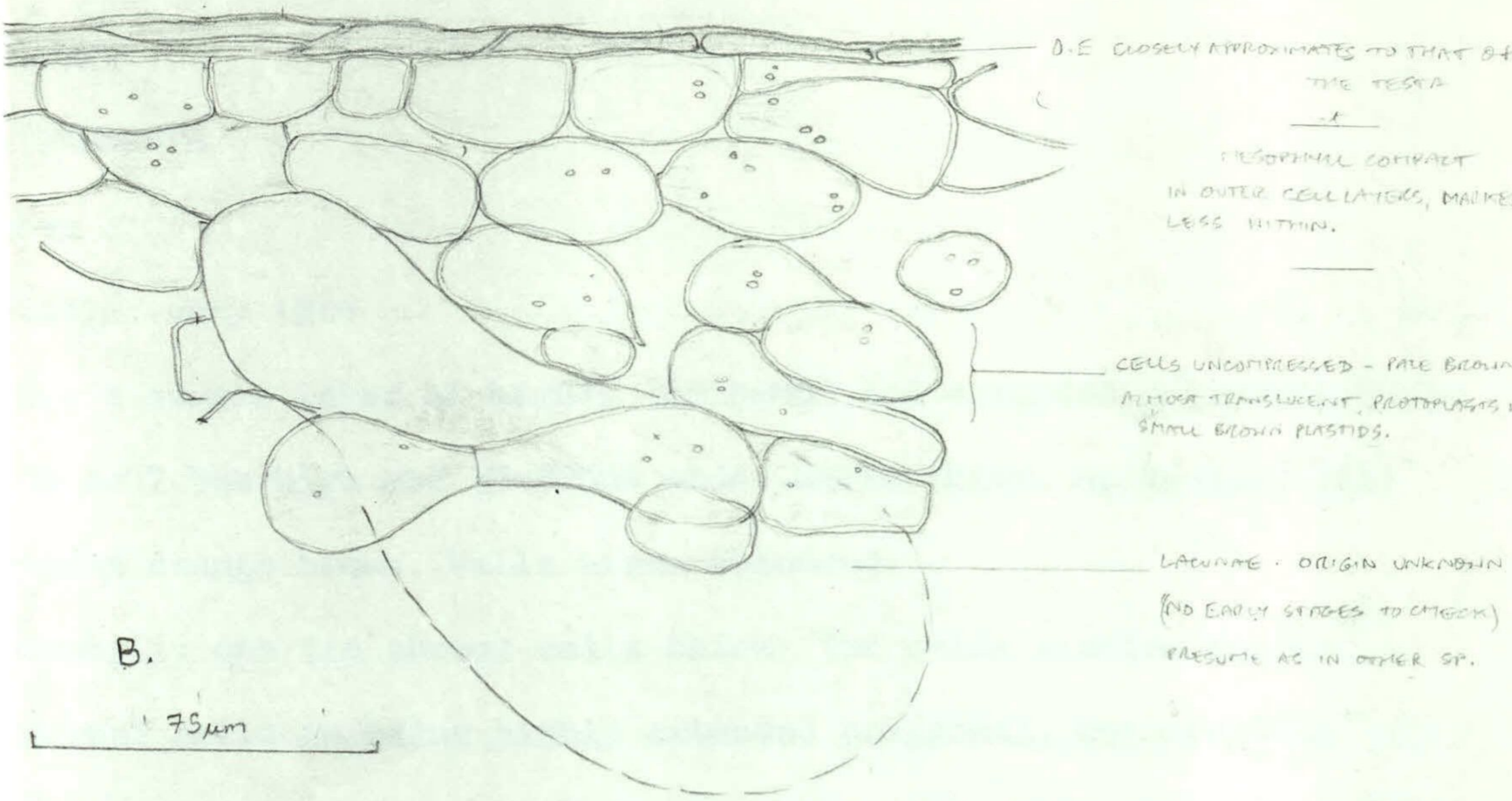
CHISOCHETON SARAWAKANUS

SEED-COAT ANATOMY: THE PACHYCHALAZA.

A. UPPER PART OF FLESHY, AERENCHYMATOUS TISSUE.

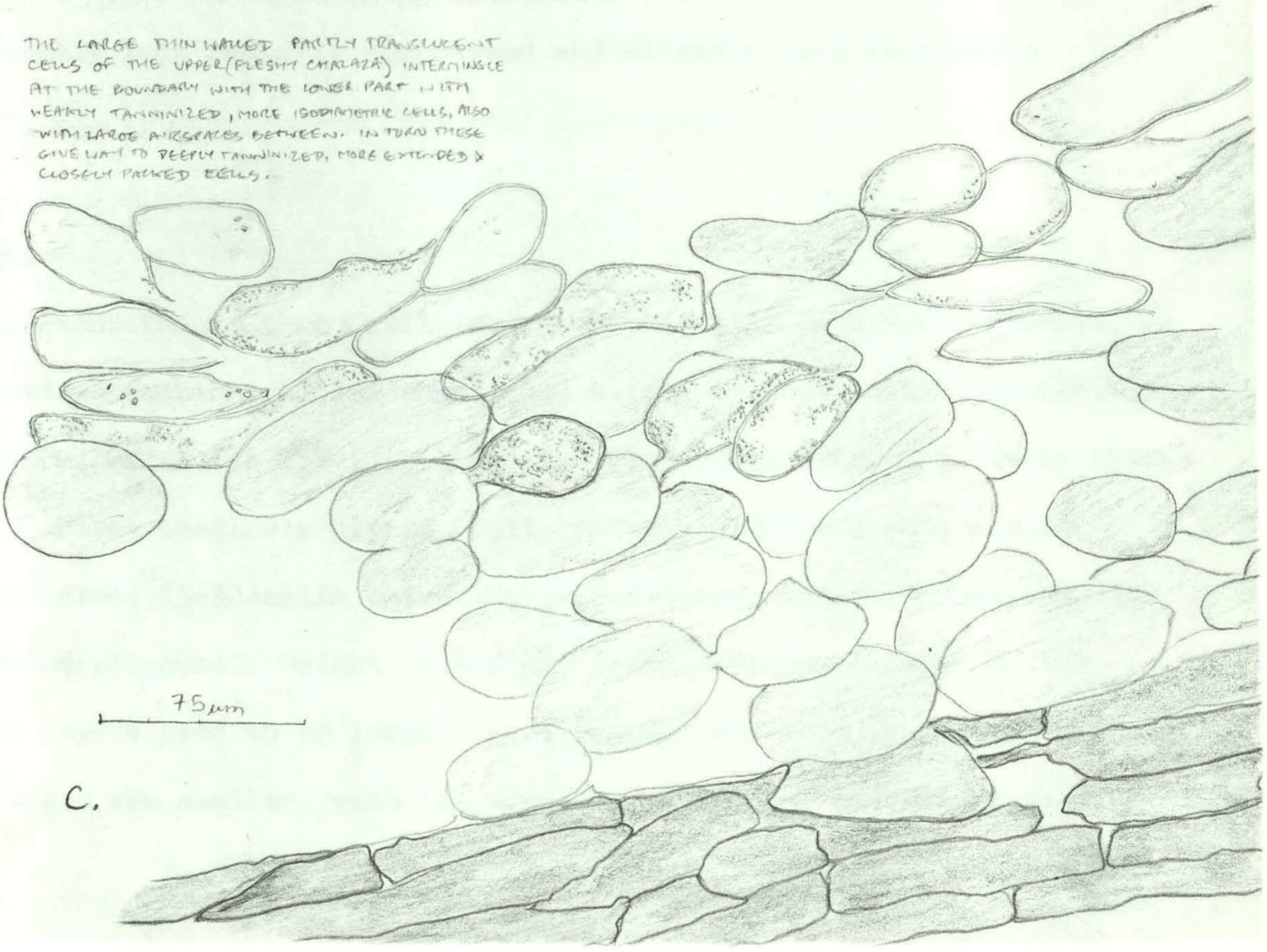
B. JUNCTION OF LOWER AND UPPER PART. NOTE TRANSITION FROM FLESHY PARENCHYMA TO TANNINIFEROUS ENDOTEGMOID CELLS BELOW.

B. CHALAZA - UPPER PART.




C. CHALAZA - LOWER PART

THE LARGE THIN WALLED PARTLY TRANSLUCENT CELLS OF THE UPPER (FLESHY CHALAZA) INTERMINGLE AT THE BOUNDARY WITH THE LOWER PART WITH WEAKLY TANNINIZED, MORE ISODIAMETRIC CELLS, ALSO WITH LARGE AIRSPACES BETWEEN. IN TURN THESE GIVE WAY TO DEEPLY TANNINIZED, MORE EXTENDED & CLOSELY PACKED CELLS.



ANATOMY

INTEGUMENTS

Testa

Cuticle: very thin

O.E.: a single layer of highly flattened and extended polygonal cells 4.5um to 7.5um high and 35-105um wide. Walls thick, up to 3um; cell contents orange brown. Walls straw coloured.

Mesophyll: one (to three) cells thick. The cells similar to the epidermal cells in being highly extended polygonal, but are less radially flattened (often 7.5um tall.) and with walls slightly thinner (1.5-2um). Contents living, translucent, never brown.

I.E.: a single layer of cells, virtually identical to th O.E., marginally less radially compressed and slightly less tanninized.

Tegmen

Exotegmen: two to three cell layers thick. Cells prostrate, fibroid, in transverse section, taller than long; height 16-28um, width (in L.S.), 36-114um, width (in T.S.), 9-16um. End walls largely square. Walls thick (3um) white, shallowly pitted. Cell contents a diffuse pale orange.

Endotegmen: 25-30 cells thick. Cells prostrate, tanniniferous, rounded, extended-polygonal. Height, 6.5-23um; width, 49-130um. Cells of the outer layers tend to be larger, more rounded and loosely packed. Those below are are smaller, with few airspaces. Vascular bundles frequently

run longitudinally through this layer with up to 5 vessels and support cells in diameter.

CHALAZA

Upper chalaza: cuticle: very thin.

O.E.: one (in very short and intermittent parts two) cells thick. Cells very similar to those of the testal O.E.: angular, prostrate extended polygonal-markedly flattened. Height, 5-8um; width 34-42um ; walls rather thick, to 2um. Contents deeply stained.

Cortex: 12-20 cells thick (deepest below the hilum). The cells are large and thin walled, usually prostrate extended polygonal. The outer layers are quite compact and rectangular in cross-section, the inner more rounded, often with 'arms' (aerenchymatous) linking with other cells and large intercellular spaces and lacunae. Cells 65-75um long, 19-23um broad.

At the lower boundary of the upper chalaza, the transition to the tegmoid layer is not abrupt. Before petering out, the elongated and branched mesophyll cells intermingle with a zone of large ellipsoid, lightly tanninized cells which in turn merge with the lower chalaza proper.

The lower chalaza, usually 18-20 or so cells thick, resembles the endotegmen very closely, in fact, the cells tend to be very slightly larger and the tissue more highly vascularized and less tanninized than the endotegmen.

TRANSITION ZONE

The histology of the transition from integuments to chalaza is most interesting: at the confluence of the integuments, the exotegmen becomes thicker and appears to invade the inner base of the testa, the testal I.E. disappearing. Proceeding towards the boundary of the fleshy layer, the endotegmoid layer dwindles from seven to one cell in thickness, whilst the testal mesophyll above correspondingly increases, until, about 1mm in from the chalaza boundary, it appears to proliferate rapidly giving rise to uncompressed thin walled parenchyma which is continuous with the bulk of the fleshy upper chalaza. At the point of proliferation, the exotegmoid fibres peter out altogether.

The boundary between the fleshy mesophyll tissue and the endotegmoid cells below (i.e. between upper and lower chalaza) appears initially to be marked by a single intermittent layer of translucent prostrate parenchyma, but this distinction is soon lost.

The tanniniferous endotegmen is of all integumentary parts, least changed by the transition, retaining all of its characters and merely becoming narrower and more penetrated by vascular bundles.

SUB-SEED-COAT

?Endosperm(#5): the uppermost part of a single layer of small isodiametric to slightly radially elongate (columnar) unstained, thick-walled cells. 8-13um tall, 6-8um wide, walls 2um thick.

The lower part of about 6-7 cells thickness. The cells ± spherical and medium sized: 10-25um tall, 13-29um wide with thin walls (0.5um). The contents living and translucent, air spaces frequent and quite large.

EMBRYO

#4, the well differentiated epidermal layer of the outer part of the cotyledon consists of two to three layers of cells. These are small, isodiametric to slightly tangentially extended, densely packed cells, 8-11.5um tall and 10-21um wide. The walls are relatively thick (1um), the contents living, stained brown with nuclei often present. In macro-section these cells appear as a narrow black line.

#3.The cortex below of four to seven cells depth, this apparently depending on the development of layer #2 beneath. The cells large, slightly radially elongate polygonal, thick-walled and angular. 45-68um tall, 23-29um wide, walls 1.5um thick. The walls brown, contents a pale yellow brown, living, with nuclei usually present. Air spaces few, cells tightly packed.

#2. A continuous band of sclereids four to six (exceptionally 3-8 cells) thick. Height, 24-65um; width 23-42um; wall thickness 4-5um. The thick walls are heavily pitted. Contents are absent. Shape: sub-isodiametric, highly angular.

#1. The innermost layer, of thin-walled isodiametric cells 26-55um long and 23-59um broad. The walls (1-1.5um thick) are rounded at the corners, at which small airspaces are frequent. The contents are pale grey and finely granular.

PLATE 88

CHISOCHETON GRANATUM

A-D FRUITS. APPÀRENTLY TARDILY DEHISCENT

E-J SEEDS; SARCOTESTAL.

C. GRANATUM 7911

## GROSS MORPHOLOGY - FRUITS & SEEDS

OBLIQUE LATERAL VIEW

SURFACE SUB-VERRUCATE

SHAPE OBLATE

A.

PLAN VIEW

B

2 cm

VALVE

C.

PLACENTATION & SEPTUM

D.

SEPTUM

PLACENTA

SEED TRANSVERSE SECTION

COT. EDGE

E.

SEED, SAGITAL SECTION

HYPOCOTYL

2 cm

SEED : LATERAL VIEW

WELL DEFINED HILUM

CRACKING OF THE FRAGILE CHALAZAL SURFACE

F.

DISTAL PLAN VIEW

G.

H.

CENTRAL FURROW ON DISTAL FACE

DORSAL PLAN VIEWS (VARIATION)

I.

J.

2 cm

PLATE 89

CHISOCHETON GRANATUM

TISSUE PLAN OF SEED-COAT AND OUTER COTYLEDON.

NOTE THICK, UNITEGMIC (PACHYCHALAZAL) SARCOTESTA WITH TANNINIZED CELLS (LOWER CHALAZA).

NOTE LARGE CLUSTERS OF SCLEREIDS IN OUTER COTYLEDON.

# SEED SURFACE - TISSUE PLAN

C. GRANATUM TDP 7941

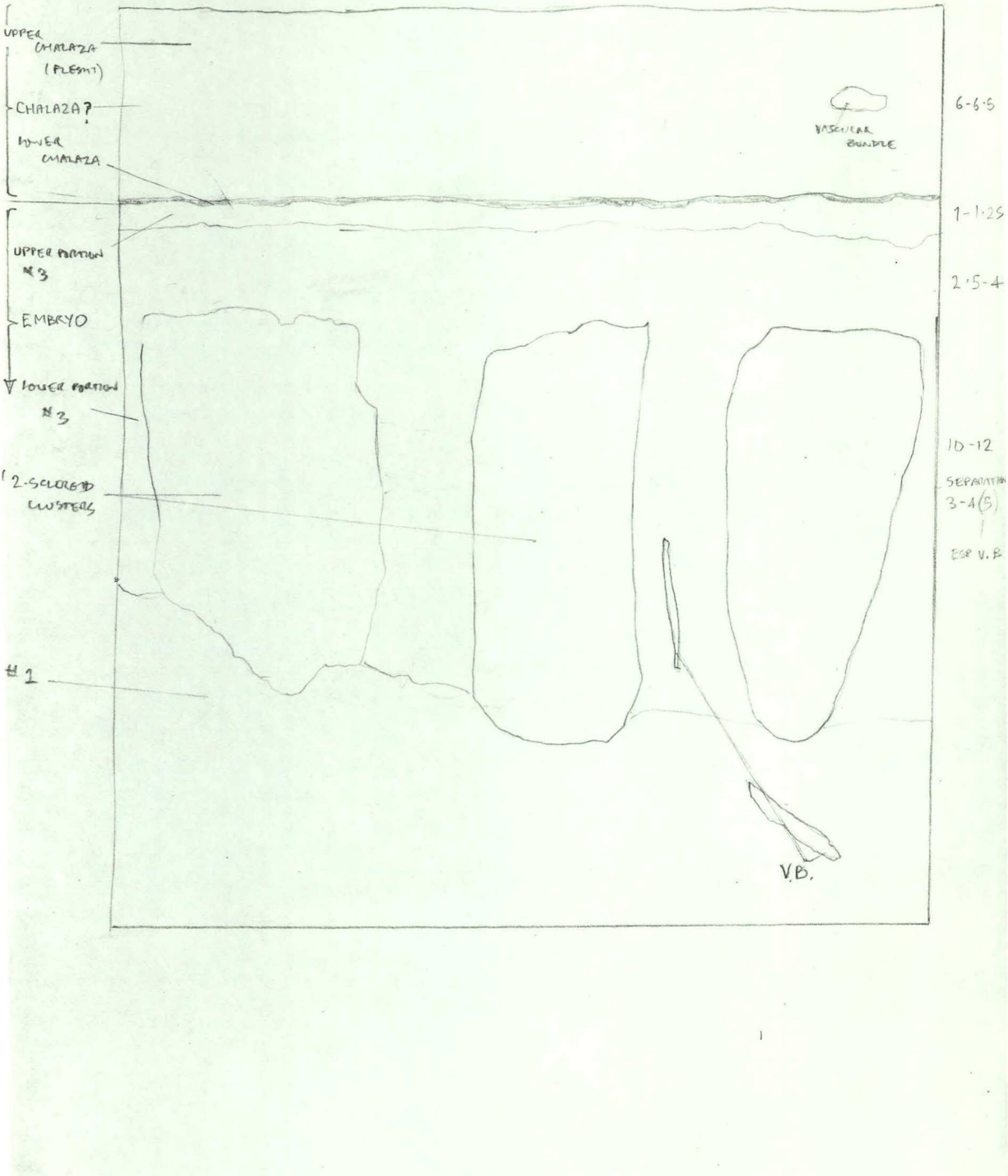


PLATE 90

CHISOCHETON GRANATUM

SEED-COAT ANATOMY. ENTIRE SEED-COAT UNITEGMIC, PROBABLY PACHYCHALAZAL. THE OUTER PART FLESHY, WITH THIN-WALLED PARENCHYMA CELLS, THE INNER PART ('LOWER CHALAZA') WITH HARD, TANNINIFEROUS CELLS.

NOTE THE VARIATION IN THE UPPER ZONE (#1) OF THE OUTER EMBRYO.

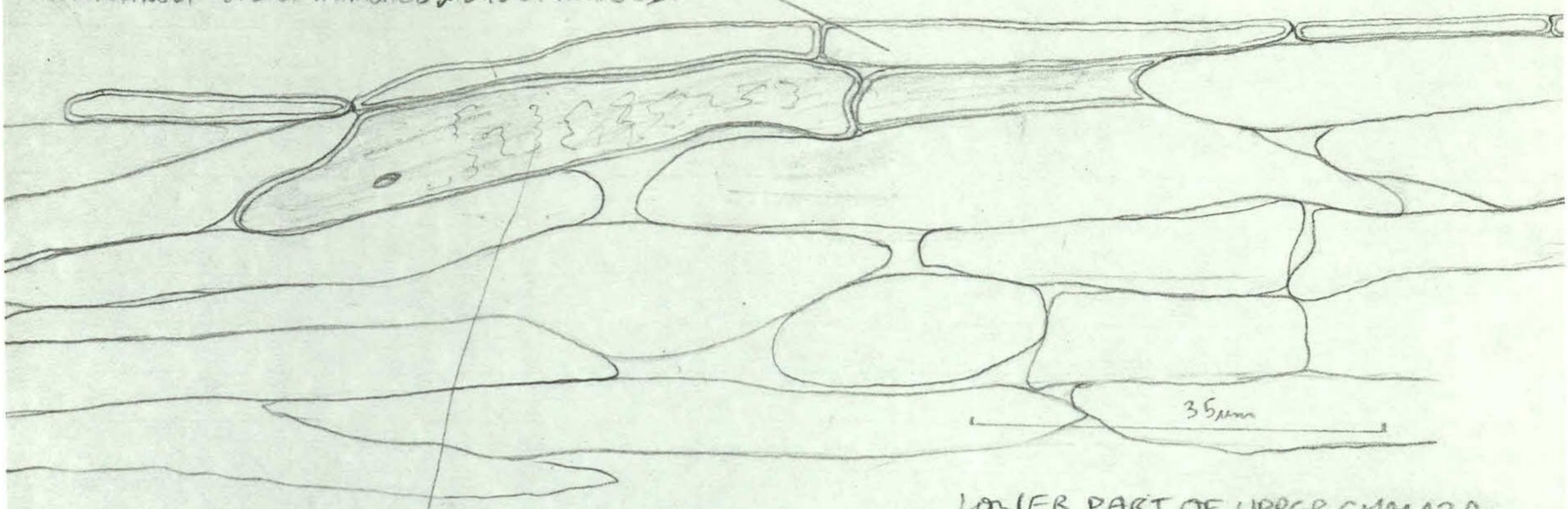
TDP

90.

# C. GRANATUM 7941

## OUTER CHALAZA - L.S.

EPIDERMAL. PROSTRATE, THIN WALLED ( 1 µm ) x V. NARROW
6-8 µm ; MAXIMUM LENGTH 35 µm . APPARENTLY ISODIAMETRIC.
COMPARATIVELY LOOSELY ATTACHED & EASILY DAMAGED.




MESOPHYLL: 35-50 CELLS THICK, LARGE RECTANGULAR (BUT COMPRESSED & THEREFORE ROUNDED & BUCKLED, IN OUTER LAYERS) PROSTRATE WITH FATE CONTENTS. LARGE AIRSPACES, THOUGH REDUCED IN THE INNER LAYERS. IDIOBLASTS ± ABSENT. LACUNAE ?
VASCULAR BUNDLES OCCASIONAL - MUCH SUPPORT TISSUE.

## LOWER PART OF UPPER CHALAZA, LOWER CHALAZA & EMBRYO (#3) - L.S.

LOWER PART OF UPPER CHALAZA, 3-4 CELLS.
SL. SMALLER, MORE RIGID, ANGULAR, UNCOLLAPSED.
LOWERMOST CELLS WITH CRYSTALS, USUALLY 5-6 PER CELL, 2-6 µm (TO 27 x 14 µm)

LOWER CHALAZA, SOMETIMES NIL, BUT USUALLY 4-10 CELLS, DEEPLY STAINED, PROSTRATE, DISC SHAPED CELLS, COMP. SMALL, CLOSELY PACKED, NO AIRSPACES - CELL WALLS HARD TO DETERMINE. HIGHLY STRUCTURAL

? ENDOSPERM (V. RARE)
SINGLE LAYER SL. RADIALLY ELONGATED CELLS. ROUNDED, LARGE AIRSPACES, GRANULAR CONTENTS DENSE, OFT SHRUNK FROM WALL

BAND OF 3-5 ALMOST SPHERICAL CELLS WITH LIVING, GRANULAR CONTENTS, OCCASIONALLY IN SOME PARTS SEED, STAINED BLACK. NEAREST LAYER - SEED COAT DETACHES EASILY HERE. LARGE AIRSPACES - LOOSELY PACKED.

INTERMEDIATE BAND, WITH CHARACTERS OF THOSE ABOVE & BELOW, ESPECIALLY DIMENSIONS 1-3 LAYERS

#3

BAND OF LARGE, ANGULAR CELLS WITH FAIRLY THICK WALLS & FEW AIRSPACES. CONTENTS & WALLS STRAW COLOURED. ~~4-5 LAYERS~~ THICK OVER THE SCLEREID CLUSTERS OTHERWISE TO 10 OR MORE. to 7.

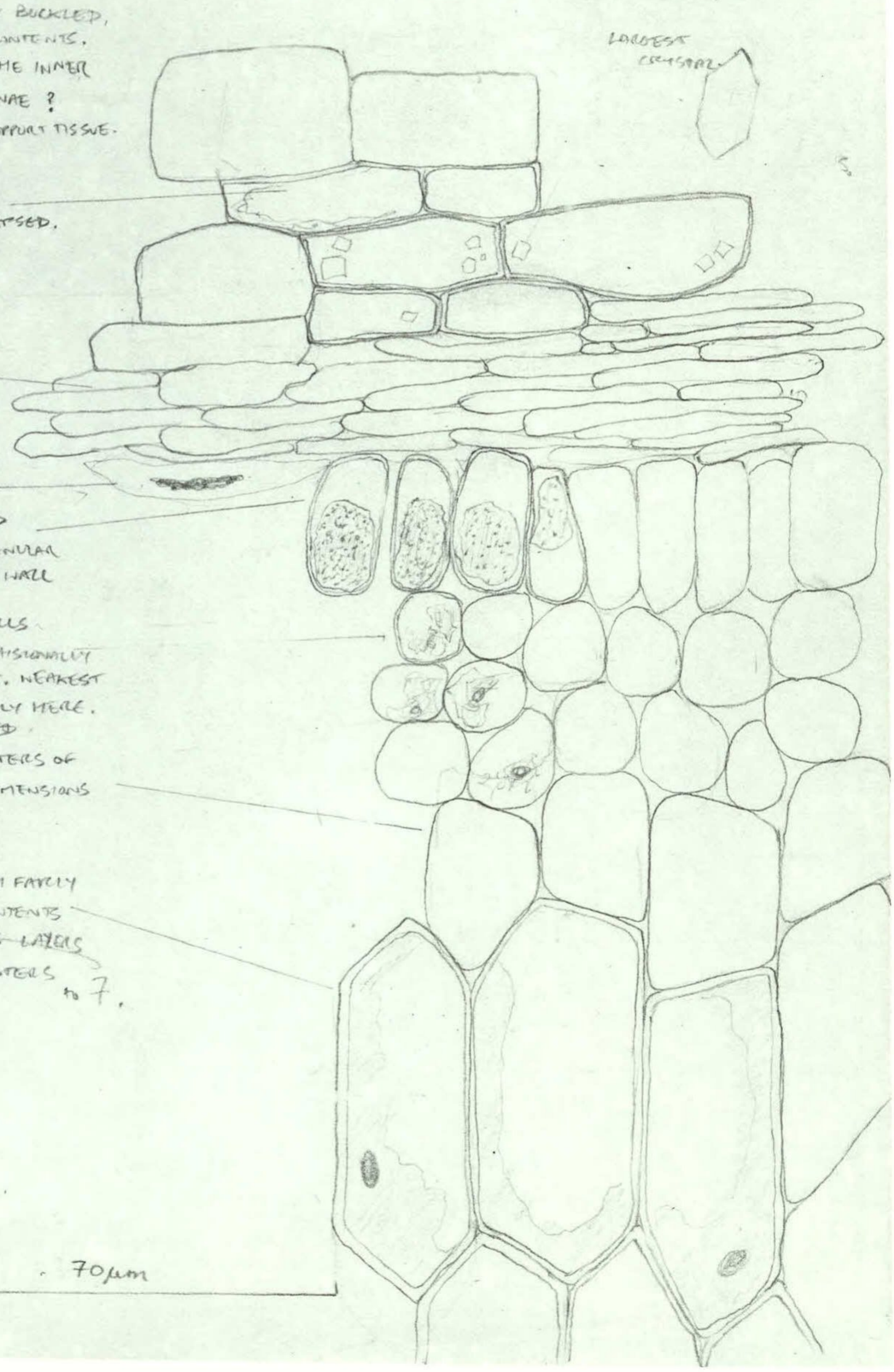


PLATE 91

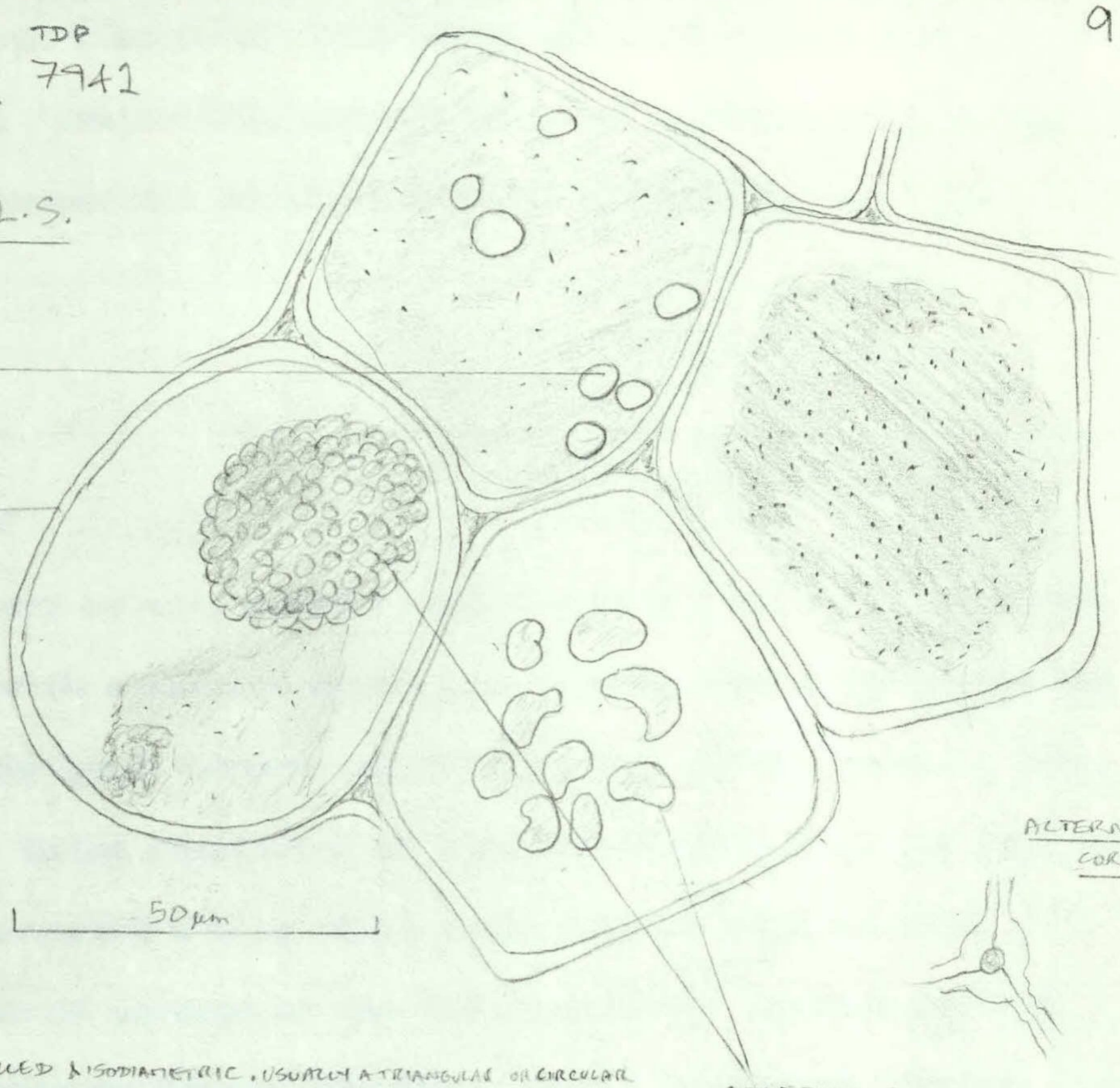
CHISOCHETON GRANATUM

CELLS OF INNERMOST EMBRYO ZONE:

DETAILS OF CONTENTS

C. GRANATUM TDP 7911

EMBRYO. #3. L.S.




CELLS THICK WALLED & ISODIAMETRIC. USUALLY ATRIANGULAR OR CIRCULAR INTERCELLULAR SPACE AT CORNERS - STAINED BROWN.
SHAPE: USUALLY 5-7 ROUNDED ANGULAR. — SQUARE & SPHERICAL.
CONTENTS: USUALLY WITH UNIFORMLY GREY (STORAGE) CONTENTS, AGGLUTINATED INTO MASSES OF VARYING Ø & P. OCCASIONALLY, LIPID GLOBULES ALSO OBSERVED. SOME EMPTY LUMEN (FALLOUT)

C.granatum Mabberley

This description based on T.D.P. 7941

Collector's notes: '4 large seeds surrounded by white meal. The seed-coat pale brown (immature). Cotyledons pink with white sap'.

Mabberley (1979) 'semina 4-5, circa 3 cm longa, scutata (ubi 4) vel formam segmentae hesperidii simulans (ubi 5), cotyledonibus laticiferibus'.

GROSS MORPHOLOGY

Seeds 4 or 5, very broadly orange-segment-shaped. In distal plan view broadly elliptic with a shallow depression running centrally across the longest part of the seed. Longest length 55-60mm, axial length c. 28mm, breadth 45 -52mm. Hilum restricted to a narrow strip 3.5 to 4cm long and 2 to 8mm broad, covering a very small proportion of seed surface, remainder of which is covered by the fleshy chalaza. Chalaza surface matt, fragile, prone to damage. Micropyle poorly developed, barely detectable.

ANATOMY (based largely on L.S.)

CHALAZA

Upper Chalaza. Cuticle extremely thin.

Outer epidermis with thin-walled (1um) highly extended polygonal and prostrate cells, 6um to 8um tall and up to 35um wide. In paradermal section, isodiametric. Contents very pale. Cell cohesion not strong, this layer usually damaged.

Cortex 35 to 50 cells thick. In material observed, cells distorted,

apparently by radial compression, cell shapes unusual, anticlinal walls especially buckled. Distortion most prevalent in outer part. Towards inner, normally developed cells, extended polygonal, largely prostrate, up to 32um tall and 56um broad, large airspaces, thin walls (1um) and pale almost translucent protoplasmic contents. No lacunae were detected, but they cannot be entirely ruled out owing to distortive effects of compression. The lowermost 2 to 4 cells are slightly smaller and noticeably closely-packed with angular walls. An unusual feature are the crystalline inclusions in each of their lumen. These usually appear cuboidal and about 2um to 6um in diameter, often with as many as 5 per cell and in one case, 27 crystals per cell. Occasionally, the crystals are fewer and larger. An hexagonal crystal 14um long was the largest observed. This trait seems characteristic of this part of the layer: it being located in both seeds investigated. However, the density of crystals varies significantly. In one section, over a millimetre span, only two crystals were located, in another, over the same span, hundreds, if not thousands, were present.

Lower chalaza. Usually of 4 to 7 cells depth, the cells prostrate extended polygonal, 3.5um to 7.5um tall and 18um to 40um wide (comparatively small). Not always developed: in some sections entirely absent for stretches of 500um. Vascular bundles very scarce in the chalaza. The cells notable for their close packing, diminutive size and high degree of tanninization.

SUB-SEED-COAT

ENDOSPERM: Traces rarely detected. The cells very irregular in shape, but on average 30um to 40um long and 6um to 8um broad. The walls thick, translucent, the contents very dense, dark brown.

EMBRYO.#3: The outer epidermal cells generally columnar, 20um to 23um tall and 8um to 14um wide. Walls thick, the contents granular, but often (see Plate 91) contracted away from the cell walls.

Below the epidermis is a cortex of 8 to 14 cells thickness, the upper and lower portions well differentiated. The upper part of spherical cells, walls fairly thin, large air spaces and loose packing of cells (this is where fracturing is most prone) together with pale brown protoplasm, is 3 to 4 cells (occasionaly 6) thick.The lower part is 4 to 5 cells thick (in some cases 7 cells), the cells much larger, radially extended polygonal with tighter packing, fewer airspaces and thicker walls than the upper part. The cells usually 60um tall and 25um to 30um broad. The protoplasts are brown, highly vacuolate with nuclei frequently present; the walls tend to be straw-coloured. This cell type extends to between the the sclereid clusters, over which the layer is naturally deeper.

#2: Sclereid clusters very well developed, usually about 12 cells tall, 15 cells wide. The individual sclereids markedly tangentially elongated: 80um to 100um tall and 30um (25um to 40um) wide. The walls comparatively thin, 4um (2um to 6 um) thick, with simple pits. An unusually high proportion with protoplasm. Sclereids at the lower and upper parts of the cluster are atypical, being smaller and almost isodiametric, 8um in diameter.

#1: Cells of large uniform size, slightly extended isodiametric 67um long and 55um broad. The walls thick (2 um) and pale orange. Air spaces

in the corners usually filled with a bright orange brown substance, the shape triangular or circular. In the latter case, the walls approach the collenchymatous state, the corners being more thickened. The contents rather variable. Generally the lumina are uniformly filled with a pale grey finely granular substance, often with sporadic oil globules, however, in some cells the contents seem to have contracted, and in others large spherical dark bodies (see Plate 90), possibly artefacts, are present. Some cells are filled with small bean-shaped, pale brown globules,these too may be monstrosities.

C.sarasinorum Harms

This description based on T.D.P. 7910.

Collector's notes: 'seed surrounded by mealy white envelope'.

Mabberley (1979): 'seed to 5cm long, like a segment of an orange, with vascular sarcotesta'.

GROSS MORPHOLOGY

Seeds 5, orange-segment-shaped. Longest length 50-55mm. Axial length 21mm, breadth 27mm. Hilum long (20-30mm) and very narrow (c.3mm) covering <1/20th of the seed surface. The rest of the seed covered by the chalaza, the outer part fleshy. Surface almost matt, in parts sub-scurfy: rather fragile. At the micropyle, the pore is well developed and part of the embryo exserted.

# PLATE 92

## CHISOCHETON SARASINORUM

A-C FRUITS, NOT DEHISCED.

D-F SEEDS, ORANGE-SEGMENT-SHAPED, AND COMPLETELY SARCOTESTAL.

C. SARASINORUM 7910.

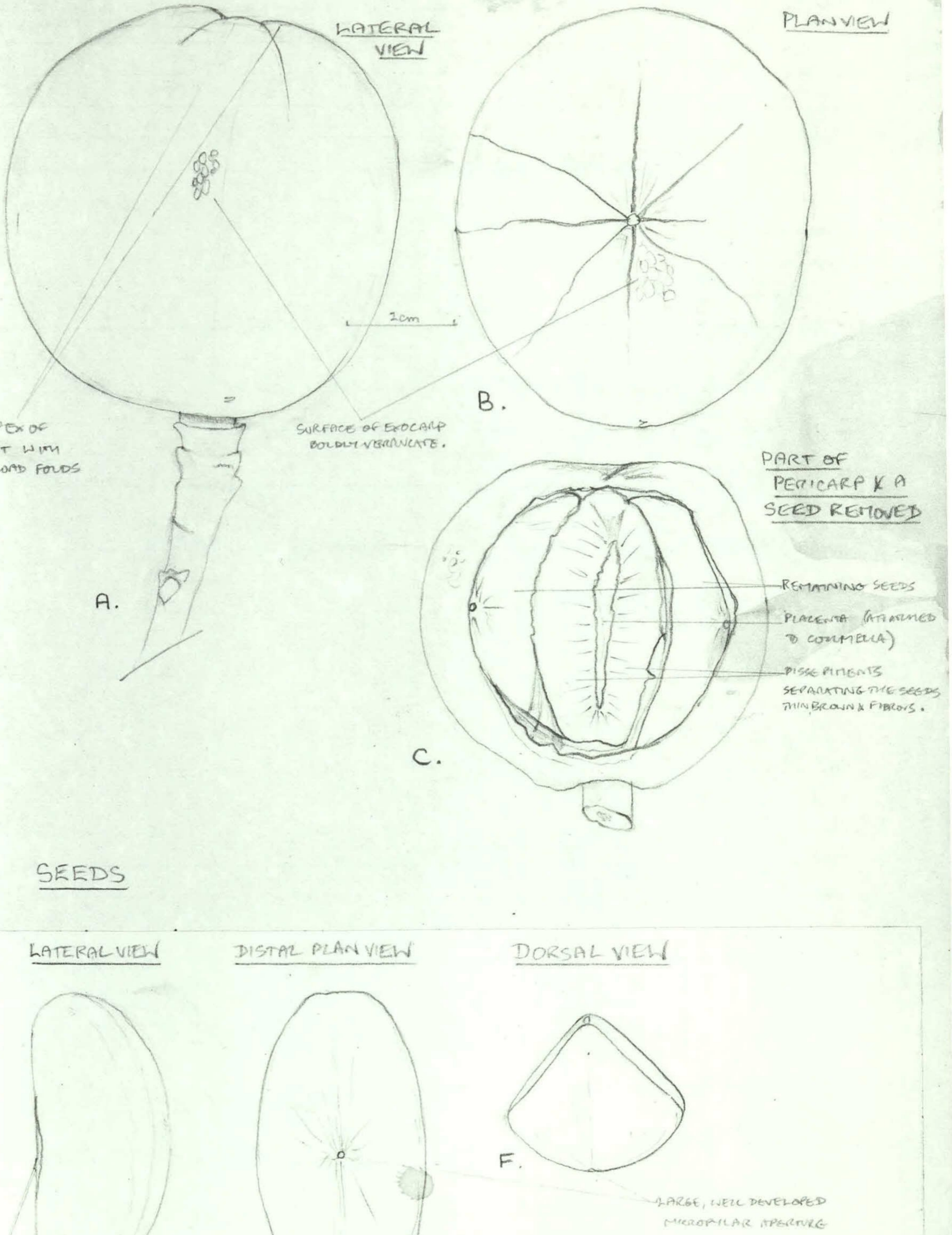


## GROSS MORPHOLOGY - FRUITS & SEEDS

FRUIT

LATERAL VIEW

PLAN VIEW




PART OF PERICARP & A SEED REMOVED




## SEEDS

PLATE 93

CHISOCHETON SARASINORUM

SEED-COAT ANATOMY: TISSUE PLAN. NOTE UPPER, FLESHY PART OF PACHYCHALAZAL SEED-COAT, WITH VASCULAR BUNDLES IN LOWER, MORE MECHANICAL PART. NOTE LARGE CLUSTERS OF SCLEREIDS IN UPPER EMBRYO. VERY SIMILAR TO C. GRANATUM IN ANATOMY - c.f. PLATE 89.

C. SARASINORUM 7910



L.S SEED SURFACE

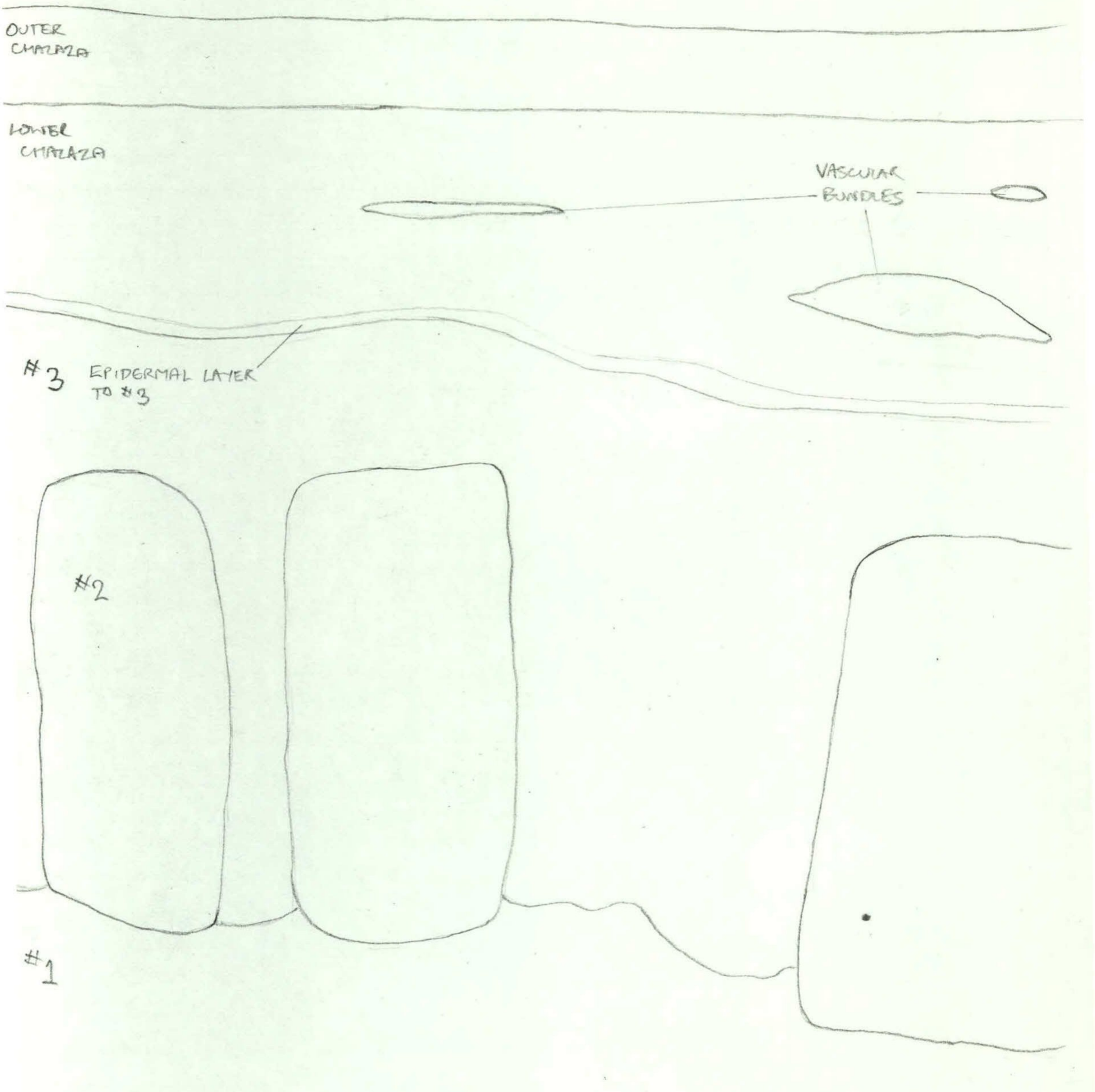


PLATE 94

CHISOCHETON SARASINORUM

SEED-COAT (UNITEGMIC-PACHYCHALAZAL) ANATOMY:

NOTE UPPER PART FLESHY, OF THIN-WALLED CELLS,

LOWER TANNINIFEROUS. NOTE LACK OF CHARACTERS

C. SARASINORUM 7910

L.S. CHALAZA



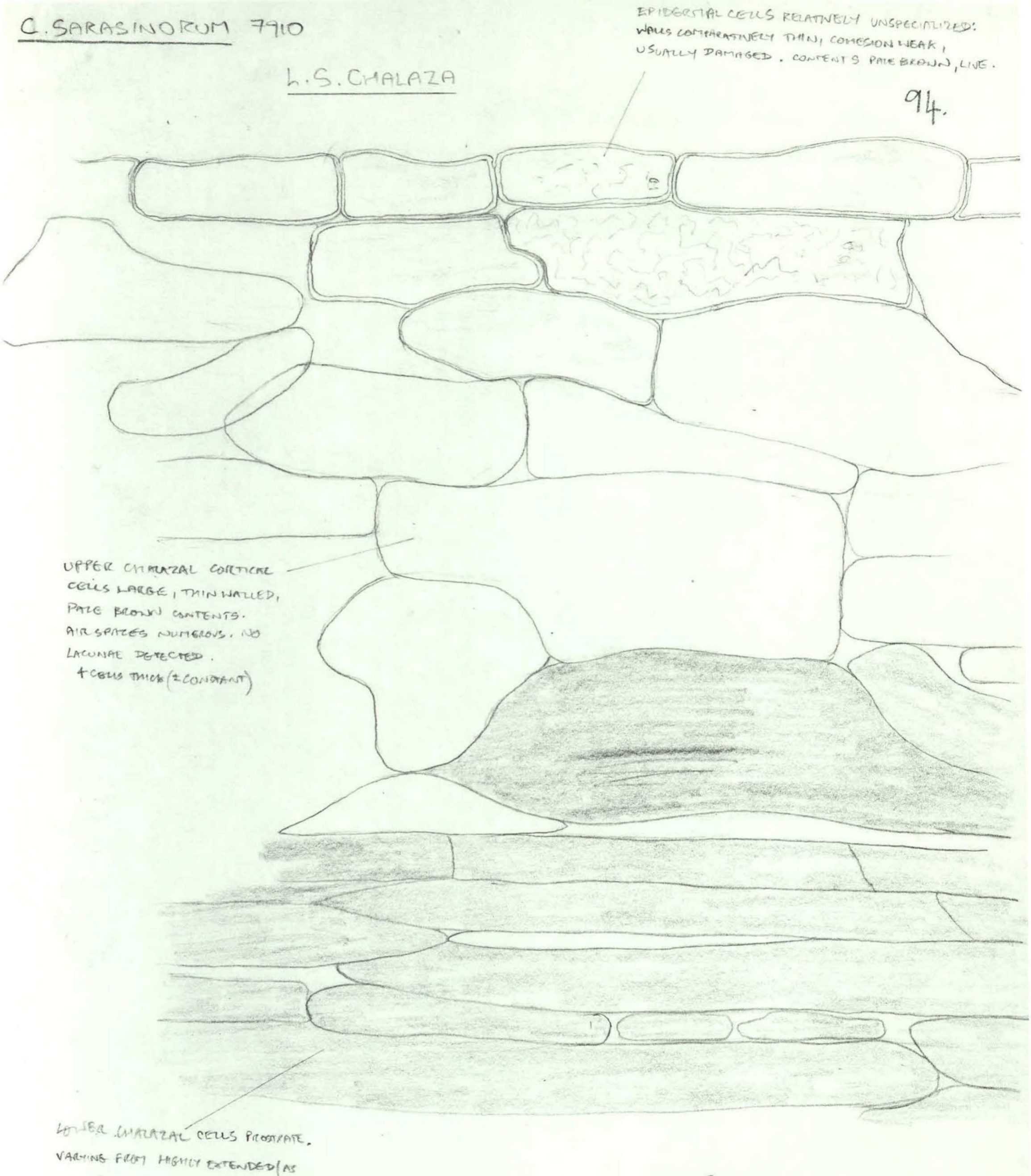


PLATE 95

CHISOCHETON SARASINORUM

OUTER EMBRYO ANATOMY: VARIATION IN CELL STRUCTURE.

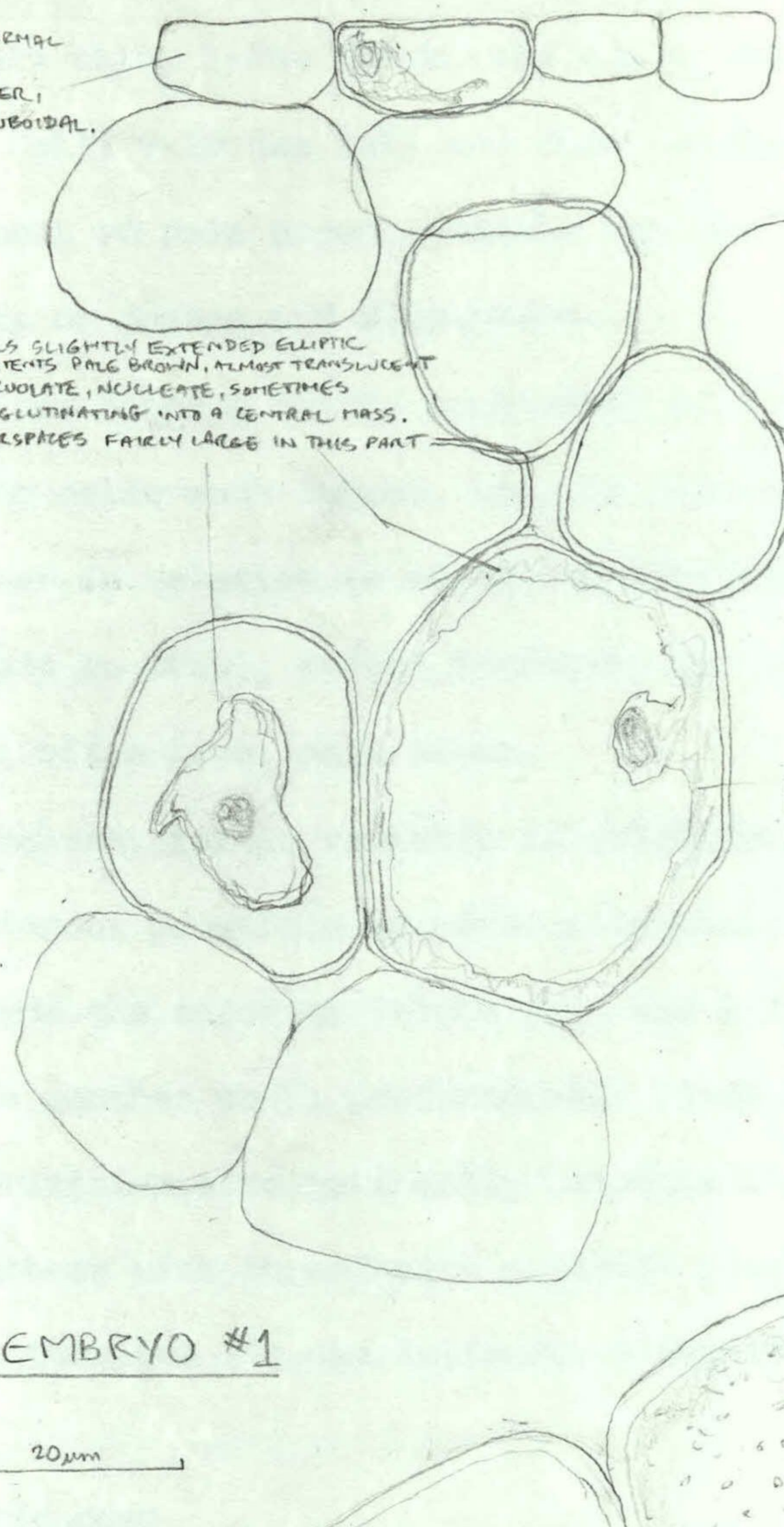
C. SARASINORUM 7910

# EMBRYO - #3

## UPPER X MAIN PORTION

EPIDERMAL CELLS SMALLER, SUB-CUBOIDAL.

CELLS SLIGHTLY EXTENDED ELLIPTIC CONTENTS PALE BROWN, ALMOST TRANSLUCENT VACUOLATE, NUCLEATE, SOMETIMES AGGLUTINATING INTO A CENTRAL MASS. AIRSPACES FAIRLY LARGE IN THIS PART

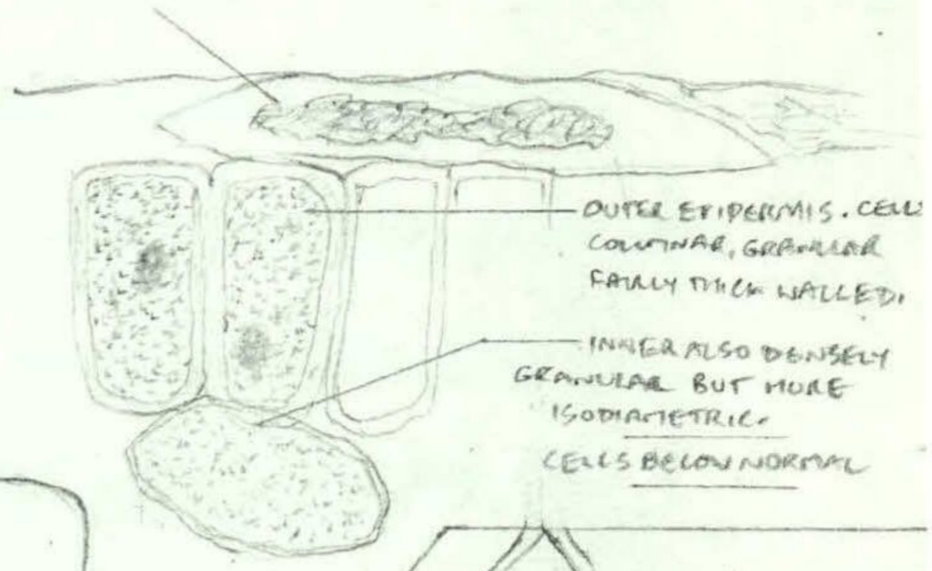


## ALTERNATIVE EPIDERMAL LAYER (& ? ENDOSPERM)

95.

ISOLATED ?ENDOSPERMAL CELL, THICK TRANSLUCENT WALLS, DENSE LUMEN.

20μm



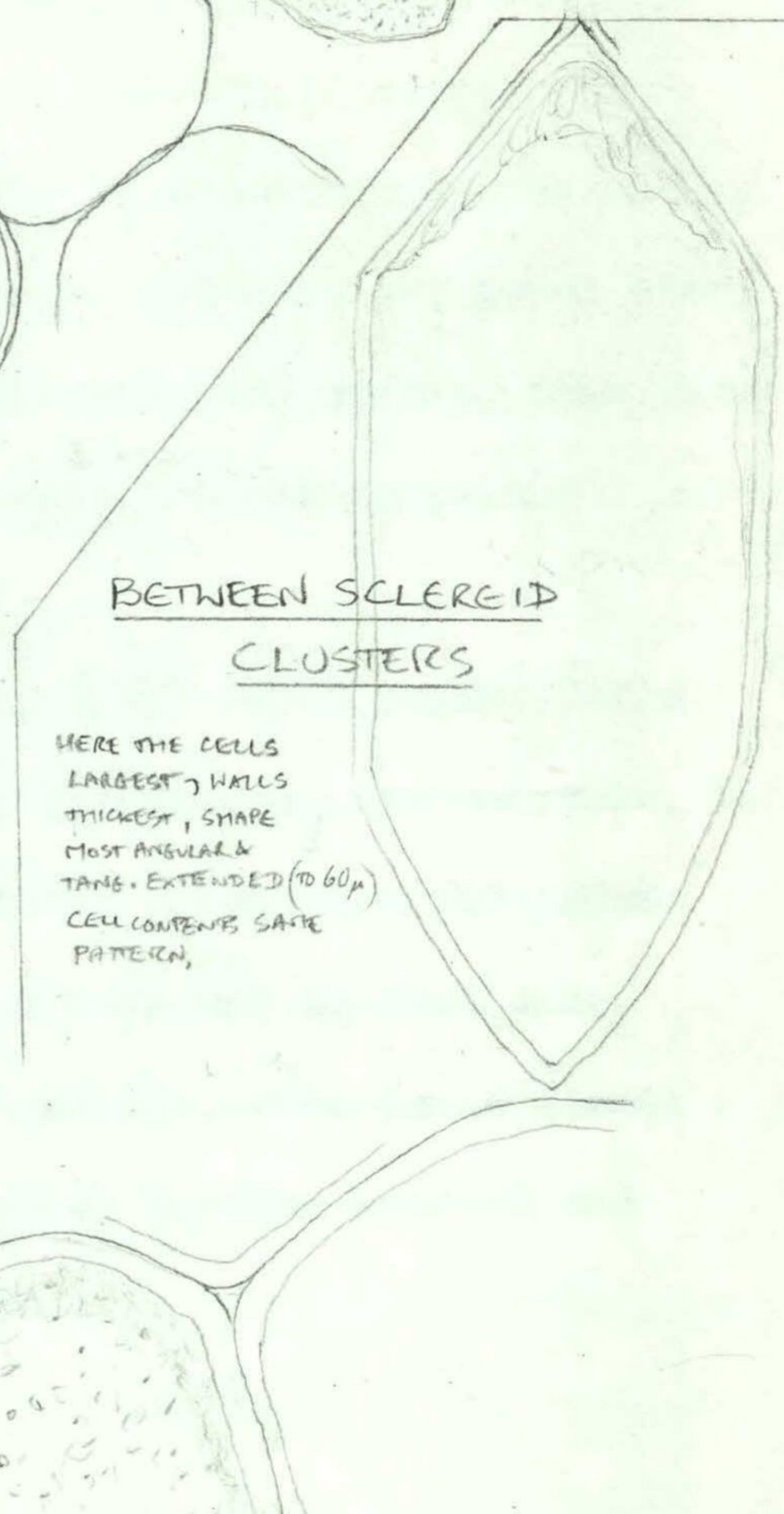
OUTER EPIDERMIS. CELLS COLUMNAR, GRANULAR FAIRLY THICK WALLED.

INNER ALSO DENSELY GRANULAR BUT MORE ISODIAMETRIC.

CELLS BELOW NORMAL

## BETWEEN SCLEREID CLUSTERS

HERE THE CELLS LARGEST, WALLS THICKEST, SHAPE MOST ANGULAR & TANG. EXTENDED (TO 60μ) CELL CONTENTS SAME PATTERN,



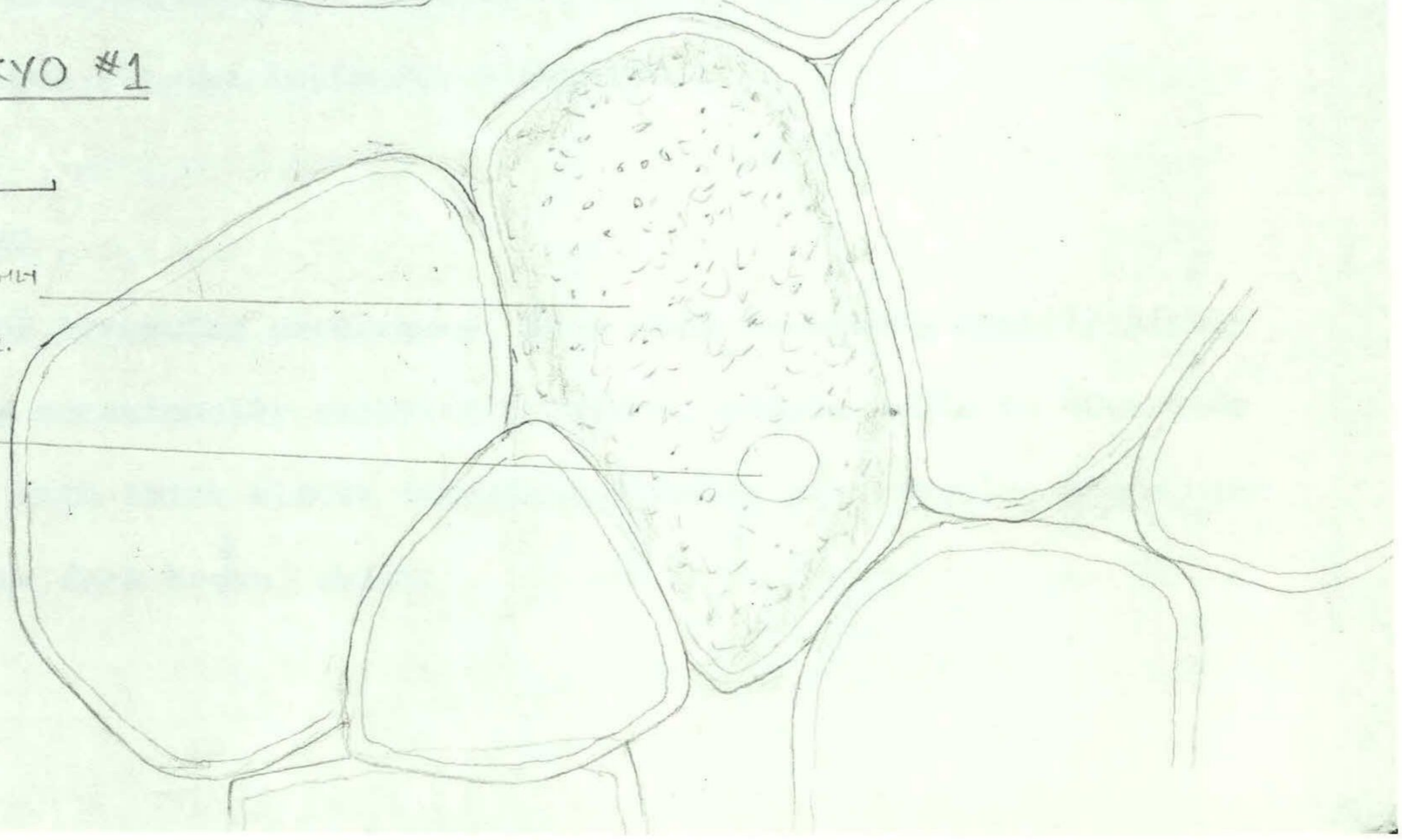
## EMBRYO #1

20μm

CONTENTS UNIFORMLY GREY FINELY TO COARSELY GRANULAR. VACUOLE POORLY DEVELOPED.

LIPID GLOBULES OCCASIONAL.

SOMETIMES AS THIS (CELL) DENSER AT EDGE



ANATOMY

CHALAZA

Upper Chalaza: cuticle ± nil or very thin.

O.E. a single layer of prostrate extended polygonal cells. Walls relatively thin, 1-2um thick, the o.p.w. not very much thicker than the others. Cells 9-10.5um tall and 35um (20-45um) wide. Contents living, translucent to pale brown, notable for the lack of cohesion and the frequency of damage and disruption.

The cortex beneath fairly constantly of 4 cells thickness (occasionally 3-5), the cells much larger, usually prostrate, extended polygonal also, but taller in relation to width: 20-30(-35)um tall and 30um to 55um wide (sometimes to 60um), rather variable. The walls 1-1.5um thick,the contents often live, pale brown.

Lower chalaza: fairly variable in thickness, 12-17 cells thick. Cells tanniniferous prostrate extended polygonal. Dimensions very variable, in some seeds the majority 7-10um tall and a large proportion 100-120um wide, in another seed, predominantly 15-20um tall and 60-70um wide. Vascularization also noticeably variable in extent, some parts almost free, others with three quite separate vascular bundles storied and running parallel (in one instance, 4 bundles.)

SUB-SEED-COAT

ENDOSPERM: of irregular occurrence. Even when detected, usually highly crushed. Very occasionally relatively intact, single cells to 40um wide and 8um tall with thick almost translucent walls of irregular shape, the contents dense dark brown, exist.

EMBRYO

#3. The outer epidermal cells (1-2 cells thick) always much smaller (6-9um) than those below and generally cuboidal to slightly tangentially extended. Cytoplasm brown, often agglutinated, nuclei much in evidence.

In some parts of the seed, the outermost of these cells are distinctly columnar, on average 7.5um tall and 4um wide. The contents together with those of the ± isodiametrically shaped layer below densely granular. Walls fairly thick, 1um. The cortex beneath of 5-8 or 8-11 cells thickness (depending on part of seed) over the sclereid clusters. The walls rounded isodiametric to slightly extended polygonal, the smaller sub-cuboidal cells of 15um diam., most numerous in the upper part, the large cells 34um long and 25um broad, more numerous at the base. Thickness as well as cell size apparently increasing along the gradient. In the spaces between the sclereid clusters, cells are larger still, less rounded and more angular, more polarized and more extended, reaching 60um in height. The contents living, the protoplasts pale yellow with nuclei sometimes agglutinated.

#2. The sclereid clusters are very well developed. They vary (in section) from 13-41 cells in width and are usually 9-12 cells in height. The intervening tissue is 3 to 4 cells wide or, more exceptionally as much as 14 cells. The individual sclereids are 25-34um wide and 80-100um high (markedly radially elongate), the walls comparatively thin: 3-5um. Sclereids at the top and bottom of the cluster are smaller in diameter, and more isodiametric. No crystal cell idioblasts were detected in association with this layer.

#1 Uniform, slightly extended polygonal cells 53um long, 35um broad (relatively little variation). Walls fairly thick, 1.5um. Lumina filled uniformly with grey granular contents, occasional lipid globules.

# PLATE 96

## CHISOCHETON MEDUSAE

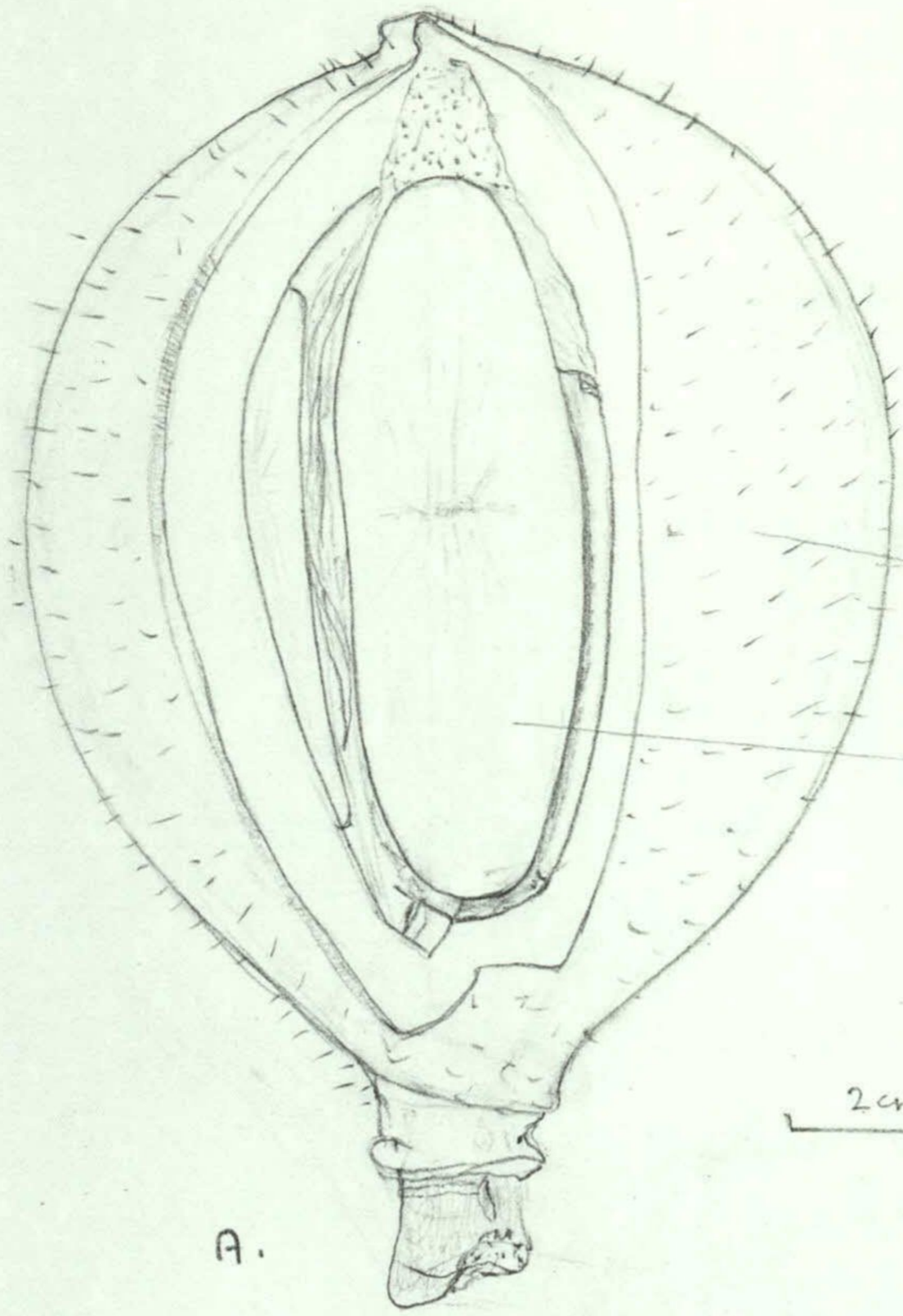
A FRUIT - POSSIBLY INDEHISCENT.

B-E SEEDS - SARCOTESTAL AND ORANGE-SEGMENT-SHAPED.

C. MEDUSAE 8002

## GROSS MORPHOLOGY

## FRUIT & SEED.



FRUIT - LATERAL VIEW, PART OF FRUIT WALL REMOVED

NO SUTURES VISIBLE ON FRUIT SURFACE

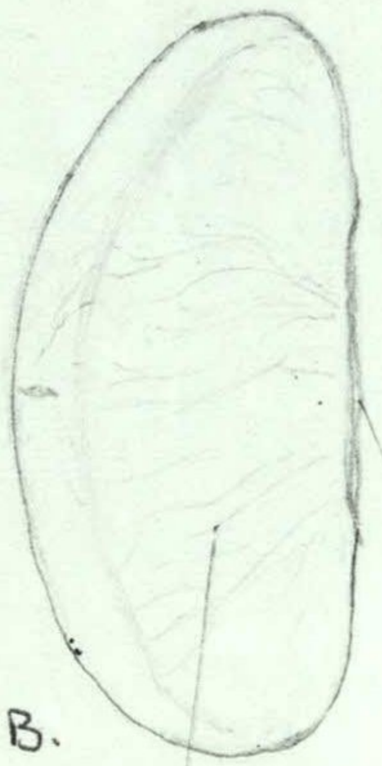
SEEDS: 7 OR 8 PER CAPSUE

2cm

A.

## SEEDS.

LATERAL VIEW

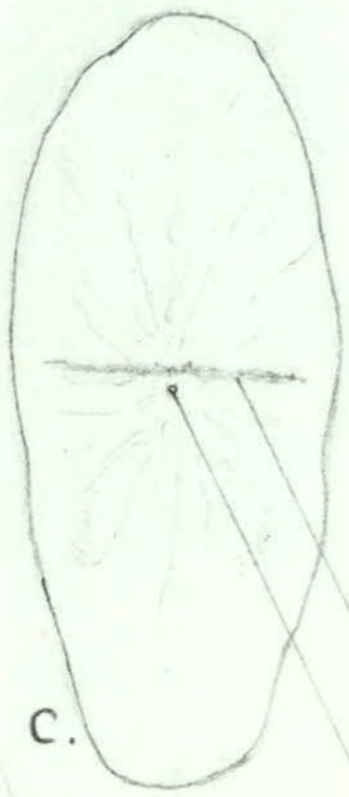


B.

VASCULAR BUNDLES CLEARLY VISIBLE ON SURFACE RADIATING FROM HILUM, CONVERGING ON THE MICROPYLE.

HILUM: NARROW & LONG

DISTAL PLAN VIEW



C.

TRANSVERSE DEPRESSION IN SEED SURFACE MARKING DIVISION BETWEEN CULLATERALS.

MICROPYLE - VERY SMALL. (c. 0·5mm ø)



D.

DORSAL PLAN VIEWS (VARIATION)



E.

2cm

PLATE 97

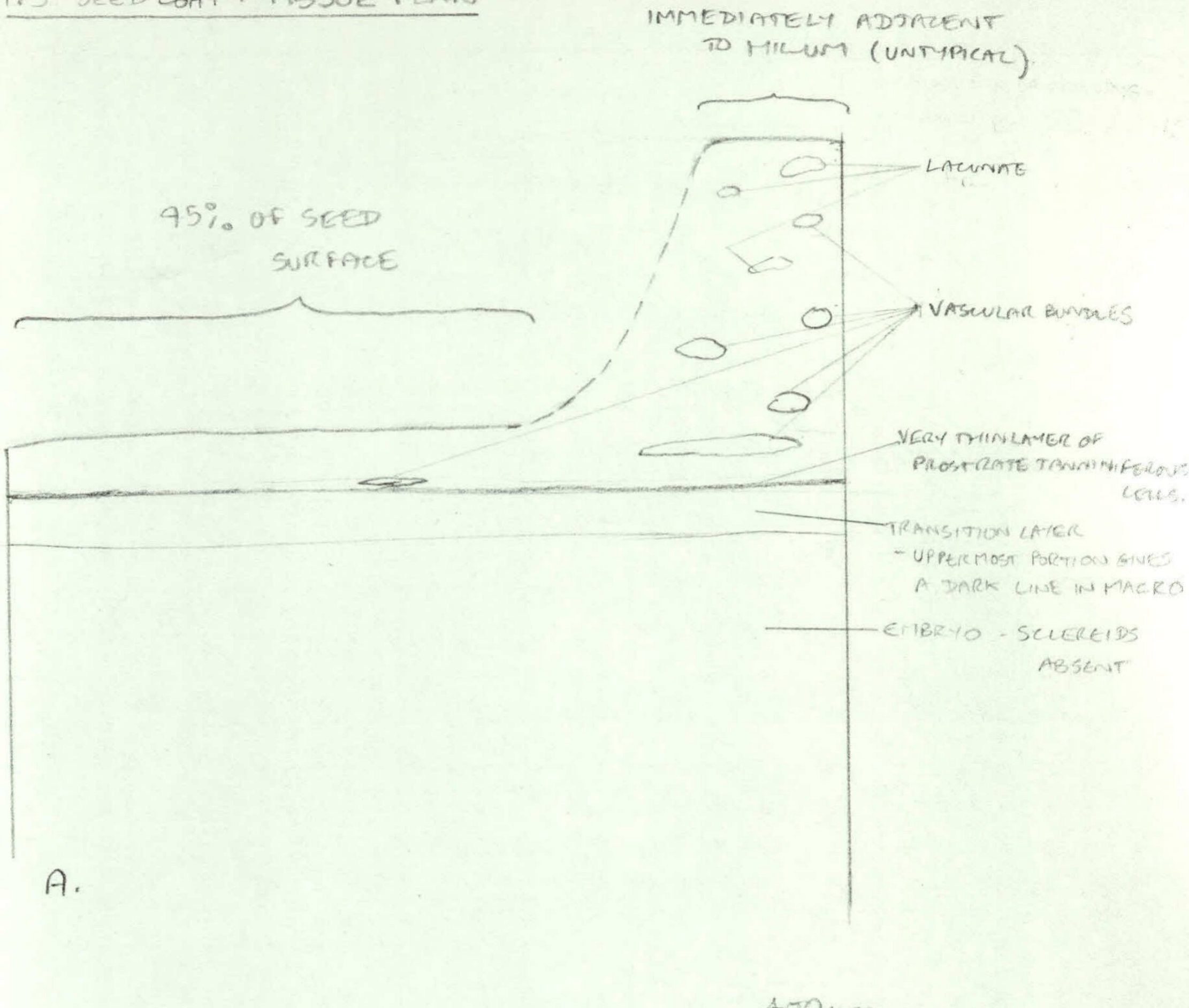
CHISOCHETON MEDUSAE

A. VARIATION IN STRUCTURE OF SEED-COAT.

B. DISPLACEMENT OF MICROPYLE FROM COTYLEDON SUTURE.

MEDUSAE 8002.

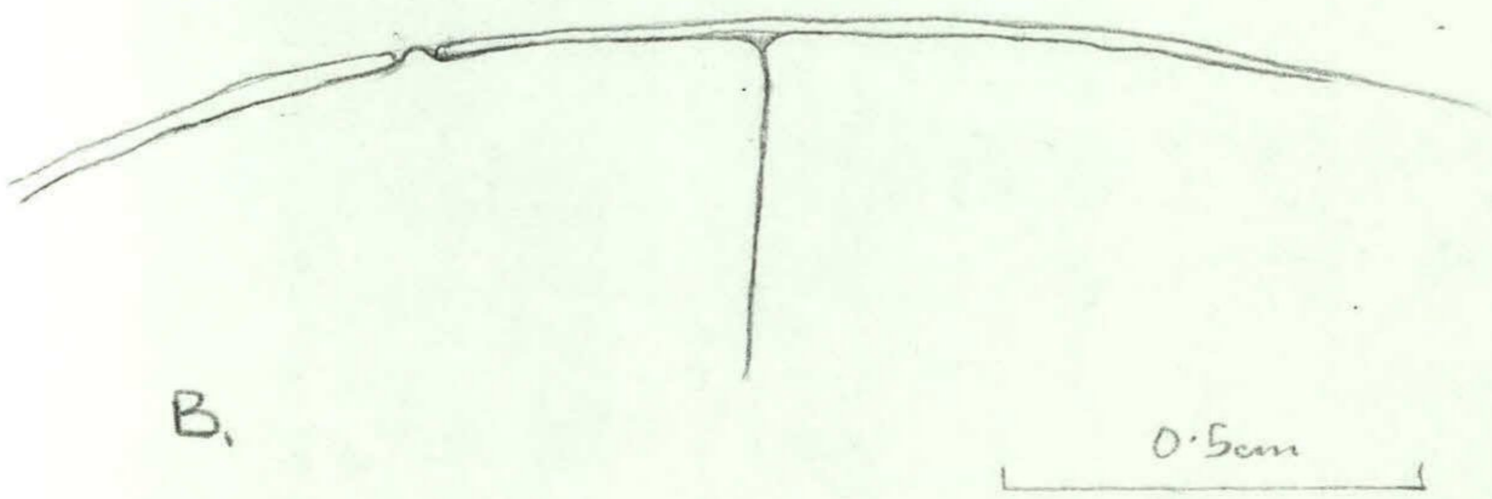
## T.S SEED COAT . TISSUE PLAN




A.

## COTYLEDON JUNCTIONS & MICROPYLE

NOTE: MICROPYLE DISPLACED FROM COTYLEDON SUTURE




B.

# PLATE 98

## CHISOCHETON MEDUSAE

A-D. SHAPE OF AERENCHYMATOUS CELLS FROM UPPER CHALAZA: NOTE INTERCELLULAR ARMS.

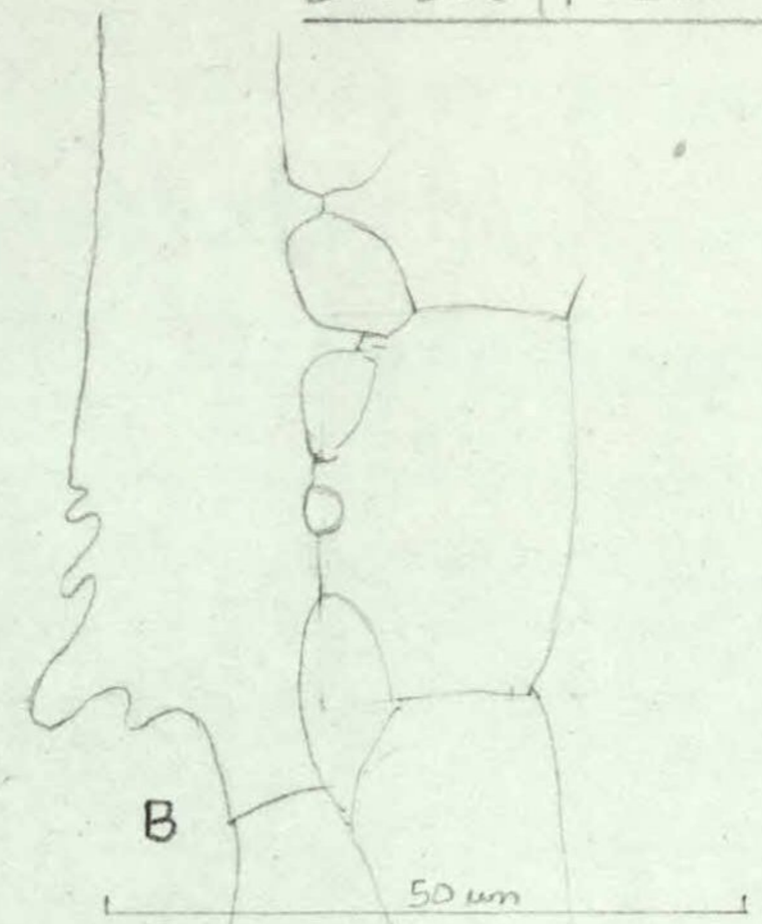
E. STRUCTURE OF OUTER EMBRYO. NOTE ABSENCE OF SCLEREIDS.

# C. MEDUSAE 8002

PLAN VIEW EPIDERMAL CELLS




UPPER (FLESHY) CHALAZA




VERY TYN WALLED, PALE BROWN, GRANULAR CONTENTS. TISSUE V. EASILY DESTROYED IN SECTIONING. IN THICK SECTIONS, NO DETAIL. CELLS HIGHLY ARMED.

CORTICAL CELLS




ARMS BETTER DEVELOPED

NOTE: THE TREND FOR CONVENTIONAL INTERCELLULAR CONNECTIONS ON ENDWALLS, & ARM CONNECTIONS ON LONG WALLS.




DRUSE IDIOBLAST
HOST CELL LESS EXTENSE

# L. S. EMBRYO

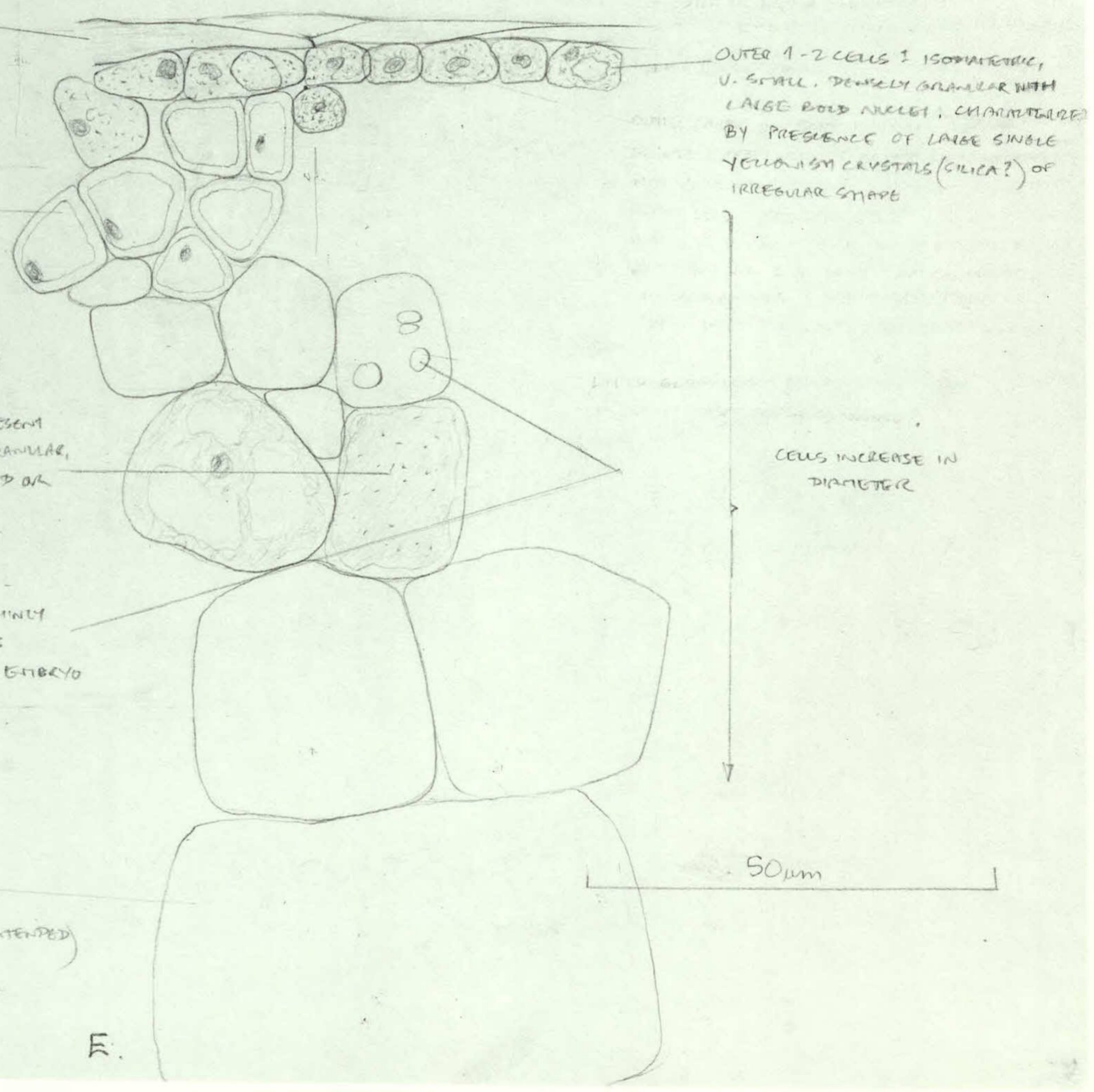


PLATE 99

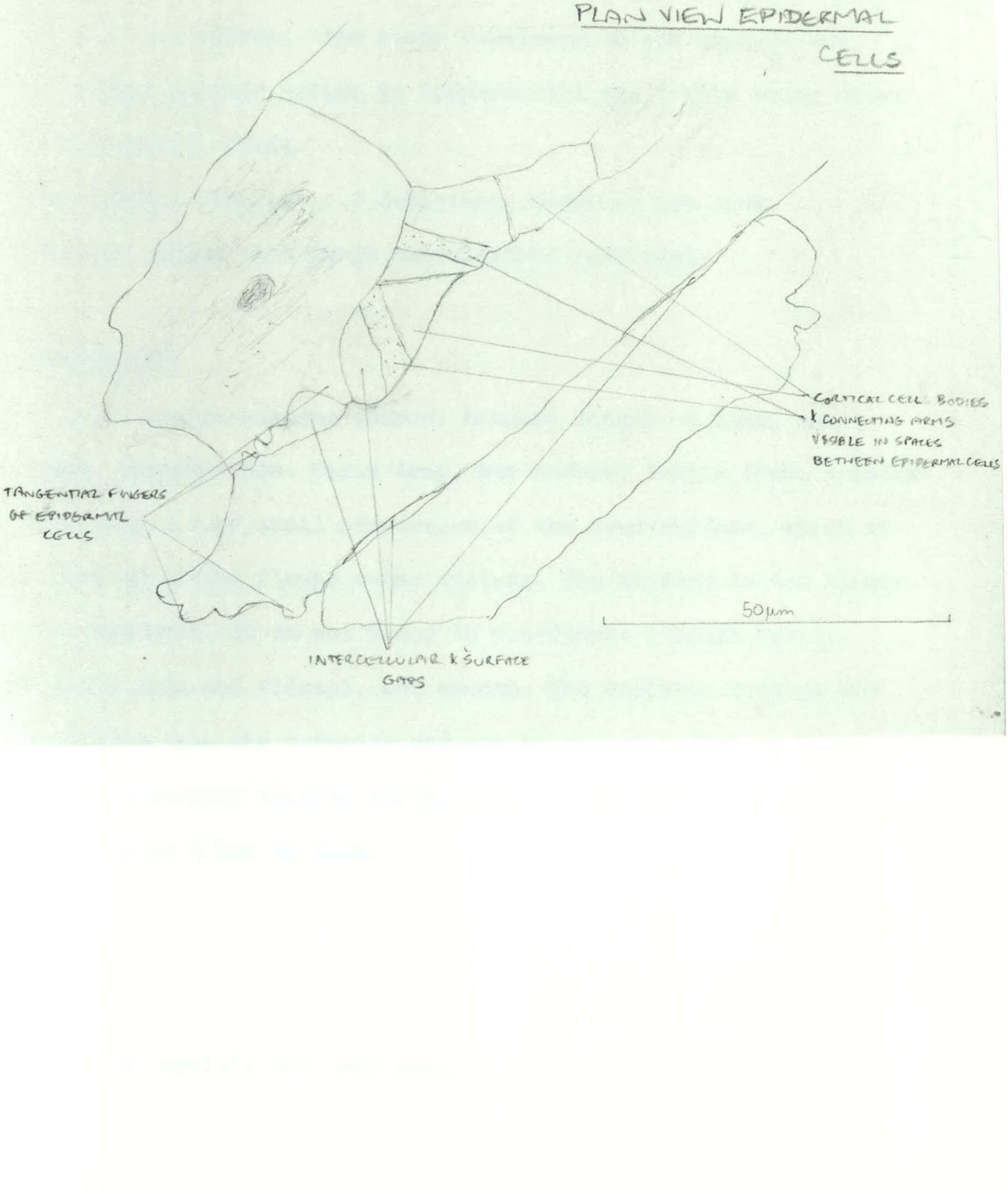
CHISOCHETON MEDUSAE

TESTAL O.E.: NOTE LARGE INTERCELLULAR GAPS (c.f. PLATE 66A OF MICROMORPHOLOGY).

C. MEDUSAE . 8002.



PLAN VIEW EPIDERMAL CELLS



C. medusae Airy Shaw

This description based on T.D.P. 8002

Collectors notes are absent for seeds from this collection, indeed from three of the four spirit collections at FHO, perhaps suggesting tardy dehiscence. Mabberley (1979) suggests that dehiscence is delayed until sometime after the abscission, descent and impact of the fruit. One collection, (T.D.P.7913), mentions that the fruits dehisce on the tree, dehiscing into 3-4 valves, 'the seeds remaining in the capsule and rotting', whilst another refers to (apparently) the fruits being eaten by squirrels (T.D.P. 7912).

Mabberley (1979): 'fruits....? dehiscent; seeds to 5cm long, orange-segment shaped with dense vascularized sarcotesta'.

GROSS MORPHOLOGY

Seeds 7 or 8, orange-segment-shaped. Longest length to 55mm, axial length 25mm, breadth 25mm. Hilum long, but narrow: length 25mm, breadth 3-4mm, covering a very small proportion of the seed surface, which is largely made up of the fleshy outer chalaza. The surface is not glossy, rather, a fine matt. It is not prone to scurfiness (though easily damaged being thin and flimsy), but smooth. The vascular bundles are clearly visible from the exterior and can be traced radiating from the hilum, then converging towards the micropyle. The micropylar pore is very small, about 0.5mm in diam.

ANATOMY

CHALAZA

Upper chalaza: cuticle not detected.

Epidermal cells: large, radially flattened, extended polygonal. Height 10um, width in t.s. 20-25(-30um), in L.S. 80um to 160um. The cells remarkable for their extremely thin walls (1um) and digital projections of these walls in the tangential plane(see Plates 98A, B & C) These create large apertures between epidermal cells, resulting in a perforate seed surface. Protoplast almost transparent, with nuclei.

The cortex is apparently 3 to 10 cells thick. The cells are very similar to the epidermal in dimensions, 10um tall and 22um or 120um broad depending on the plane of cutting. These cells also with projections, but these much longer and more frequent than those of the epidermis, the connecting arms with mean width c.6um. Walls about 0.5um thick. Lumina with almost transparent and rather large nuclei. Large (on average 16um) cluster crystals occur singly in less extended (but still digitate) cells and seem characteristic of this layer. Lacunae occur near the hilum in the limited area where the seed-coat becomes much thicker (see tissue plan) but this region has anatomy untypical of the rest of the seed surface.

This rather aerenchymatous tissue is extremely difficult to section being very easily damaged owing to its delicate construction.

Vascular bundles, with larger vessel diameters and less support tissue than in other species seen, occur between the upper and lower chalaza.

Lower chalaza: very poorly defined. At the base of the aerenchymatous tissue, 1-3 layers of prostrate lightly tanninized cells can be detected. These are extremely thin, 3-4um high and 20-30um long.

SUB-seed-coat

ENDOSPERM: none detected.

EMBRYO: the outer 1 to 2 cells smallest, cuboidal or slightly tangentially extended. occasionally columnar, 6-8um high and 8-10(-15um) wide, the walls to 1.5um thick. Contents densely grey-brown, granular with large nuclei. The layer characterized by containing large yellow crystals; one per cell, often occupying most of each lumen. Owing to the density of the protoplasm, these objects are normally only discernible by the yellow glow they refract, the shape(irregularly isodiametric) being obscured.

Below the epidermal layer, the cells are ± isodiametric, though sometimes slightly extended (but not polarized). The outer 2-3 cells have thicker walls (to 2um) but walls further in are decidedly thin, less than 1um. Cell size gradually increases from 11um diameter below the epidermal layer to 50um(-70um) lower in the embryo. The contents are very pale grey, almost transparent, and finely granular, sometimes with lipid globules.

Dysoxylum descriptions are in MSS at Kew-the drawings (plates 105-121) are self-explanatory if considered together with the discussion.

Synoum glandulosum(Smith)A.Juss.

This description based on Symons 1491.

Collector's notes: none made.

GROSS MORPHOLOGY

Fruits loculicidally dehiscent, leathery capsules, 3(-4) locular, strongly 3(-4) lobed, roughly oblate, slightly sunken at base and tip, 15-19.5mm wide, 13-16mm long, pericarp wrinkled transversely outside, c. 0.6mm thick, inner third of fibrous endocarp, inner surface glossy,

continues on page 340.

337 - telephone call

PLATE 100

SYNOUM GLANDULOSUM

A-C FRUITS: 3-4-LOCULAR, DEHISCENT.

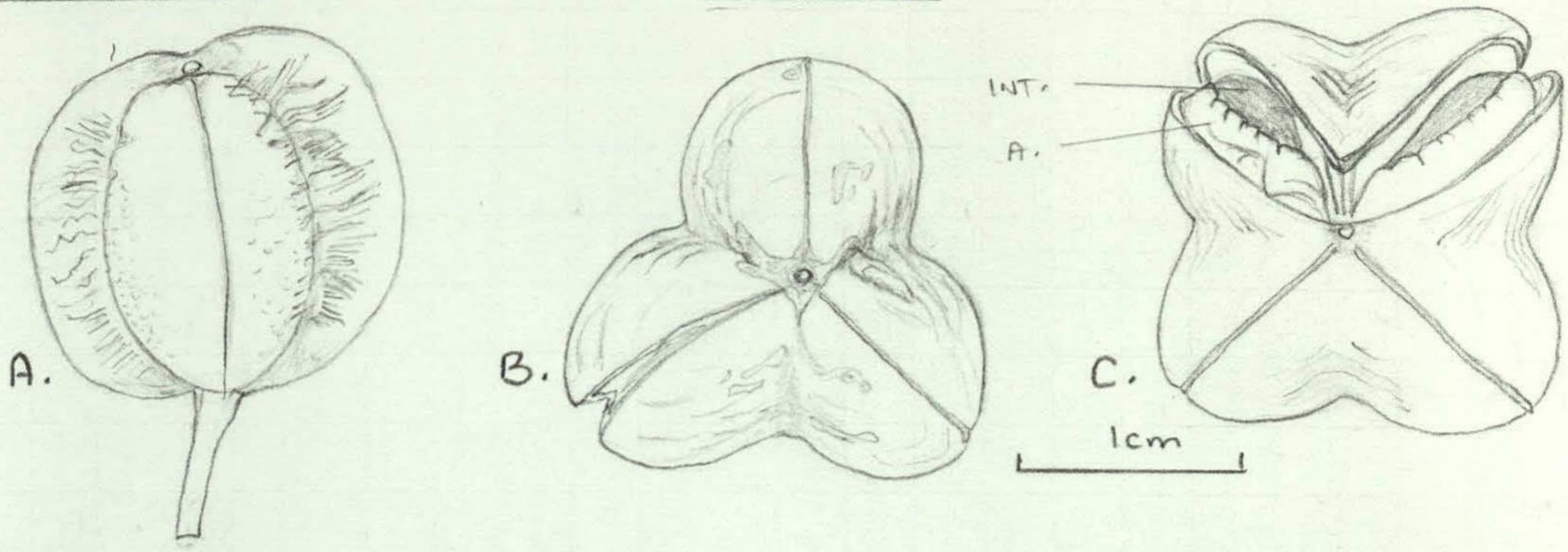
D-I SEEDS: UNITED BY A COMMON FUNICULAR-RAPHE-ARIL. NOTE THAT CHALAZA NOT FLESHY (H), RAPHE BUNDLES NOT UNITED (G), BUT HILUM COMMON (E). NOTE ALSO FOLDED COTYLEDONS (G) - BUT NOT ALL COLLECTIONS, AND SLIGHTLY INCLUDED RADICLE (J-K).

# Synoum glandulosum

VARIATION: 4 LOCULAR FRUIT, PLAN VIEW

FRUIT, LATERAL VIEW

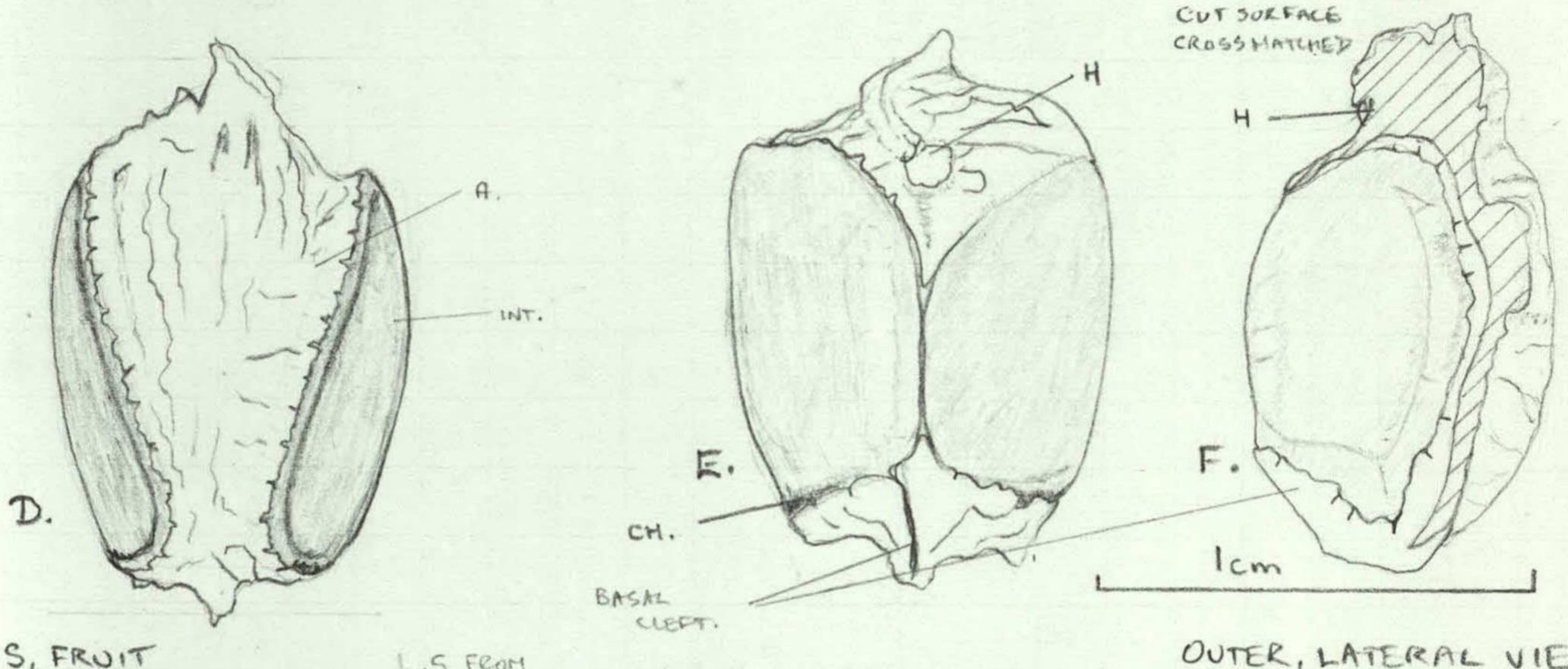
PLAN VIEW




SEED PAIR: DORSAL VIEW

SEED PAIR: VENTRAL VIEW

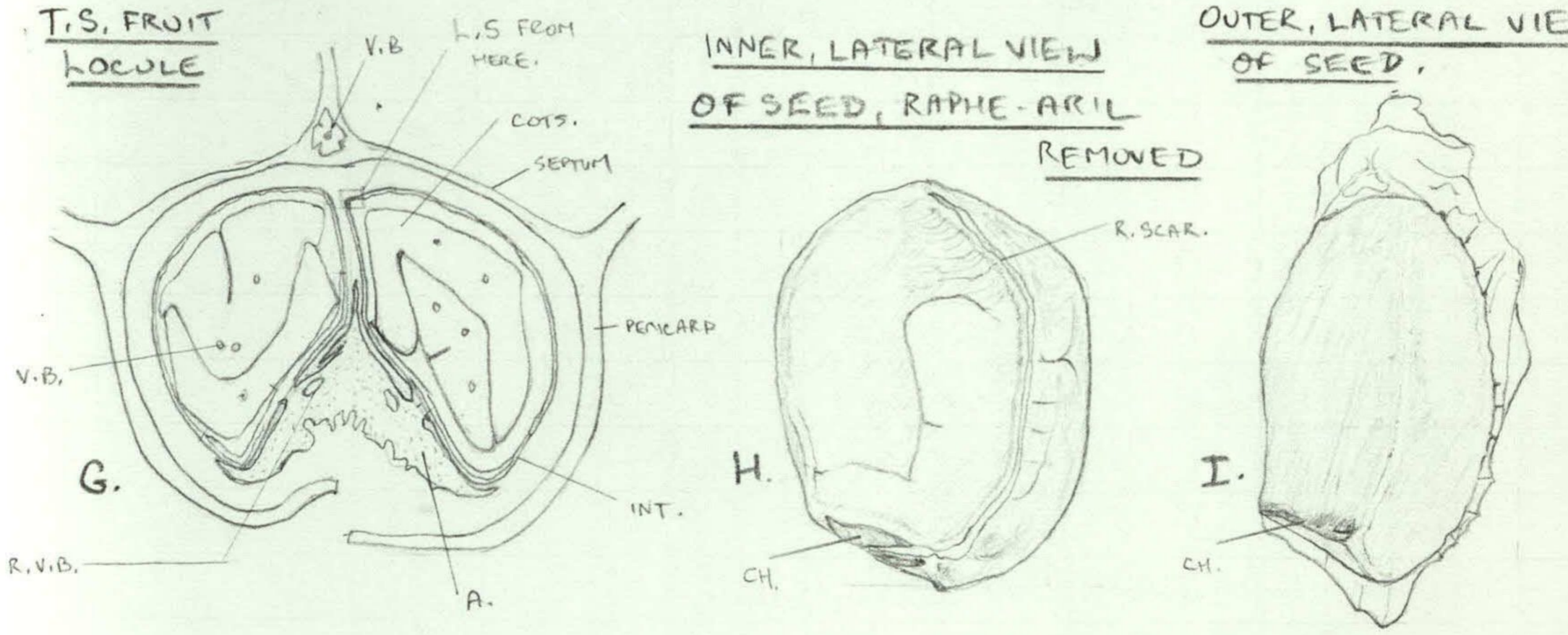
L.S. SEED PAIR




T.S. FRUIT LOCULE

INNER, LATERAL VIEW OF SEED, RAPHE-ARIL REMOVED

OUTER, LATERAL VIEW OF SEED.




EMBRYO UNFOLDED

EMBRYO INTACT

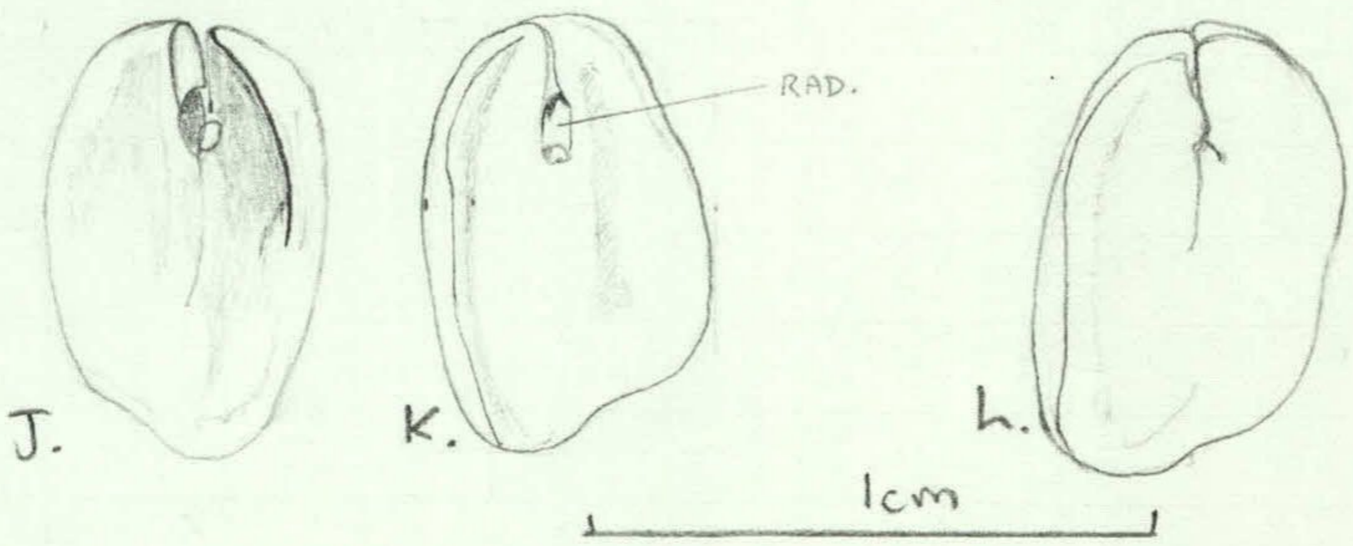


PLATE 101

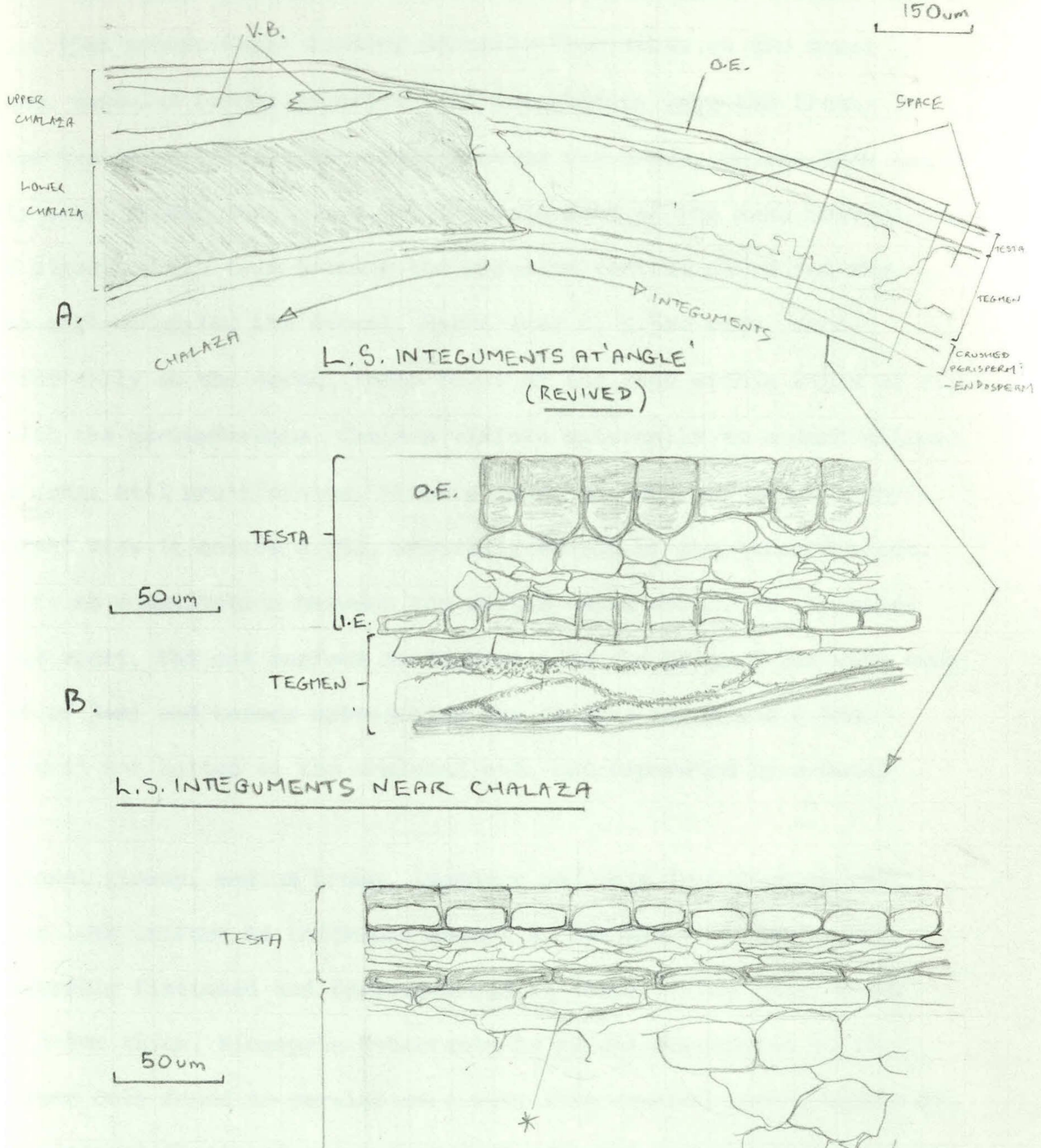
SYNOUM GLANDULOSUM

A-C SEED-COAT ANATOMY. NOTE BITEGMIC CONSTRUCTION, TESTAL I.E. WITHOUT CRYSTALS AND SIMILAR IN SHAPE TO O.E. (NOT USUAL IN MELIACEAE, BUT SEEN IN e.g. CHISOCHETON) AND WEAKLY DEVELOPED TEGMIC FIBRES, SOME OCCURRING IN THE TEGMIC I.E.

# Synoum glandulosum

## L.S. TRANSITION ZONE OF CHALAZA : INTEGUMENTS

### TISSUE PLAN



pale. Septum 0.2mm thick. Placenta c.1.5mm thick, vascular bundle 3-4 armed.

Seeds (1-)2 per locule, pendulous epitropous, collateral, with united raphe-arils. Detaching together as one unit from a common hilum c.1mm long, 1.75mm broad. Raphe running dorsally from hilum to the basal chalaza, vascular bundle exserted from integuments into the fleshy arillar tissue that fills the space between the seeds, unites them and partly wraps around them. In T.S., the main part of the seed resembles a third segment, its twin forming the opposite ventral third and the common aril occupying the dorsal. Raphe scar c. 0.5mm wide, runs longitudinally on the dorsal inner facet of the seed within 2-3mm of its rim with the circumference. Chalaza visible externally as a dark ellipse 5-8mm long. Aril proliferates, thickest over the chalaza and micropyle. In dorsal view it covers c.75%, ventrally 40-50% of the twinned seeds. There is no constriction between the united raphe-arils. If the seeds are cut apart, the cut surface is largest near the hilum ( 3mm wide over an arc of 3mm) and tapers approaching the chalaza to only c.0.5mm. Raphe-aril not united at the chalazal end, but separated by a basal cleft.

Seed-coat glossy, medium brown, leathery and thin (c.0.25mm thick), more or less uniform in thickness except at chalaza (c.0.5mm thick). Transversely flattened and faceted ovoid in shape 9-12mm long, 6-7mm wide, 3-4mm thick. Micropyle detectable by slight depression at tip. Endosperm only found to persist as a very thin crushed layer. Embryo of two collateral flattened cotyledons each with 2-3 longitudinal vascular bundles. Cotyledons usually split, plicately folded and wrapped one around the other. Radicle c.1.25mm long, included by same. Cotyledon clefts extend from micropyle to radicle, then continue as furrows.

ANATOMY

TESTA

Cuticle: present?

O.E. single layer of prostrate, shortly rectangular (to shortly columnar) cells 20-56um wide, 22-23um high, o.p.w. slightly convex or tabular, translucent medium orange, 7-16um thick; i.p.w. much thinner, anticlinals 1.5um thick, lumina pale brown, sometimes with granular protoplasm. In paradermal view, isodiametric (rarely extended to twice as long as broad), (4-)5-7-sided, width varying by factor of >2 within 2 cell breadths.

Mesophyll 3-4 layers crushed thin walled parenchymic cells. When revived, prostrate elliptic, densely packed, c.15um high, 55um long. I.E. single cell layer distinctly developed with thick, translucent brown walls, sometimes with a very well developed o.p.w., but lacking crystals. Prostrate rectangular cells 4:1 to 1.5:1, 30-50um wide, 12-20um high, o.p.w. 4-6um thick. Expression of O.E. characteristics (thick o.p.w., cells large, shape approaching cuboidal, walls thick) intermittent but regular in clusters of 4-8 cells. Cells largely 4:1 prostate rectangular with thinner walls.

TEGMEN

Near chalaza 160um thick, but crushed to 25um within a few mm of chalaza.

Largely of large, very thin-walled parenchyma cells to 28um high, 35um wide. In this collection, highly disrupted: large damaged areas, perhaps incurred in sectioning but probably by intermittent drying out in storage or absorption during seed development.

Exotegmic fibres not conspicuous, but fibroid, weakly thickened longitudinal cells do occur intermittently at both outer and inner

epidermal layers near chalaza. In most of the seed-coat, parenchymic cells crushed, only remnants of scattered fibroid cells persisting ± intact, but seem partly absorbed. Fibroid cells 60-70um long, slightly tapered, rounded at tip, c.15um diam. in T.S., walls pale brown, c.5um thick, apparently slightly pitted.

ENDOSPERM/PERISPERM: two crushed zones of cells occur below the tegmen (where intact at chalaza), probably referable to these tissues.

CHALAZA

O.E. as integuments.

Upper chalaza. c. 20-40um thick, sparse parenchyma densely packed with horizontal vascular bundles.

Lower chalaza c.60um thick, of dark, densely coloured cells c.75um long, 15um broad, tightly packed, horizontally orientated.

VARIATION

2 further collections viewed:

1. Labelled 'Synoum glandulosum. Coll. F.R.I. Canberra, Woolgoolga. 10.10.71'

These fruits ruined by dehydration. One capsule 2-locular.

2. With label completely faded, except date: 10.2.64. The distinctive seeds must belong to this genus. Perfect condition.

One capsule 2-locular. Hilum always much larger, to 6mm wide and 5mm high. Vascular bundles clearly detectable at upper boundary as a pair of horizontal ellipses c.0.5mm long, separated by c.9mm. Common aril swollen, bold dorsal ridge corresponding to fruit suture.

Embryo not properly folded, radicle not included, but with clefts and furrows.

Testal O.E. with an intermittent but well developed hypodermis. Otherwise anatomy falls into range of variation for Symons 1491. Testal mesophyll crushed and distorted here also: this character not an artefact.

Pseudocarapa championii (Hook.f. and Thoms. ex Thwaites)Hemsl.

This description based on Mrs C.V.S.Gunatilleke s.n., Sri Lanka

Collector's notes: not available.

GROSS MORPHOLOGY

Fruit (three to) four-locular dehiscent capsules, shortly obovoid, to 22mm wide, 23mm long. Apex flattened, and slightly hollowed, base slightly tapered, sub-stipitate. Calyx persistent. Fruits held on woody pedicels 11-18mm long, c.3mm diam. Pericarp surface slightly puckered, sutures sunken. Centre of the valves sometimes with a faint longitudinal ridge. Pericarp c.1mm thick near the suture, outer part leathery-fleshy, inner cartilaginous, detaching cleanly from former. Placenta c.6mm long to 4mm wide, strongly 4-angled, the distal end blunt, four-armed and much enlarged, 8.5mm across, from which issue the funicles and around which the endocarps are notched.

Seeds (one to) two, superposed, per locule, usually slightly faceted by mutual compression with twin and united by their interlocking 'arils' into a single, roughly ellipsoid unit (cf. Cabralea), 13-15mm long, 6-8mm broad.

Hard part of seed ovoid (plan view), glossy, pale-medium chestnut brown, 8-10mm long and 7mm wide in plan view, c.5mm broad. Bi-convex in TS, the radius of the outer (dorsal) surface greatest. Axis of seed sometimes dorsi-ventrally bowed.

PLATE 102

PSEUDOCARAPA CHAMPIONII

A-C FRUITS: DEHISCENT

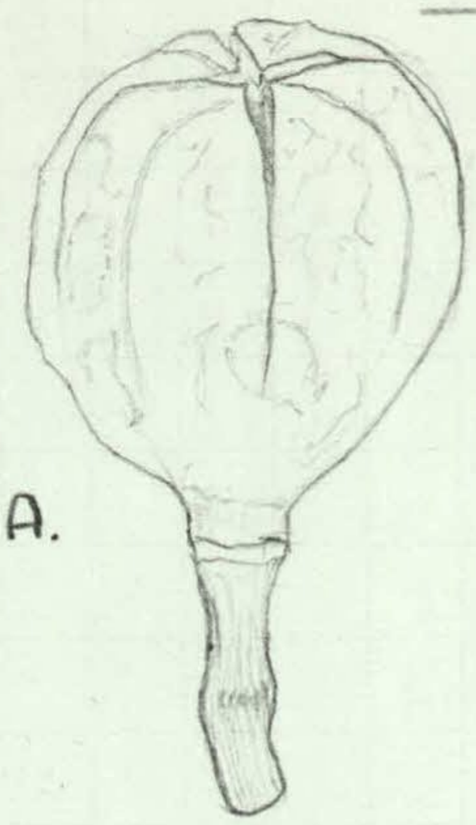
D-K SEEDS: UNITED BY ENTWINED FUNICULAR-RAPHE ARILS AS CABRALEA, BUT NOT AS SYNOUM

# Pseudocarapa championii

LATERAL VIEW
MATURE FRUIT

1cm

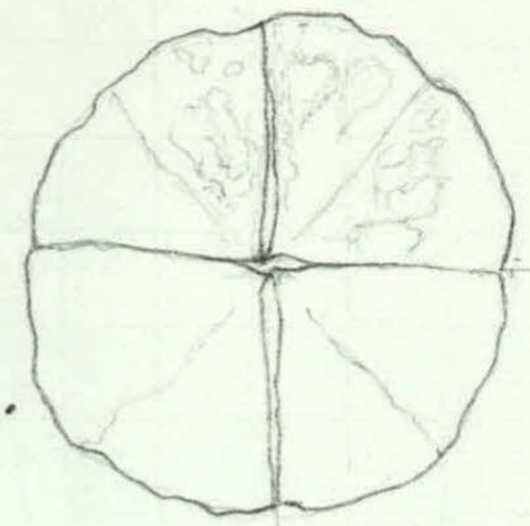
A.



MATURE FRUIT
PLAN VIEW

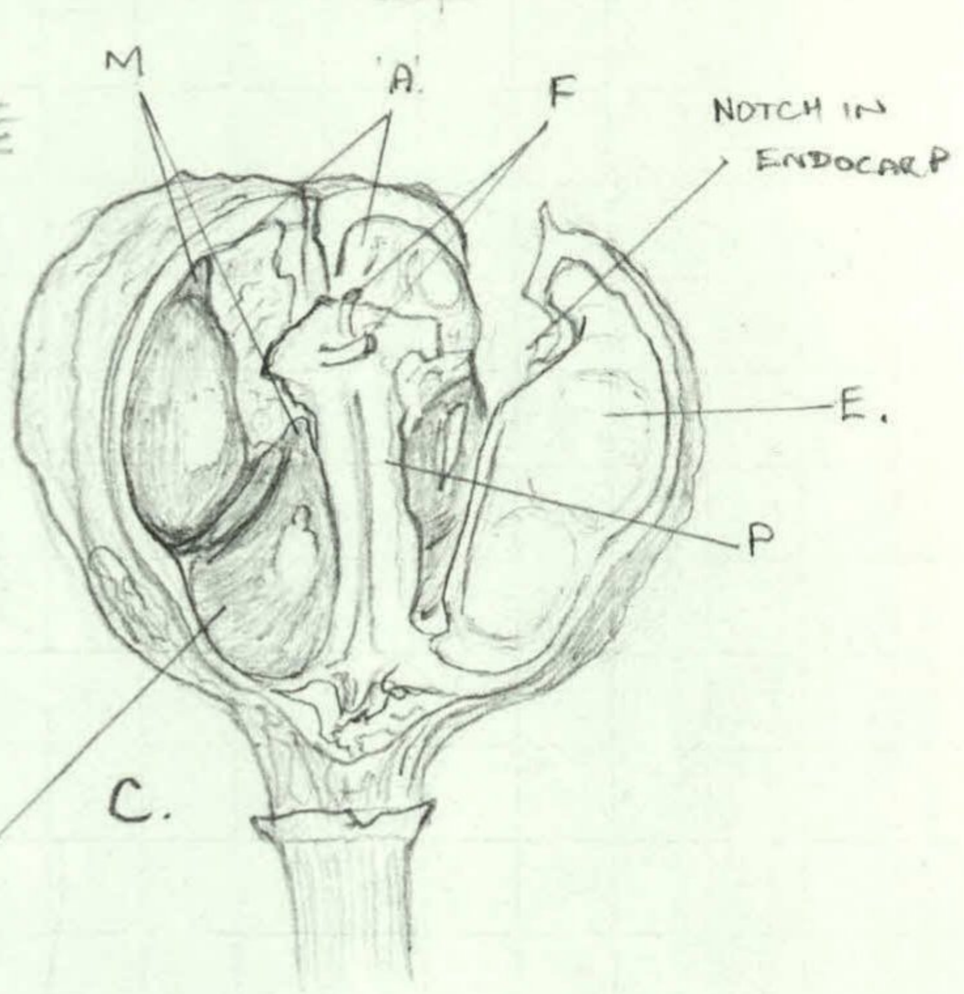
1cm

B.



LATERAL VIEW
FRUIT (ONE VALVE REMOVED)

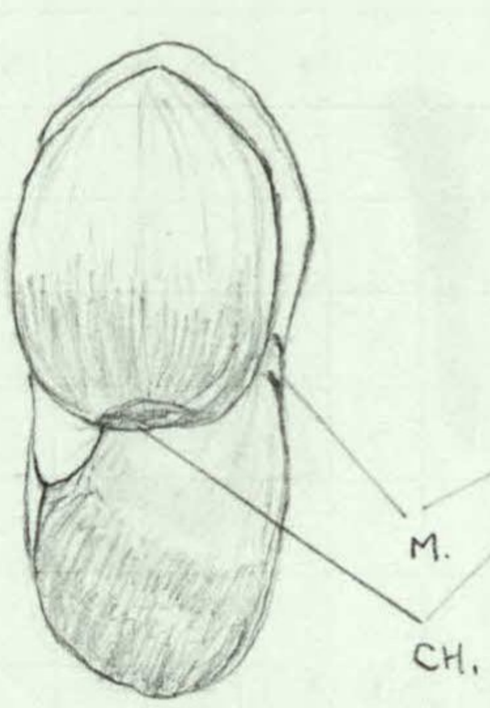
1cm




C.

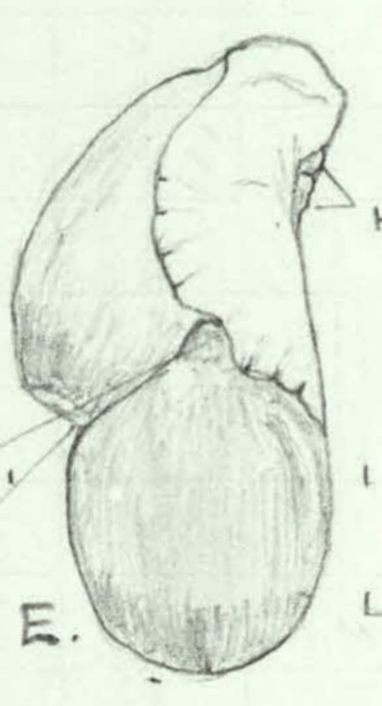
TWINNED SEEDS

DORSAL VIEW




D.

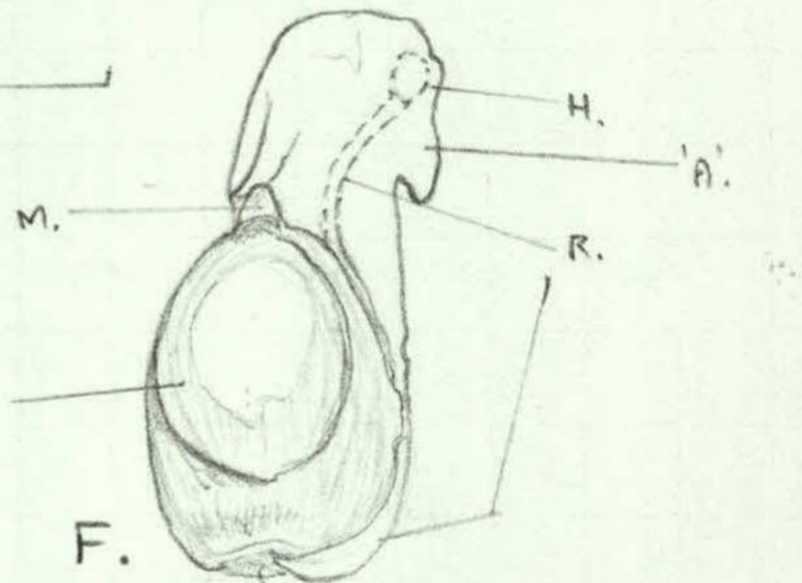
LATERAL VIEW




E.

1cm

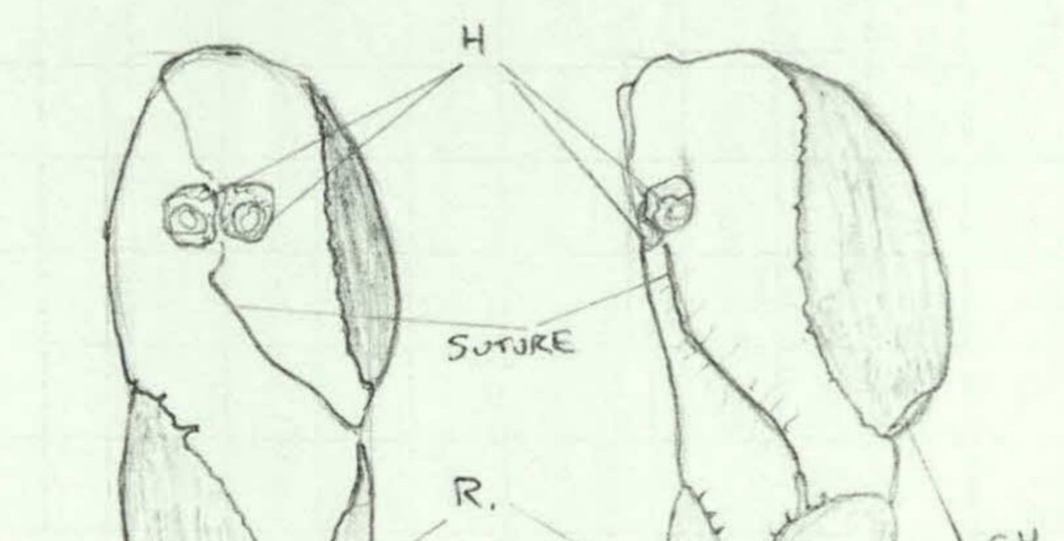
'DISTAL' SEED. VENTRAL VIEW




F.

VENTRAL VIEW

LATERAL VIEW




G.

H.

'PROXIMAL' SEED
WITH RAPHE 'ARIL'

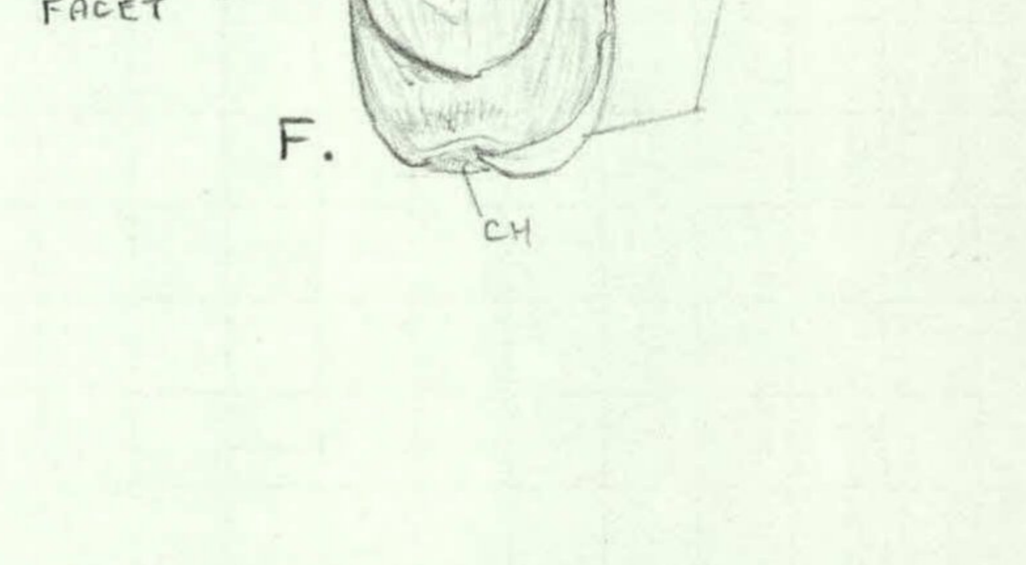
FLESHY MATERIAL REMOVED




I.

J.

L.S. PROXIMAL SEED




K.

PLATE 103

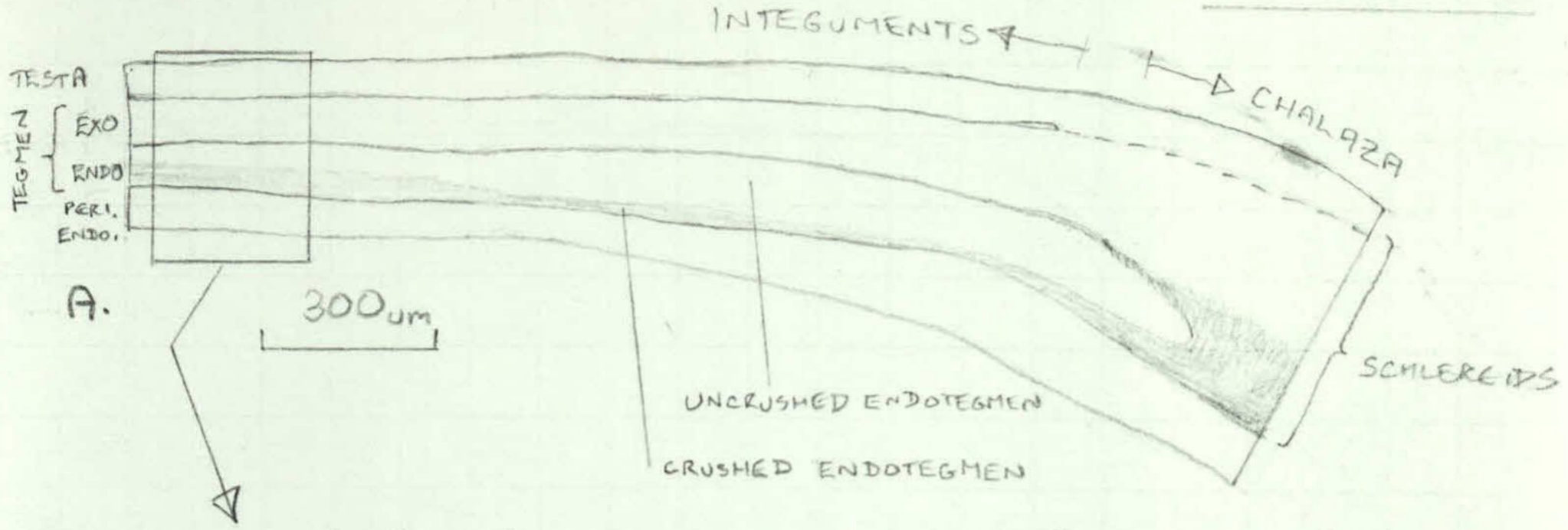
PSEUDOCARAPA CHAMPIONII

A-E SEED-COAT ANATOMY. NOTE BITEGMIC CONSTRUCTION AND STANDARD MELIACEAE PATTERN. c.f. RUAGEA AND CABRALEA

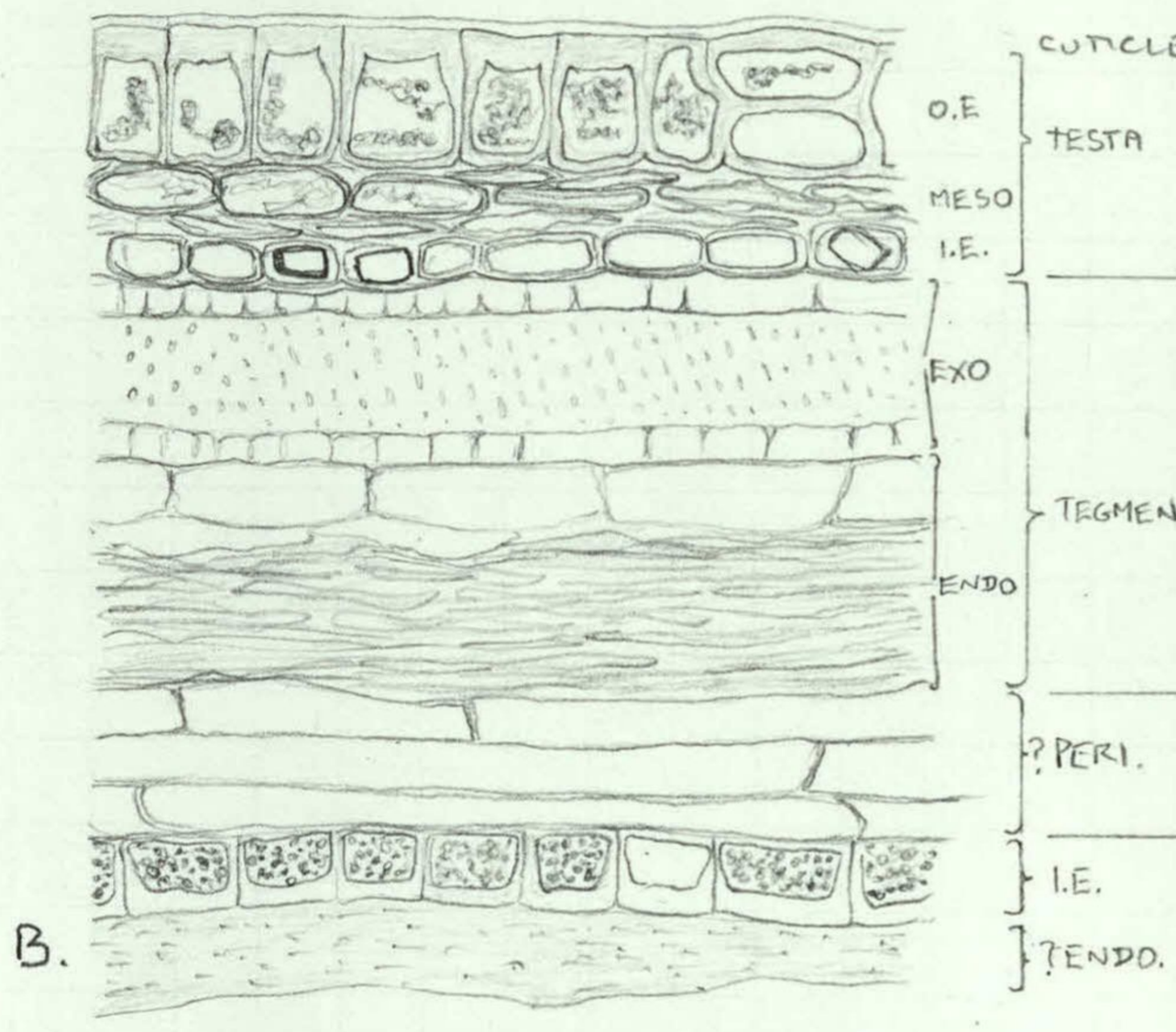
# Pseudocarapa championii

## L.S. CHALAZA: INTEGUMENTS TRANSITION ZONE

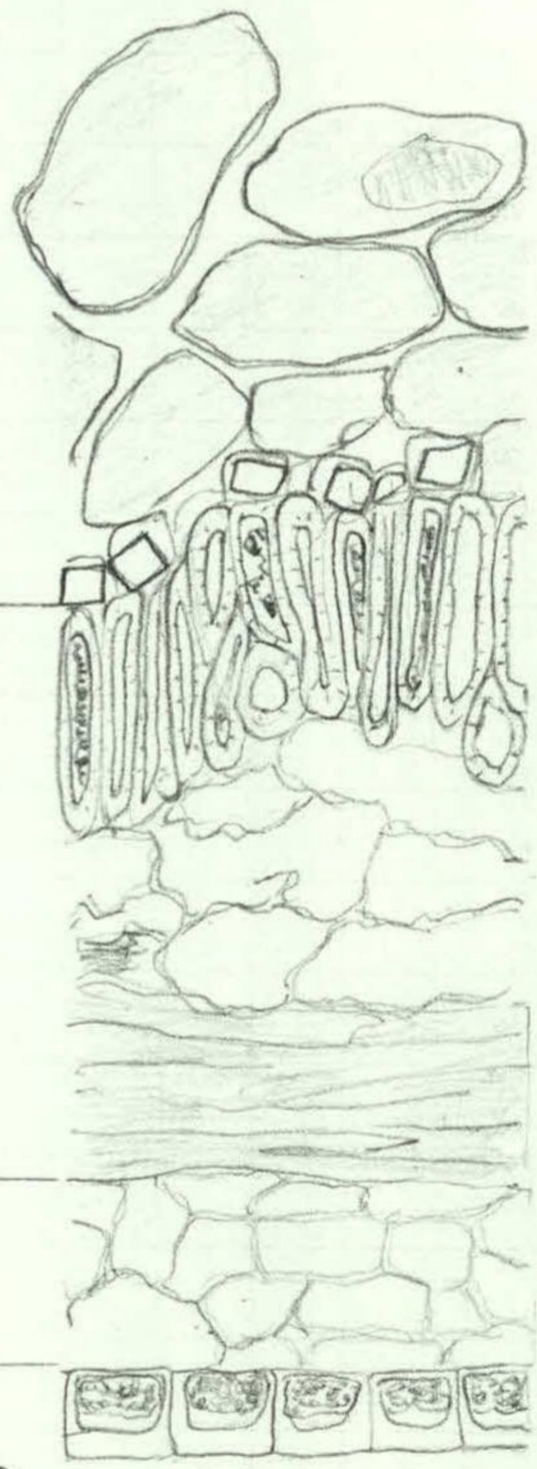
TISSUE PLAN



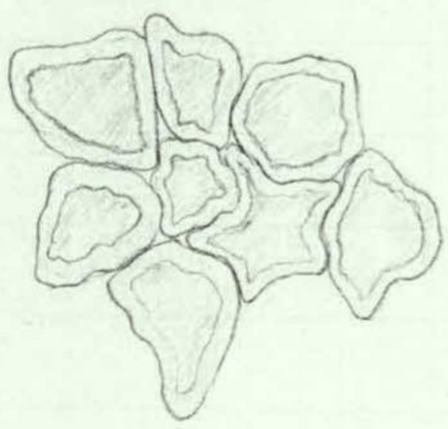

## L.S. INTEGUMENTS (DORSAL)




## T.S. RAPHE (VENTRAL)




## I.E. PERISPERM PARADERMAL VIEW




## T.S. RAPHE & INTEGUMENTS TISSUE PLAN

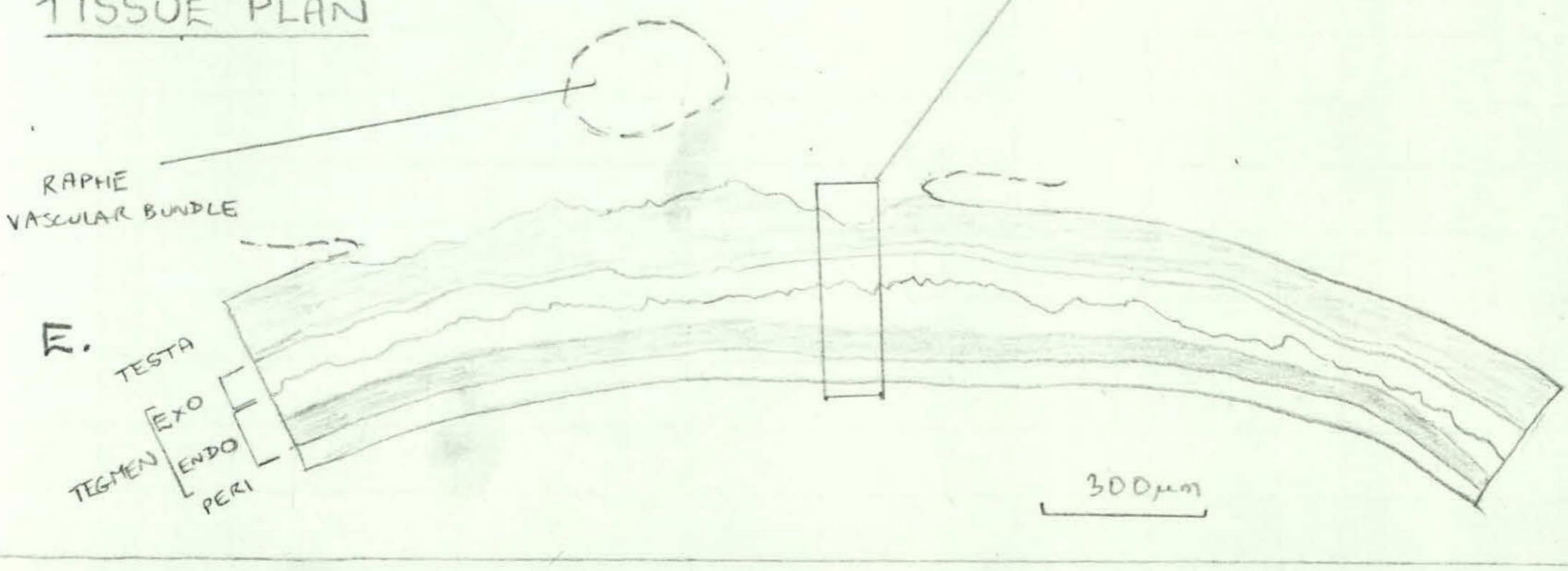


PLATE 104

(Courtesy of D.J.Mabberley)

SEED PRESENTATION IN DYSOXYLUM

A. DYSOXYLUM PARASITICUM

B. DYSOXYLUM ANGUSTIFOLIUM

C. DYSOXYLUM GRANDE

A

B

C

PLATE 105

DYSOXYLUM PACHYPHYLLUM

A-B DEHISCENT FRUITS

C-J SEEDS: PLACENTAL-FUNICULAR-RAPHE-ARILLATE.

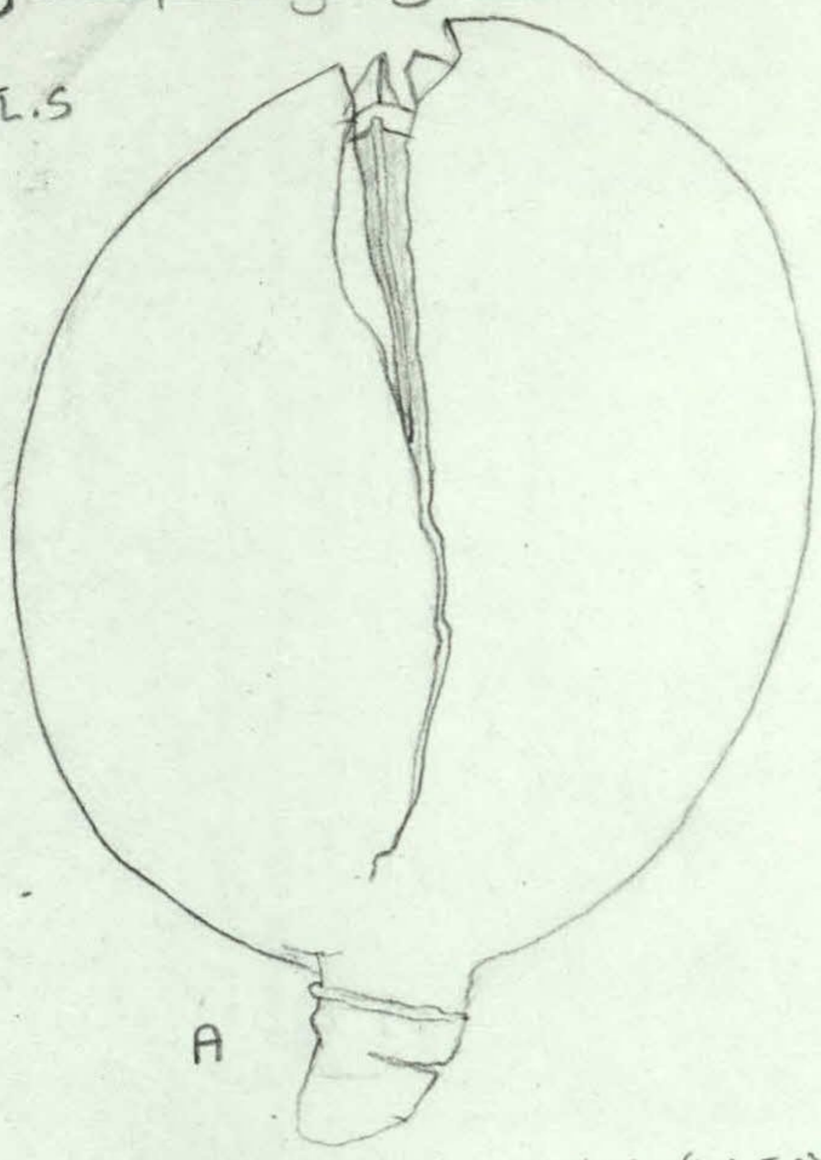
NOTE SWOLLEN, BUT HARD CHALAZA. MOST OF

`ARIL' IS THE FLESHY SEPTUM AND PLACENTA THAT

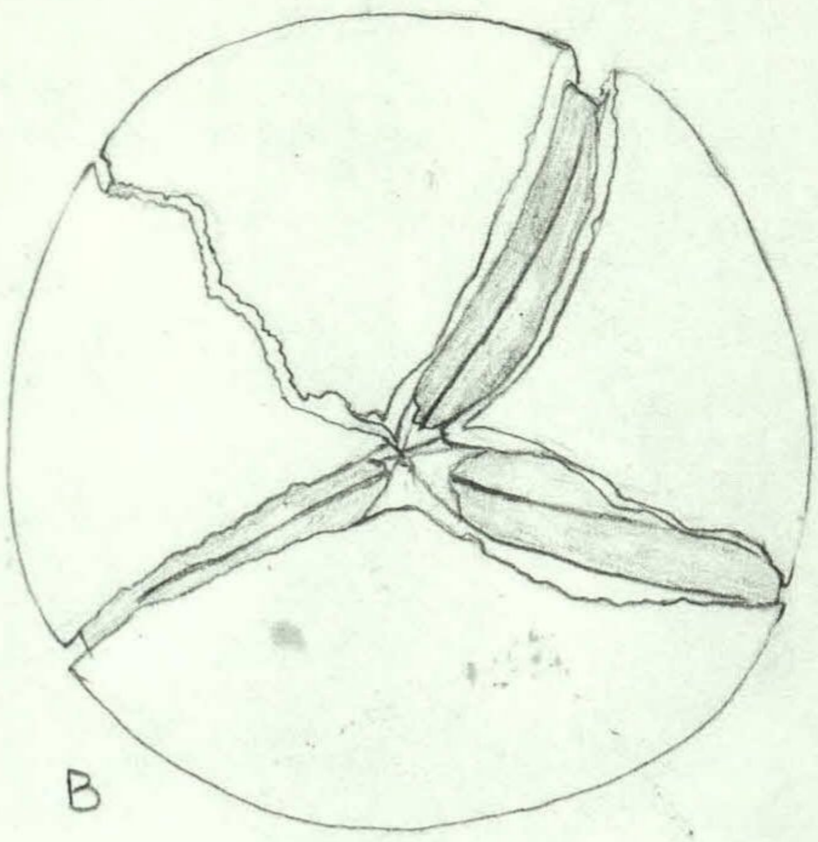
DETACHES WITH THE SEED.

# Dysoxylum pachyphyllum. Game s.n.

FRUIT, L.S
& PLAN
VIEW



A



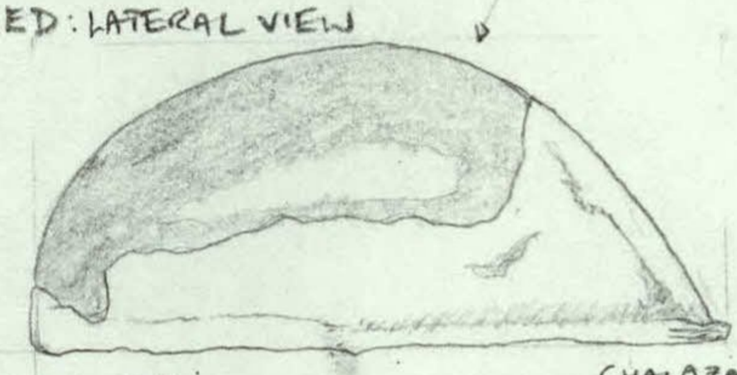
B

2cm

SEED 1. X2
WITH 'ARIL'

CUT 1 & 2, (L.S, T.S)

SEED: LATERAL VIEW



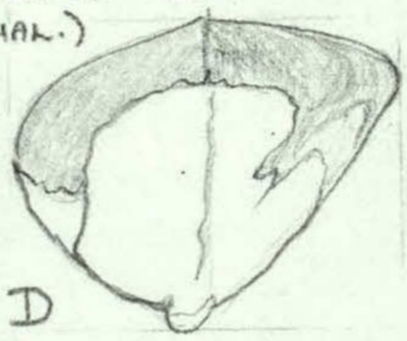
C

MICROPYLAR END

CHALAZAL END

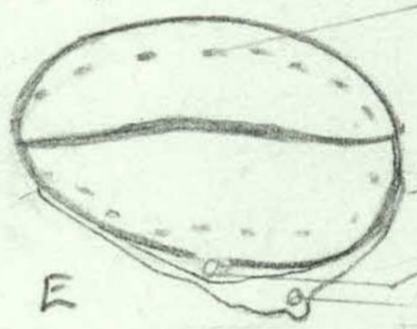
BASE

BASAL VIEW
(CHAL.)



D

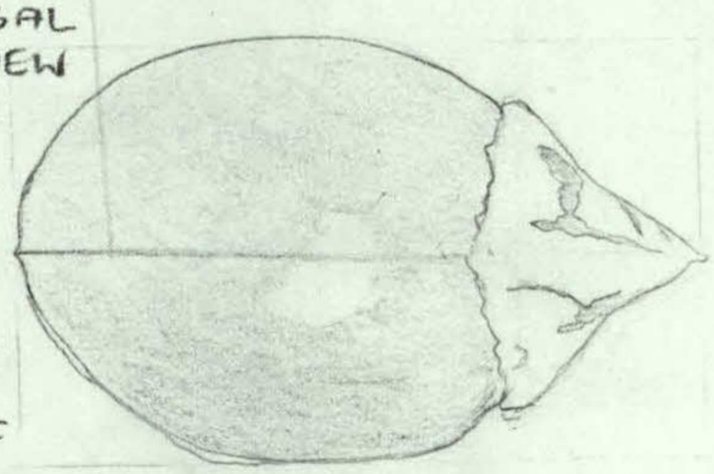
T.S.




E

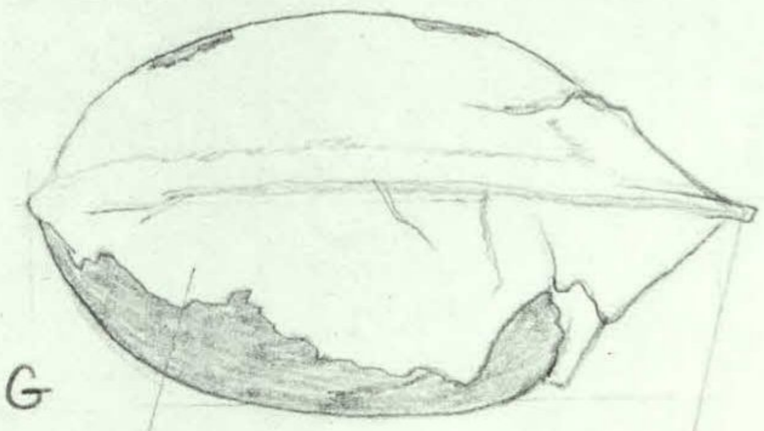
DORSAL RIDGE

DORSAL
VIEW



F

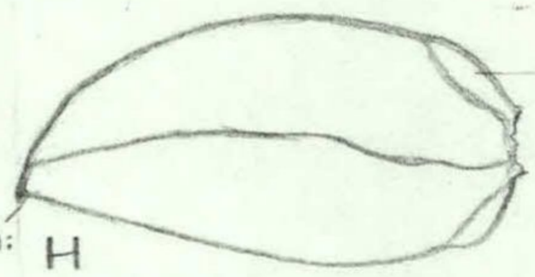
VENTRAL VIEW



G

L.S

SEED 2 x2
'ARIL' REMOVED



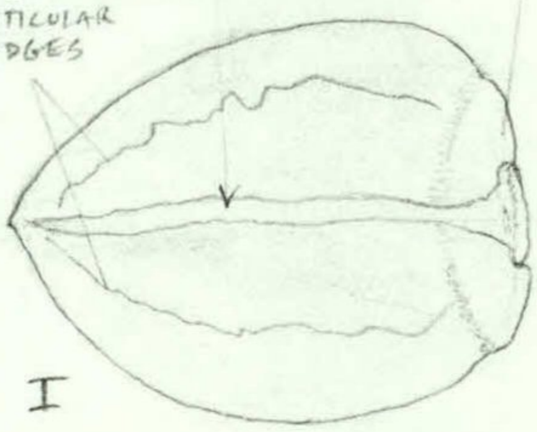
M: H

CHALAZA - SWOLLEN, BUT WITH IMPENETRABLE OUTER EPIDERMIS; NON FLESHY, EFFECTIVELY.

VENTRAL VIEW

CUT 3 (T.S)

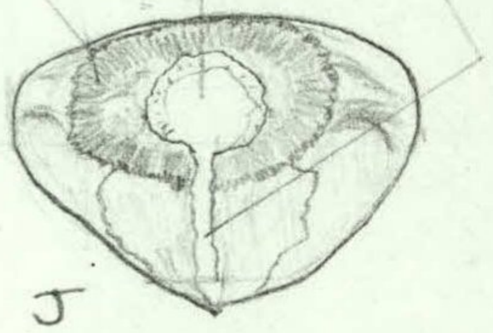
TWO IRREGULAR CUTICULAR RIDGES



I

'MAIN' HILUM

RAPHE HILUM



J

PLACENTAL
(≡ COLUMELLA) VASCULAR BUNDLE

'ARIL' DERIVED
FROM PLACENTA, ENDOCARP
& PARTLY, THE RAPHE.

PLATE 106

DYSOXYLUM PACHYPHYLLUM

TISSUE PLAN OF TRANSITION OF CHALAZA WITH THE TESTA AND TEGMEN

Dysoxylum pachyphyllum. Game s.n

L.S. TRANSITION ZONE : TISSUE PLAN

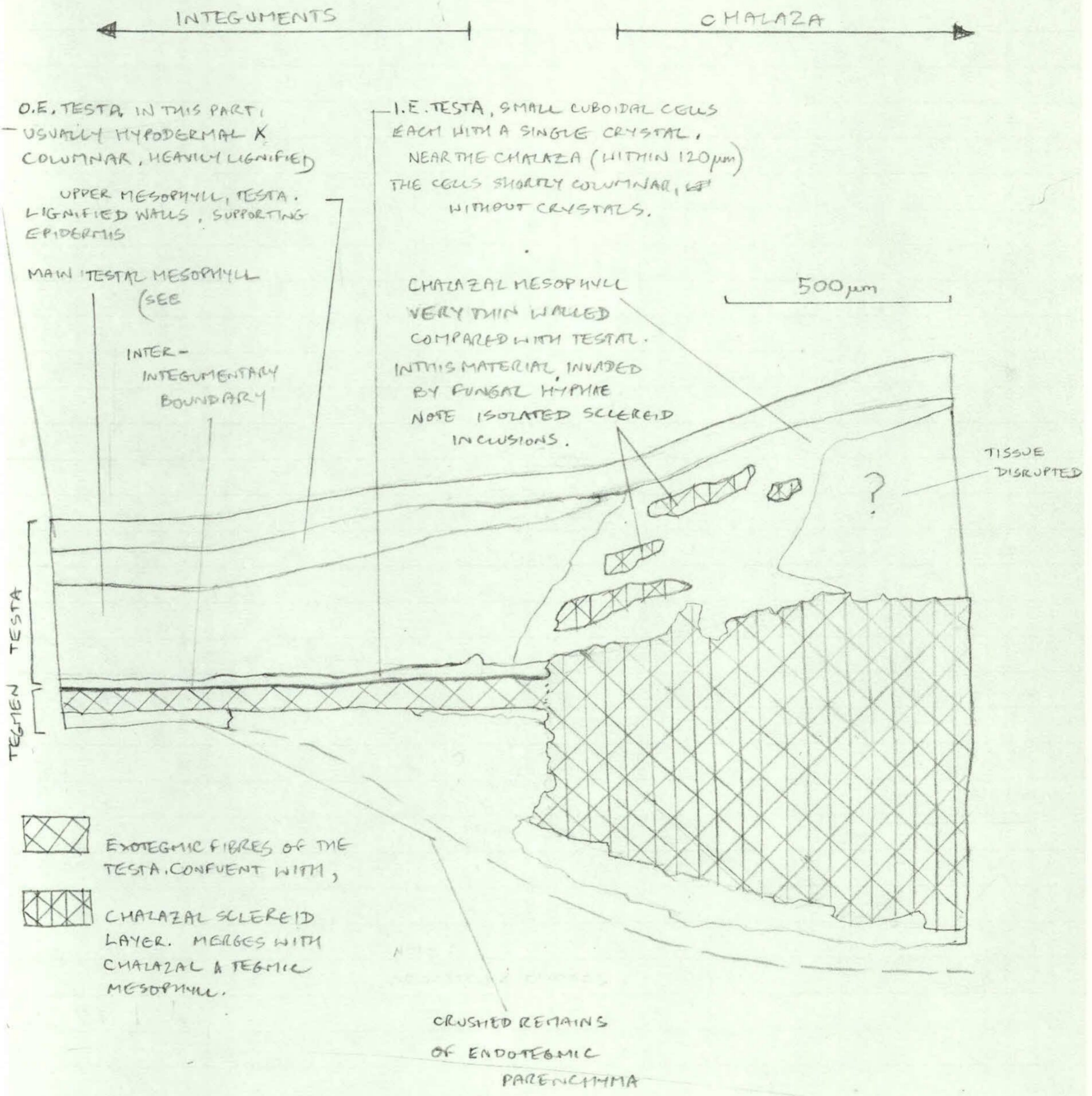


PLATE 107

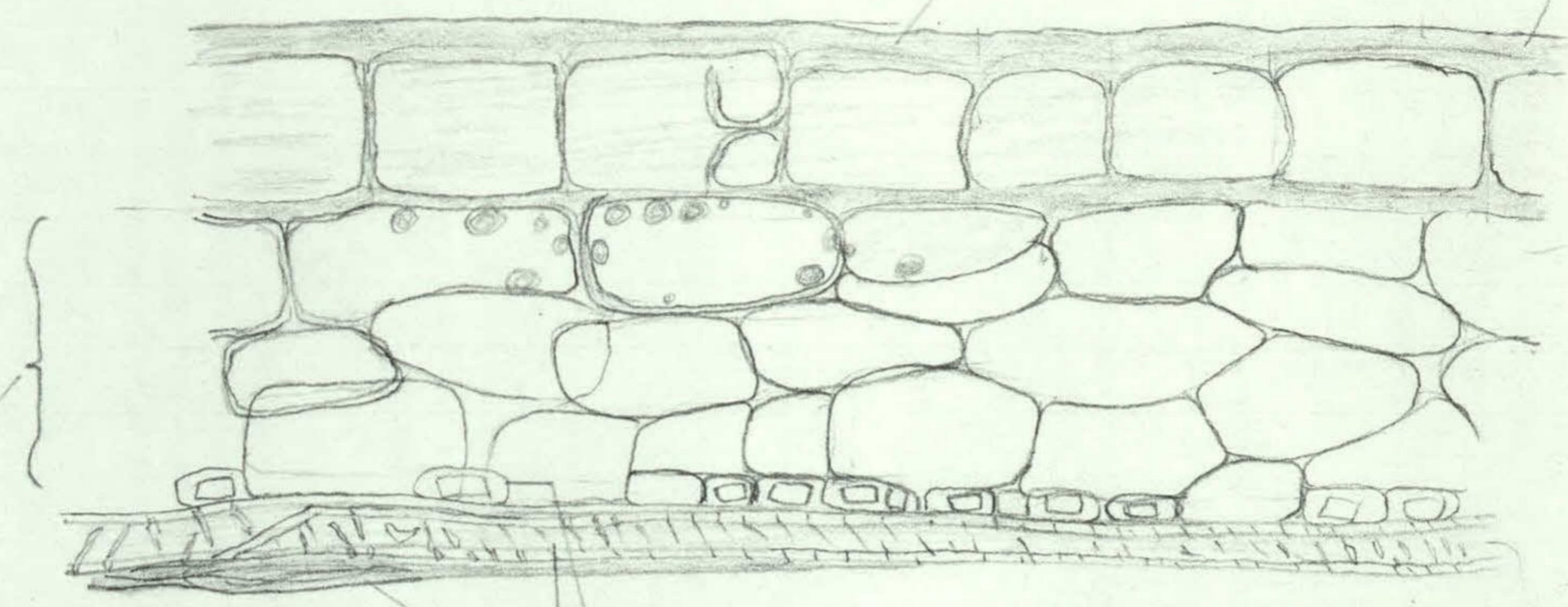
DYSOXYLUM PACHYPHYLLUM

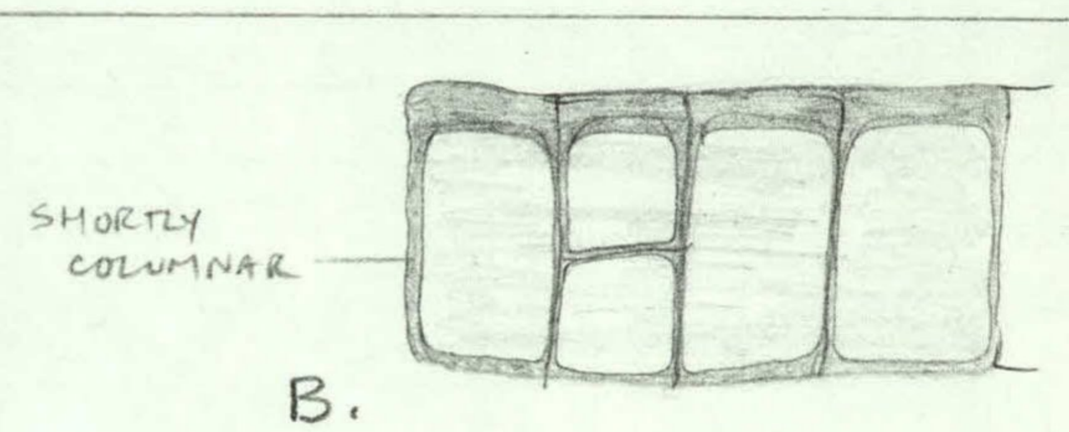
A. ANATOMY OF THE SEED-COAT (BITEGMIC PART). NOTE STANDARD MELIACEAE PATTERN AND PRESENCE OF `MARKERS': TESTAL I.E. CRYSTALS AND EXOTEGMIC FIBRES. NOTE (c.f. RUAGEA & CABRALEA) ABSENCE OF ENDOTEGMEN AND MORE WEAKLY DEVELOPED FIBROUS LAYER.

B. VARIATION IN TESTAL O.E.

Dysoxylom pachyphyllum Gamo s.n.

## L.S INTEGUMENTS




VARIATION - IN O.E. TESTA (HERE IN L.S)

100um

PLATE 108

DYSOXYLUM MACROSTACHYUM

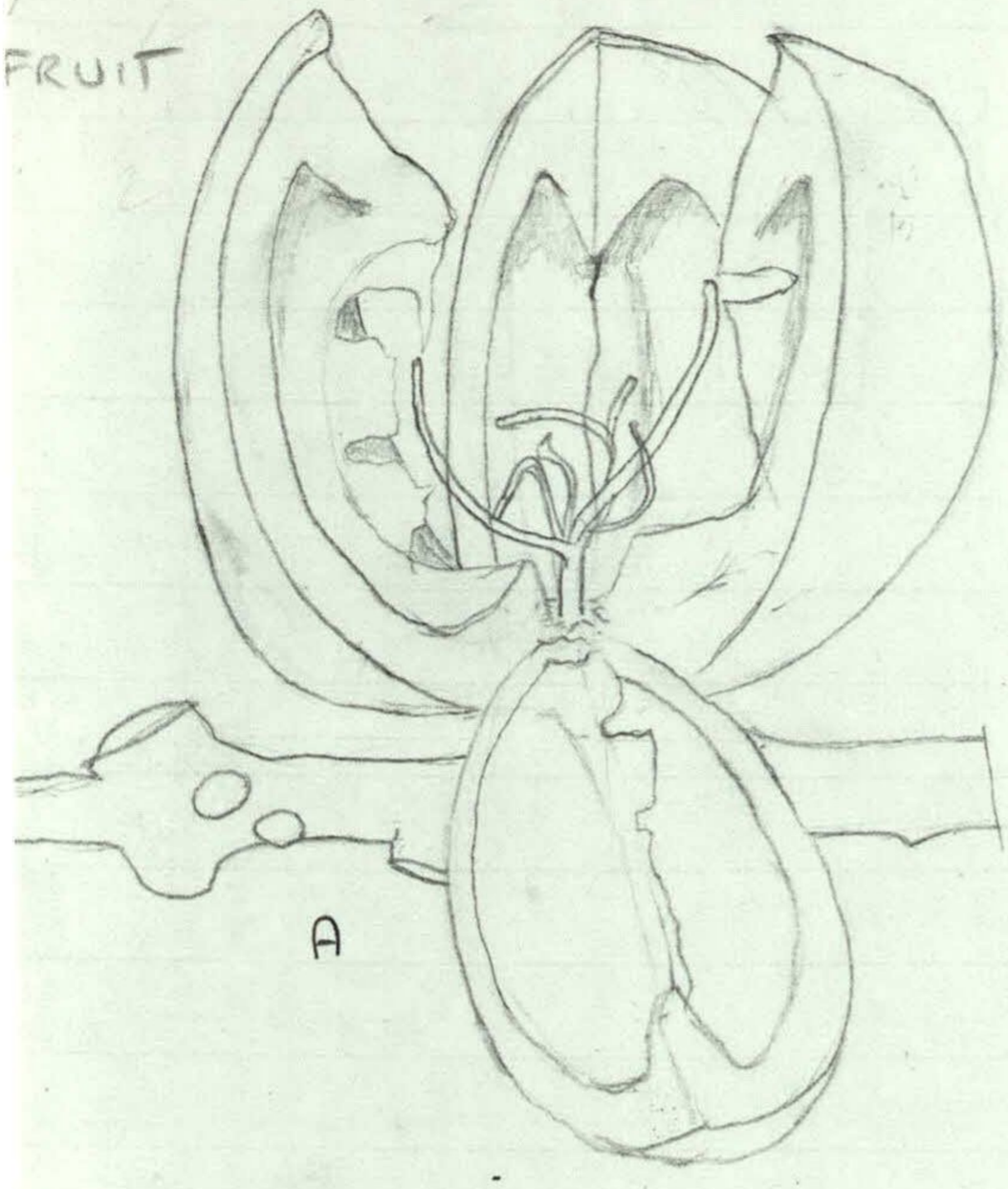
A-B DEHISCENT FRUIT.

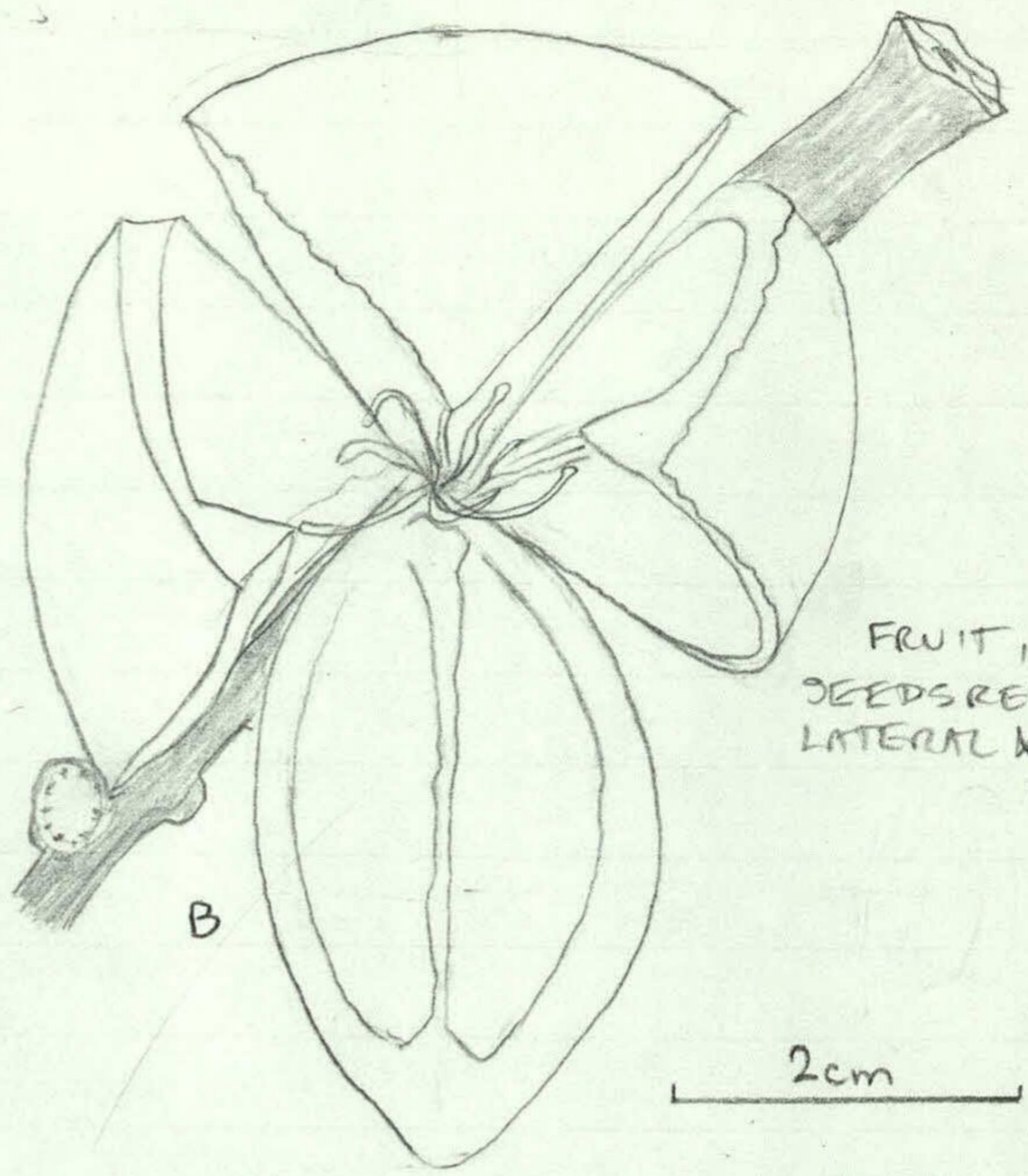
C-H SEED: SARCOTESTAL, BUT 50% OF SURFACE AREA CHALAZAL AND 50% BITEGMIC.

Dysoxylum ~~xxxxxx~~ TDP 8134
macrostachyum



FRUIT

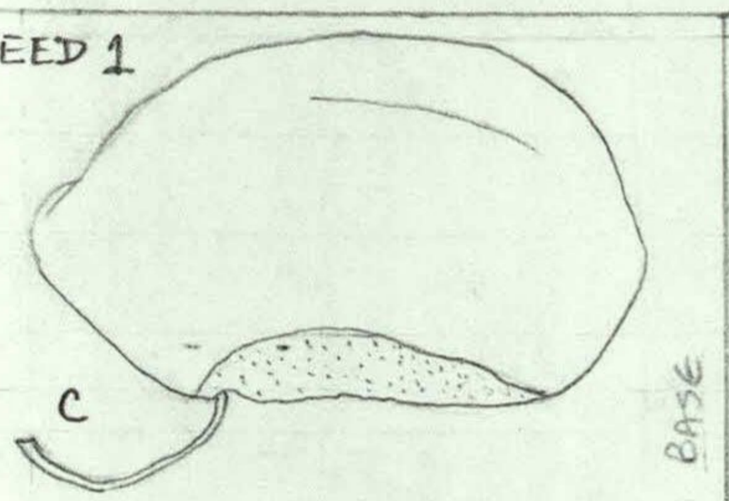


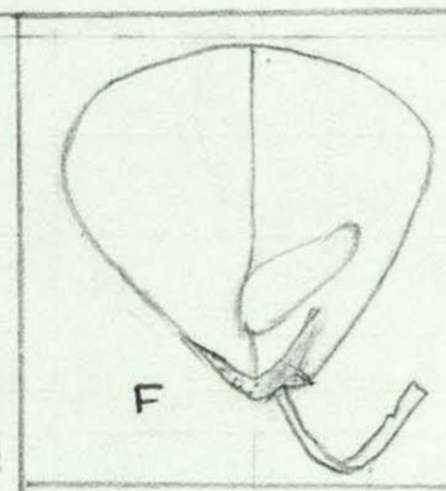



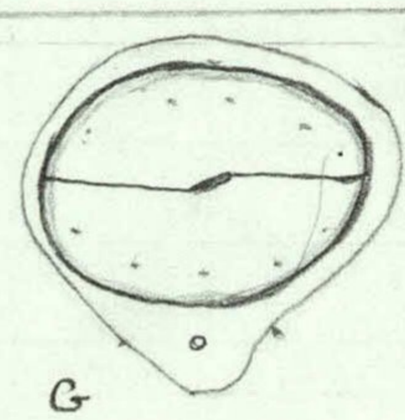

FRUIT, SEEDS REMOVED LATERAL & PLAN VIEWS.

2cm

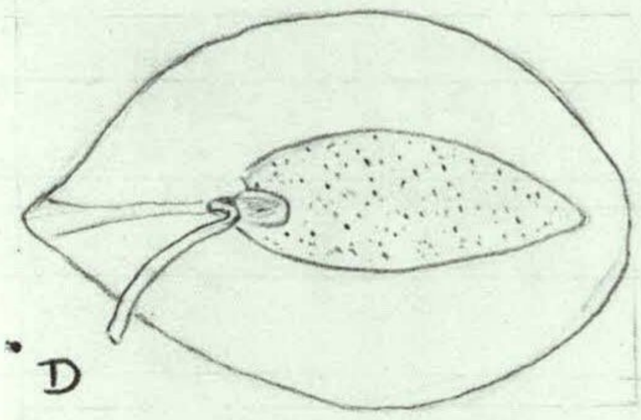
SEED 1

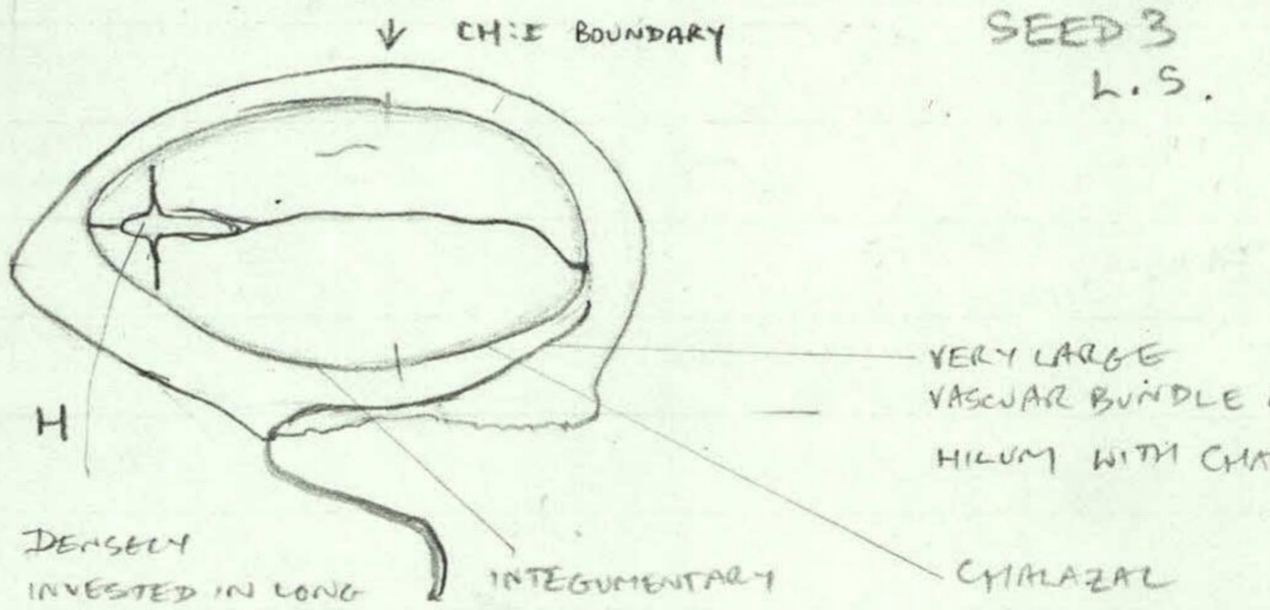


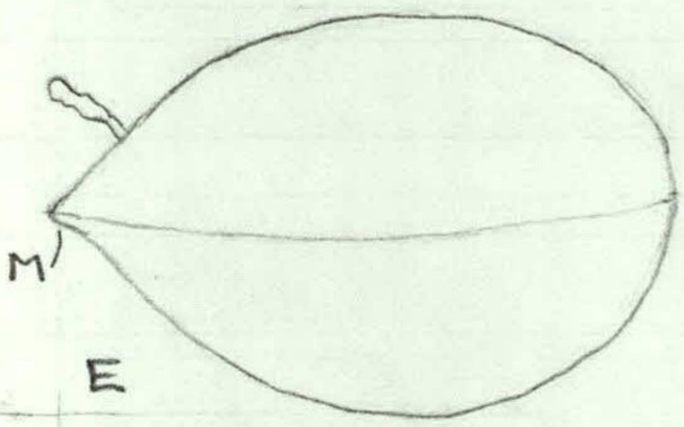




SEED 2
END VIEW X.S




SEED 3
L.S.




2cm

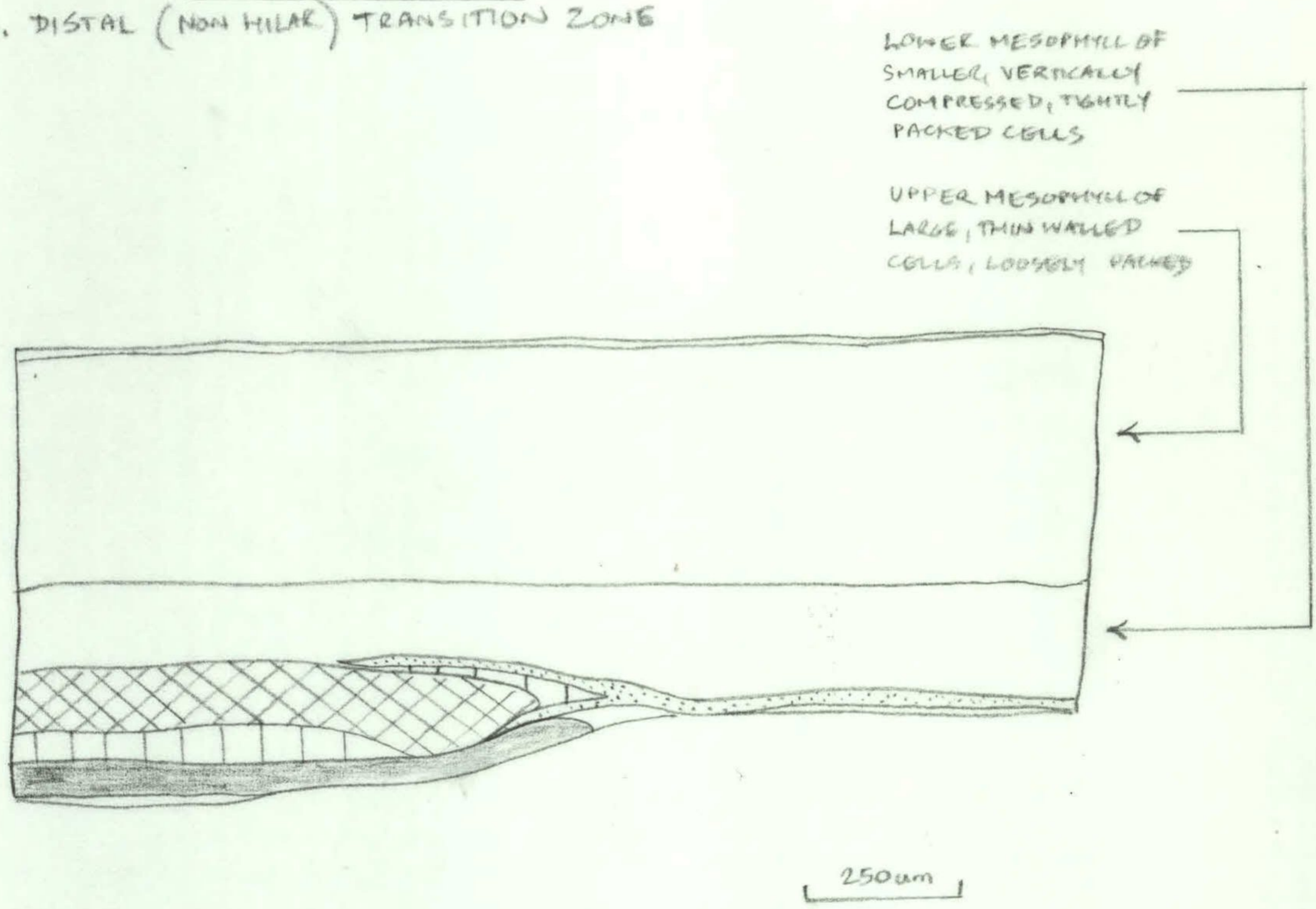
PLATE 109

DYSOXYLUM MACROSTACHYUM

TISSUE PLAN OF TRANSITION FROM BITEGMIC TO CHALAZAL SEED-COAT.

Dysoxylum ~~fraseranum~~ macrostachyum TDP 8134

L.S. DISTAL (NON HILAR) TRANSITION ZONE






EXOTEGMIC FIBRES

TANNINIZED CELLS ('CHALAZAL')

VASCULAR TISSUE

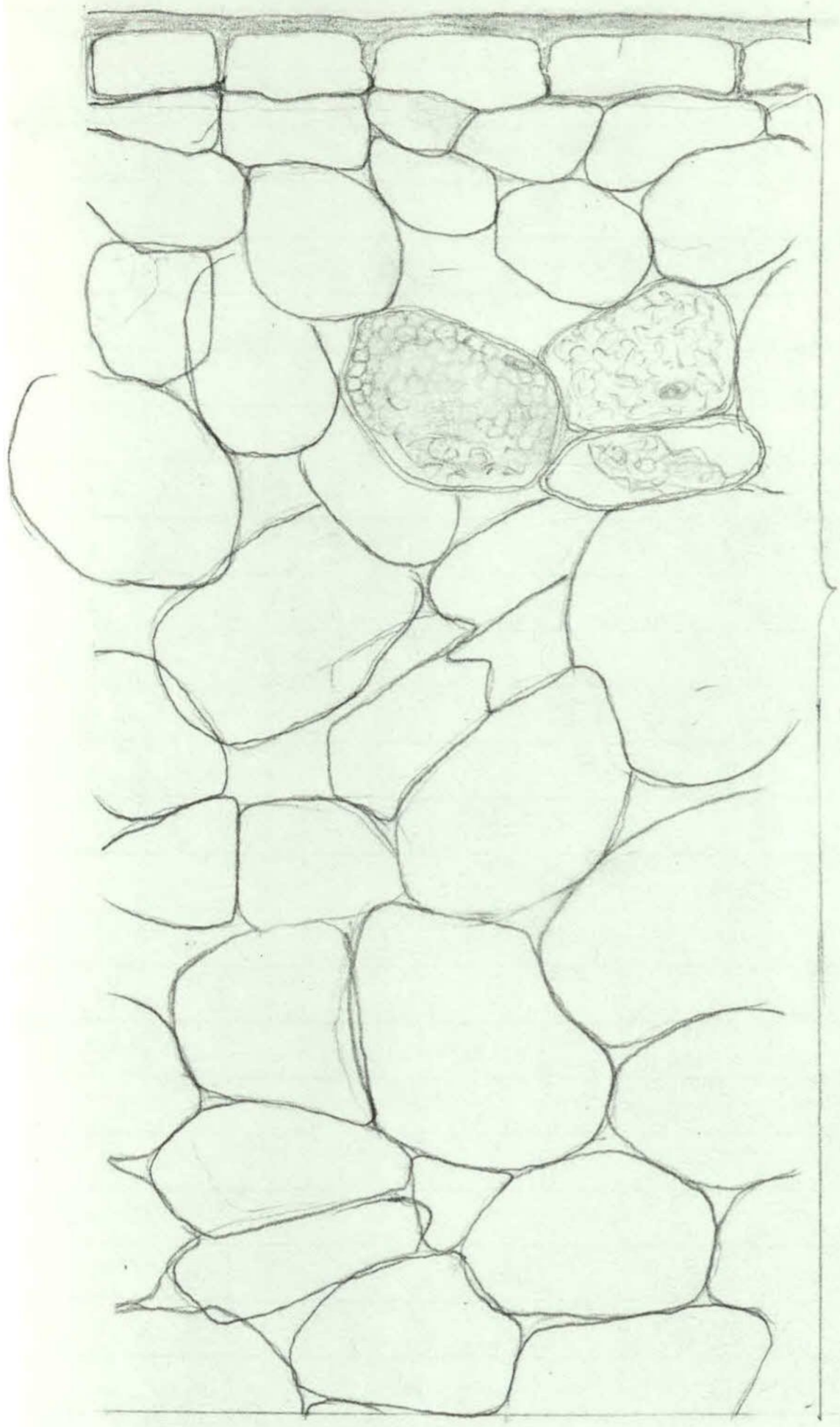
THICK WALLED PARENCHYMA

PLATE 110

DYSOXYLUM MACROSTACHYUM

ANATOMY OF CHALAZAL PART OF SEED-COAT. NOTE AERENCHYMATOUS, FLESHY UPPER PART AND VASCULAR, TANNINIFEROUS LOWER PART WITH THICK-WALLED CELLS.

Dysoxylum ~~racemum~~ macrostachyum. TDP 8134.
L.S. CHALAZA. CUT 1



EPIDERMIS. PROSTRATE IN L.S & T.S (HEXAGONAL IN Pd.S)
CUTICLE THIN. THICKENING BRICK RED, RESTRICTED TO OUTER WALL. CONTENTS LIVING, GREY GRANULAR

PARENCHYMA. SHORTLY ELLIPTIC. GREY GRANULAR LIVING CONTENTS. SOME AIR SPACES. PROSTRATE.

100 µm

BASAL ELLIPTIC PARENCHYMA, MORE THINLY WALLED & LESS DENSELY FILLED.

CRUSHED CELLS

PROSTRATE SUB-FIBROID PARENCHYMA.
SPARSE GREY GRANULAR LIVING CONTENTS

VASCULAR BUNDLES

CRUSHED CELLS

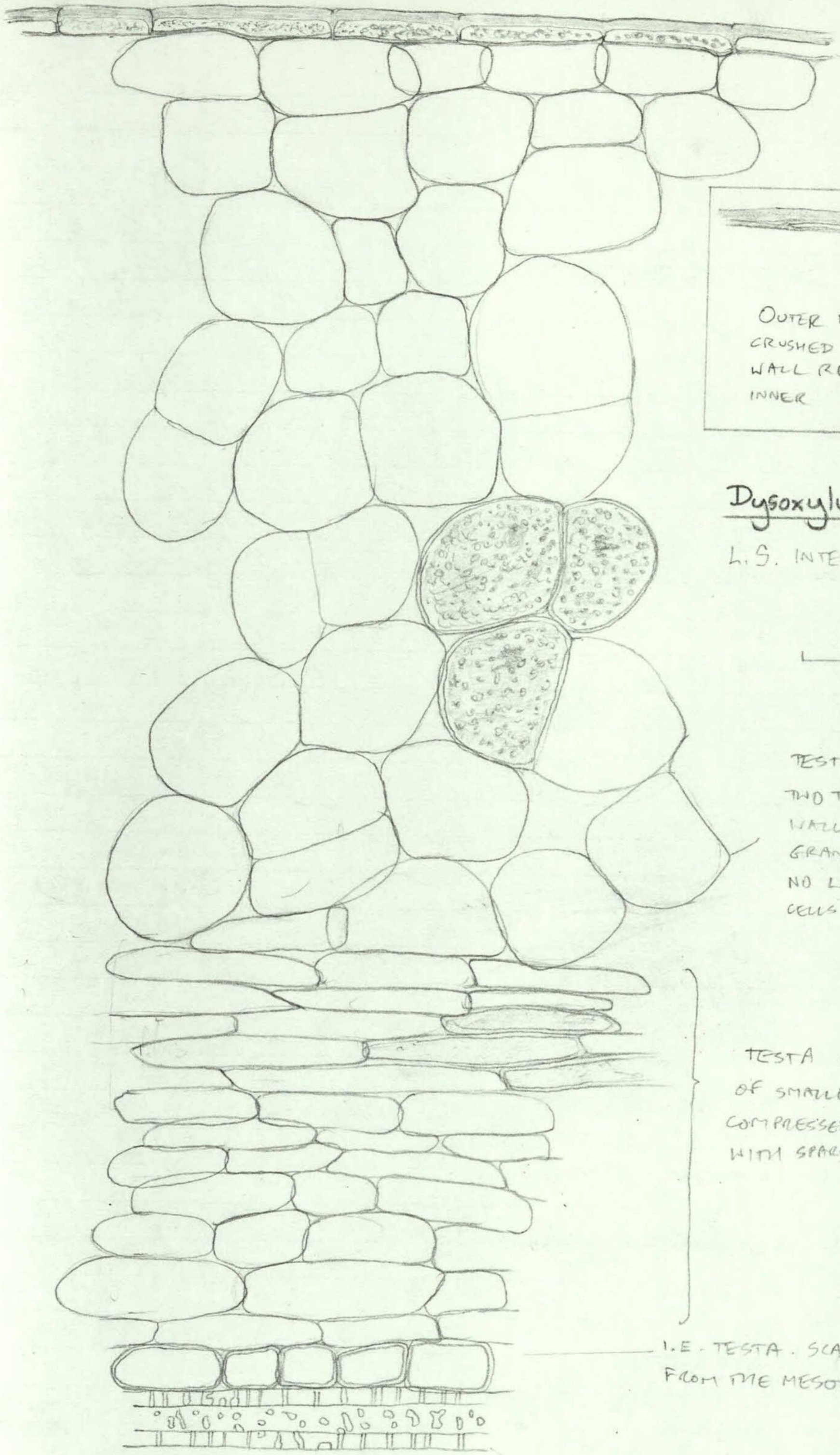
TANNINIZED PROSTRATE LIGNIFIED LAYER, 2-3 CELLS THICK FLANKED ABOVE & BELOW WITH A LAYER OF THICK WALLED VARIOUSLY TANNINIZED PROSTRATE RECTANGULAR CELLS

HIGHLY CRUSHED CELLS

PLATE 111

DYSOXYLUM MACROSTACHYUM

ANATOMY OF BITEGMIC PART OF SEED-COAT. NOTE AERENCHYMATOUS, FLESHY UPPER PART OF TESTAL MESOPHYLL AND LOWER MORE MECHANICAL PART. COMPARE WITH CHALAZA (PLATE 110) AND NOTE LACK OF THICK-WALLED AND TANNINIFEROUS CELLS. TEGMEN HIGHLY REDUCED, TESTAL I.E. WITHOUT CRYSTALS.



OUTER EPIDERMIS OFTEN CRUSHED, OUTER PERICLINAL WALL RESTING DIRECTLY ON INNER

Dysoxylum fraseum TDP 8134
macrostachyum
L.S. INTEGUMENTS CUT 3

100µm

TESTA MESOPHYLL, UPPER TWO THIRDS OF LARGE, THIN WALLED CELLS. RATHER DENSE GRANULAR BROWN CONTENTS. NO LACUNAE DETECTED. CELLS OFTEN PAIRED.

TESTA MESOPHYLL, LOWER THIRD OF SMALLER, MORE TIGHTLY COMPRESSED (VERTICALLY) CELLS WITH SPARSE CONTENTS.

I.E. TESTA. SCARCELY DIFFERENTIATED FROM THE MESOPHYLL, NO CRYSTALS

NOTE: NO V.B. DETECTED

TEGMEN: A SINGLE LAYER OF FIBROID CELLS. REMAINDER LOST BY COMPRESSION.

PLATE 112

DYSOXYLUM MACRANTHUM

A-B FRUITS

C-H SEEDS: BROADLY RAPHE-CHALAZAL ARILLATE.

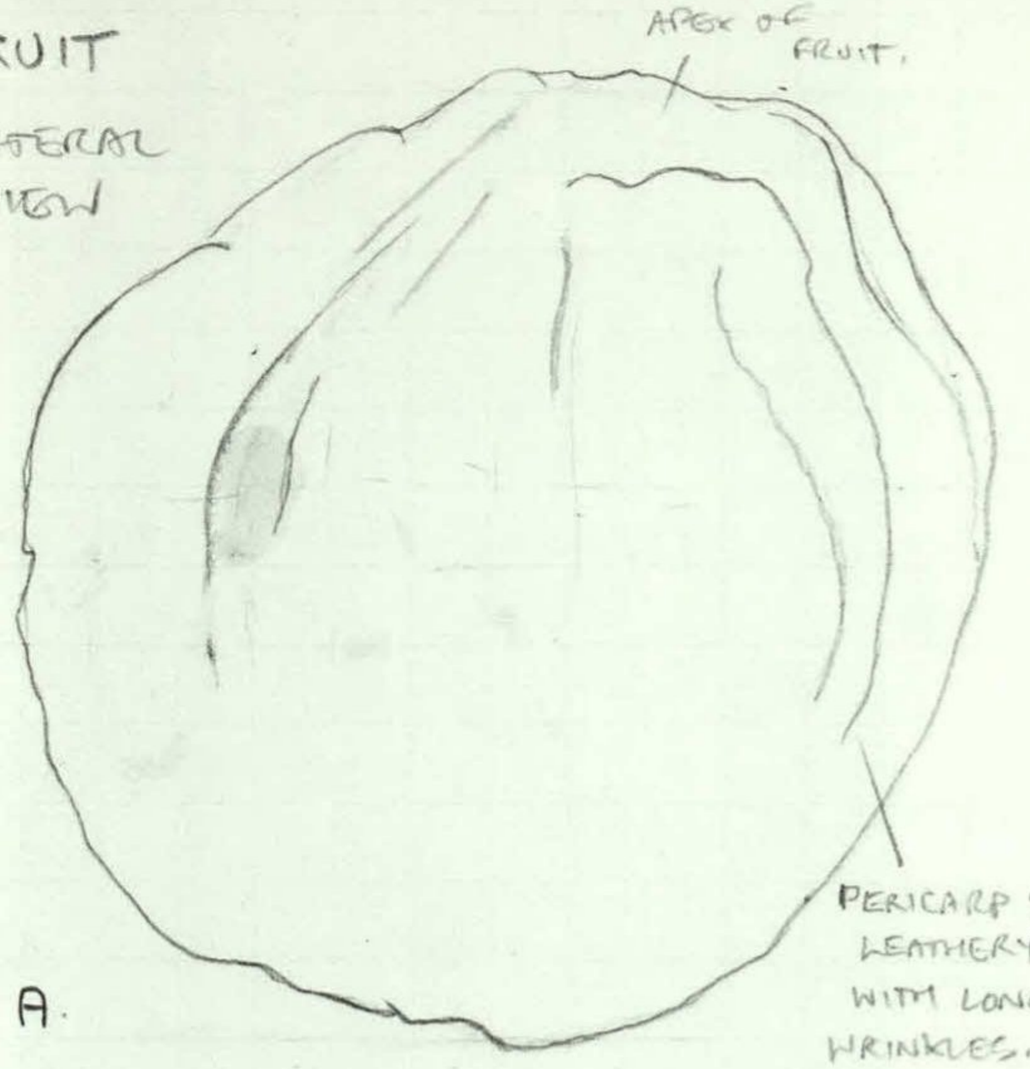
# Dysoxylum macranthum

Mackee 21130 : REVIVED & RECONSTRUCTED FROM DRIED MATERIAL.



## FRUIT

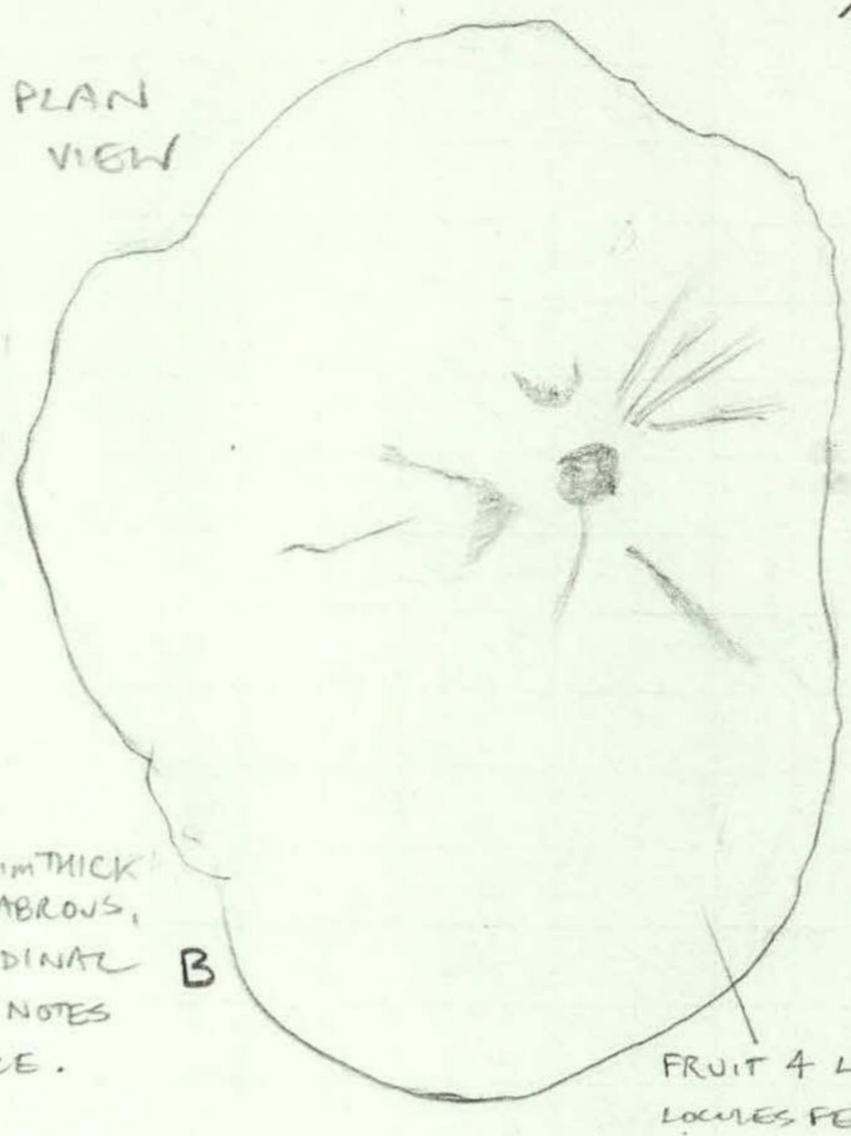
LATERAL VIEW




A.

PERICARP 2-4mm THICK LEATHERY, GLABROUS, WITH LONGITUDINAL WRINKLES. NO NOTES ON DEHISCENCE.

PLAN VIEW

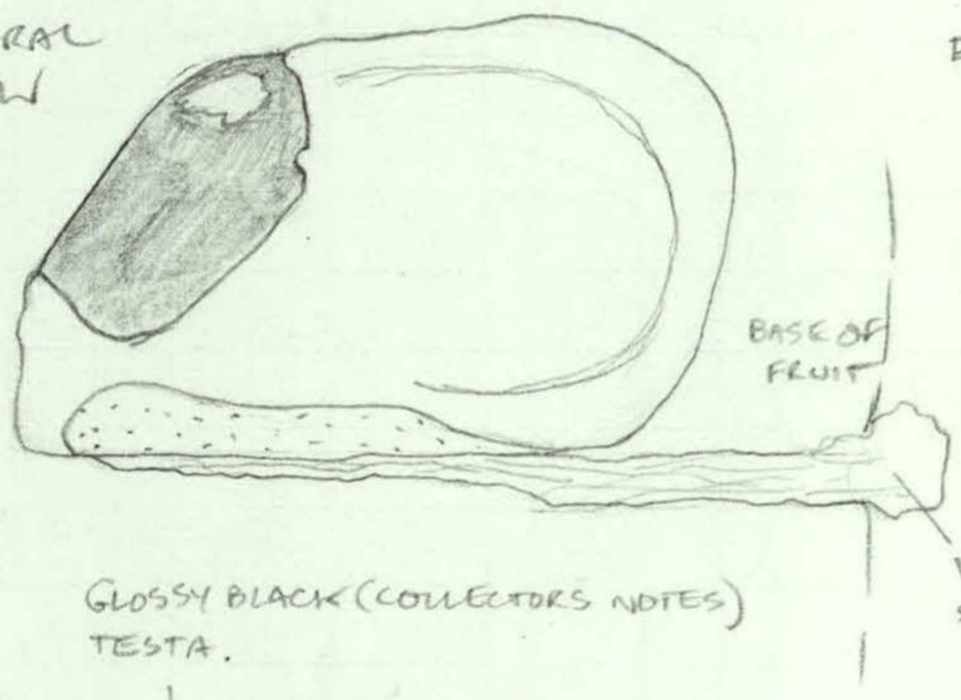


B

FRUIT 4 LOCULAR, 3 LOCULES FERTILE, 1 SEED PER LOCULE.

## SEED

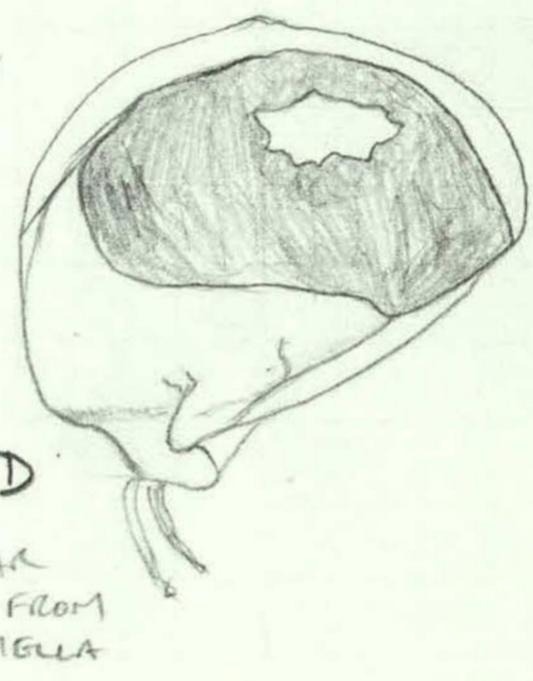
LATERAL VIEW




C

GLOSSY BLACK (COLLECTORS NOTES) TESTA.

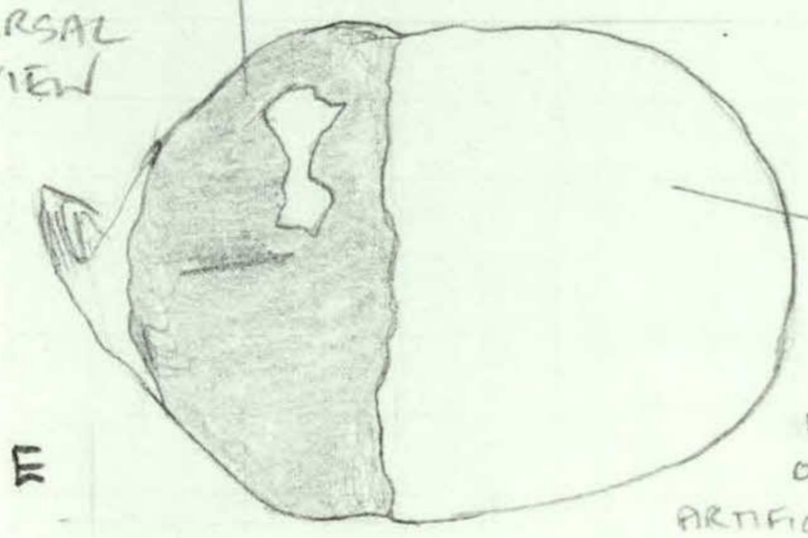
END VIEW



D

VASCULAR SUPPLY FROM COLUMELLA

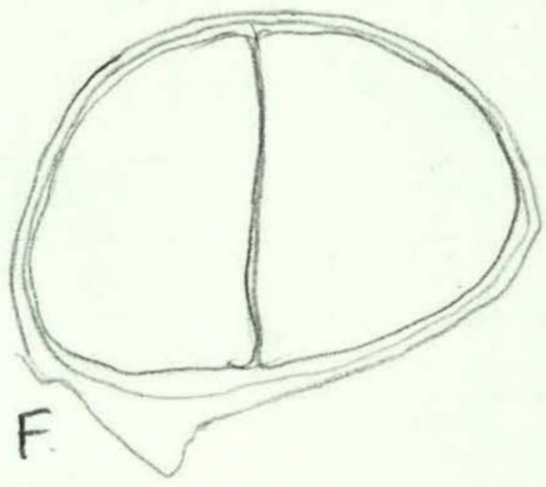
DORSAL VIEW



E

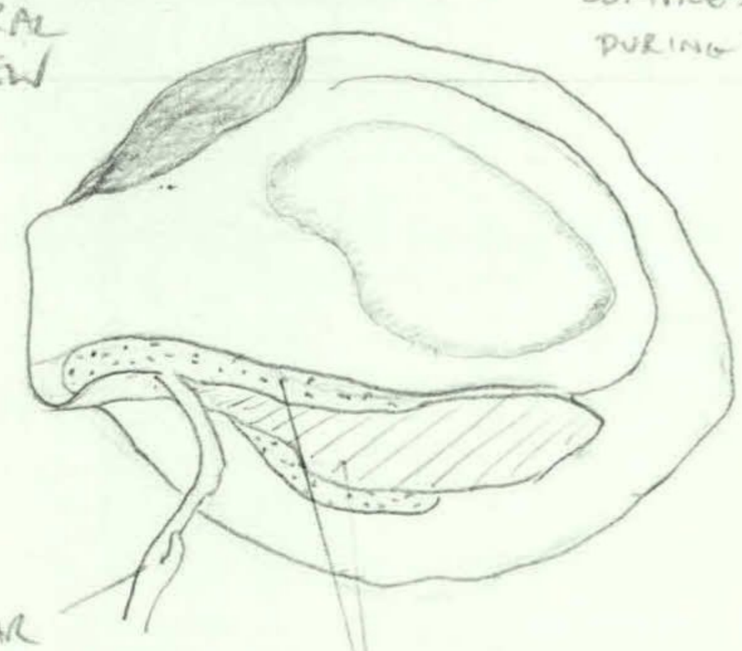
FLESHY RED (COLLECTORS NOTES) CHALAZAL 'ARIL' THIS PART WHICH WOULD PROBABLY OVERLAP THE TESTA, ARTIFICIALLY THIN DUE TO COMPRESSION OF CELLS DURING DEHYDRATION. L.S

T.S



F.

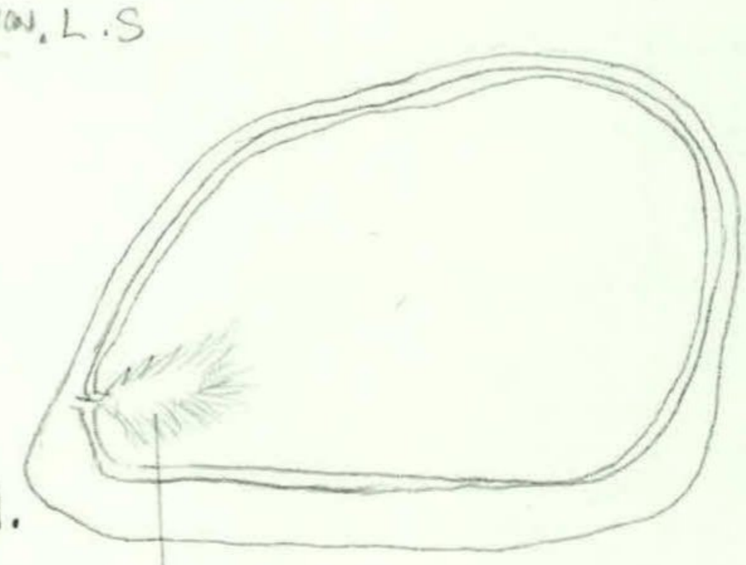
VENTRAL VIEW



G

VASCULAR CONNECTION

NARROW HILUM



H.

HAIRY EPICOTYL

2cm

PLATE 113

DYSOXYLUM MACRANTHUM

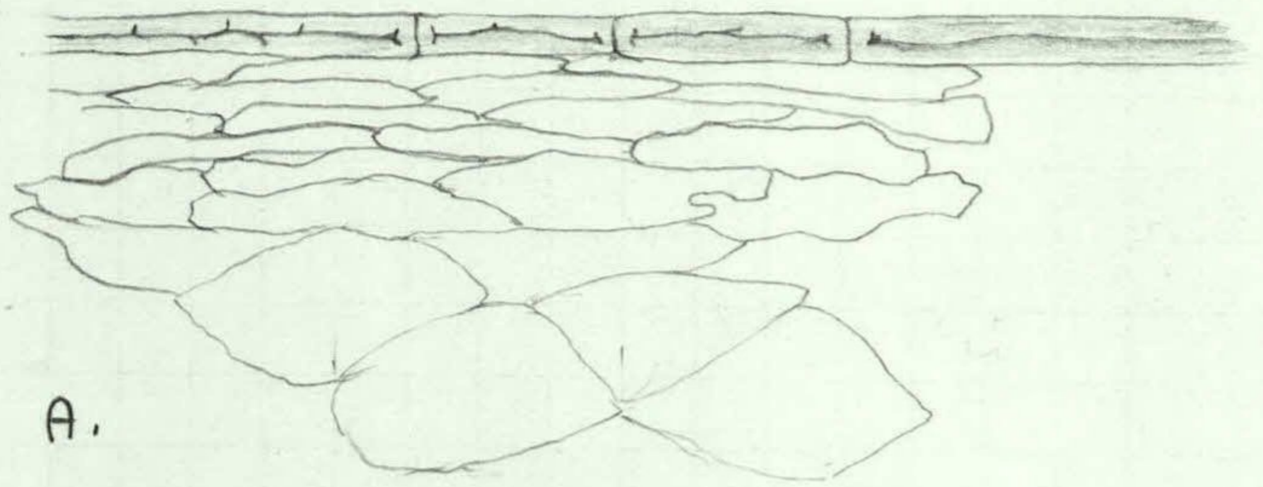
A-B ANATOMY OF THE CHALAZA (SEE PLATE 114H FOR DISTRIBUTION).

NOTE UPPER FLESHY PART, LOWER VASCULAR AND

TANNINIFEROUS, THICK-WALLED (SCLEREIDS?) PART.

Dysoxylum macranthum Mackee 21130 113

L.S. CHALAZA.

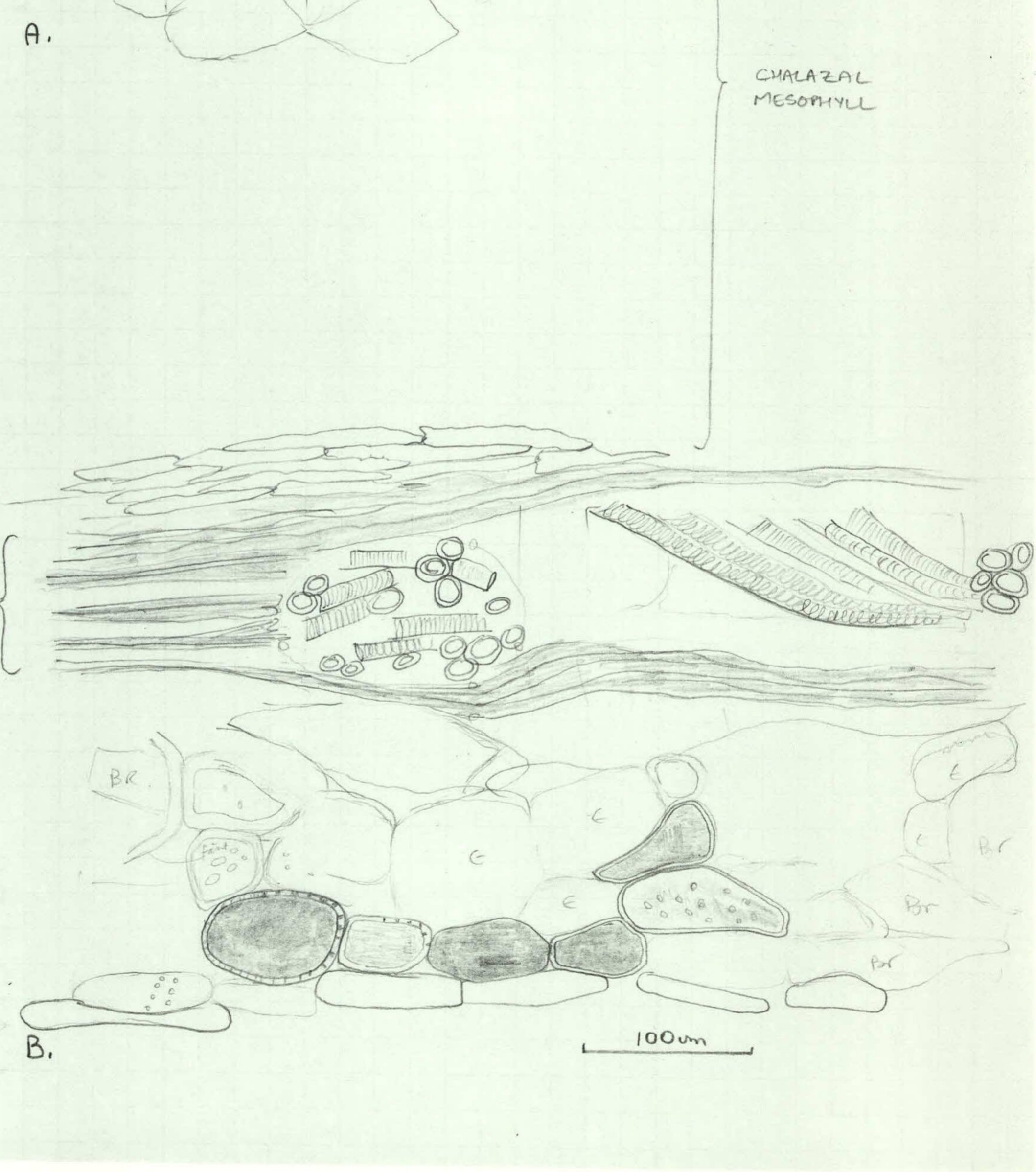


A.

CHALAZAL EPIDERMIS

CHALAZAL MESOPHYLL

VASCULAR BUNDLES & ASSOC. FIBRES




B.

PLATE 114

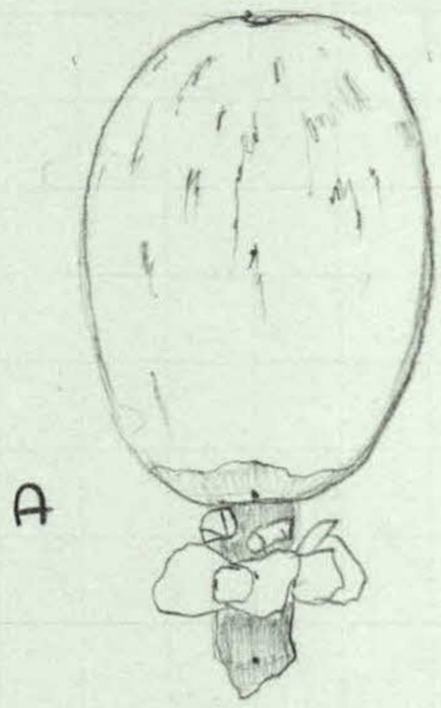
DYSOXYLUM MACRANTHUM

IMMATURE FRUITS AND SEEDS, SHOWING DISTINCTION BETWEEN CHALAZA AND BITEGMIC PART OF SEED-COAT (H).

# Dysoxylum macranthum

FRUIT: HIGHLY IMMATURE (cf PLATE 112)

LATERAL VIEW



A

PLAN VIEW

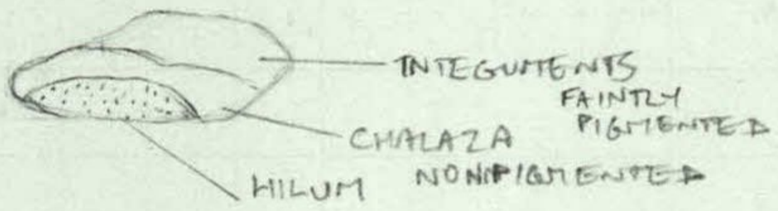


B

1cm

SEED

LATERAL VIEW




C

END VIEW



D

DORSAL VIEW



E

T.S



F

VENTRAL VIEW



G

1cm

L.S




H

1cm

PLATE 115

DYSOXYLUM CAULIFLORUM

A-B FRUITS

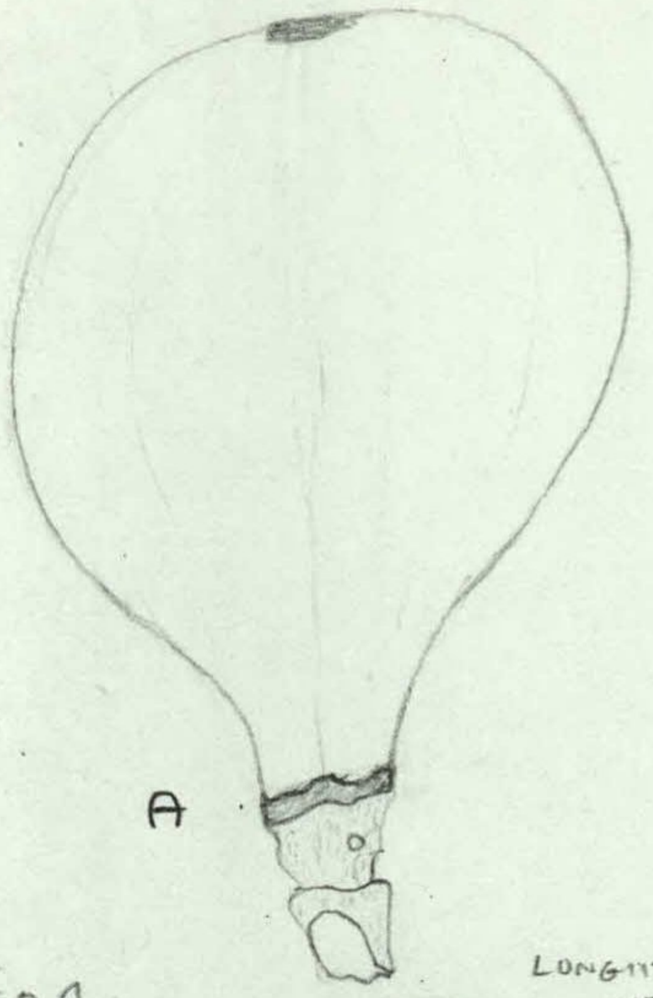
C-G SEEDS: NOTE RAPHE-CHALAZAL ARIL.

# Dysoxylum cauliflorum

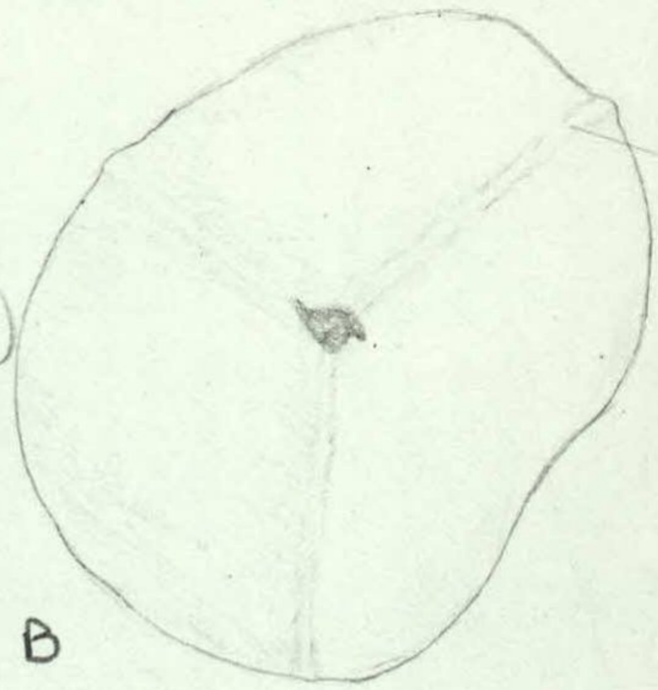
1692

115

FRUITS
LATERAL & PLAN
VIEWS.
(UNDEHISCED IN
THIS COLLECTION)



A



B

PERICARP RAISED
OVER SUTURES

1cm

SEED 1

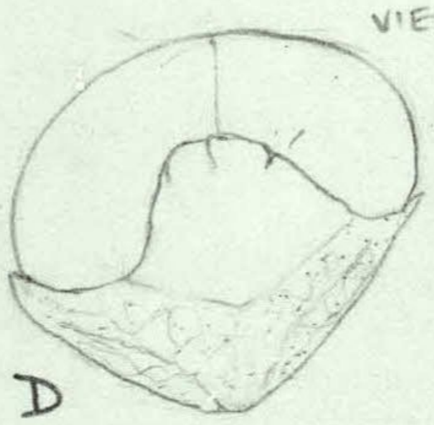
LONGIT.
VIEW



C

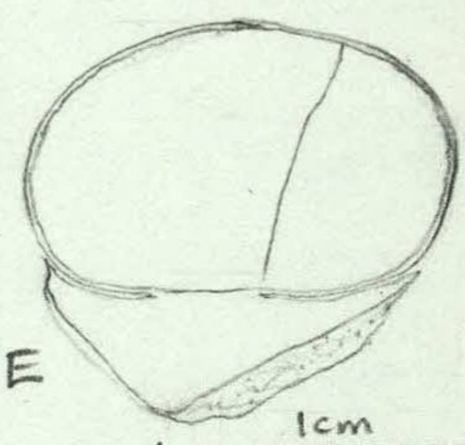
HILUM -
DIFFUSE VASCULARIZATION

END
VIEW



D

T.S

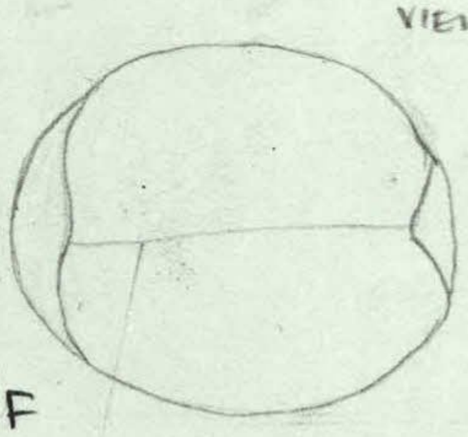


E

1cm

SEED 2

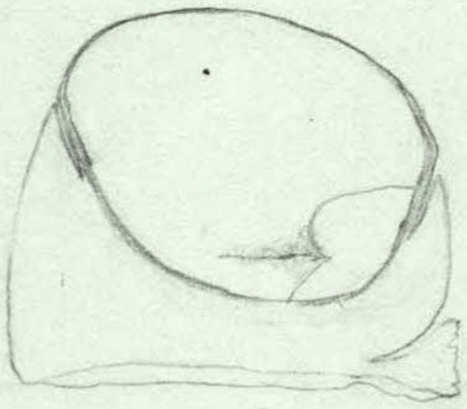
PLAN
VIEW



F

DORSAL RIDGE

L.S.



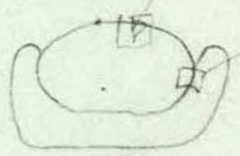
G

1cm

W

CUT 1 L.S

CUT 3 L.S



T.S

CUT 2 T.S



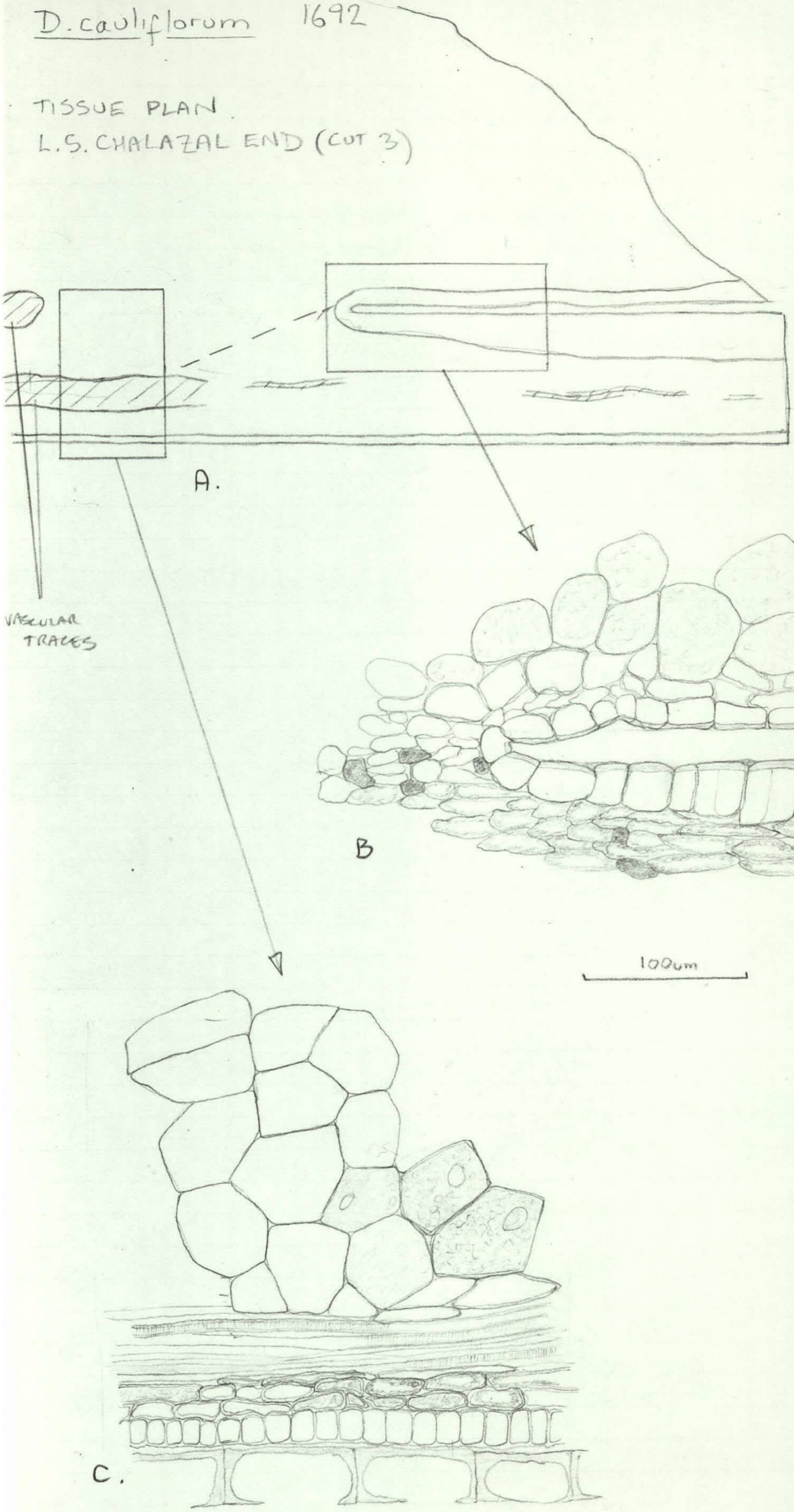
PLATE 116

DYSOXYLUM CAULIFLORUM

A. TISSUE PLAN OF TRANSITION FROM FLESHY TO NON-FLESHY PART OF SEED WITH DETAILED CELL DIAGRAMS (B-C).

D. cauliflorum 1692

TISSUE PLAN
L.S. CHALAZAL END (CUT 3)



D. cauliflorum 1692

L.S. INTEGUMENTS

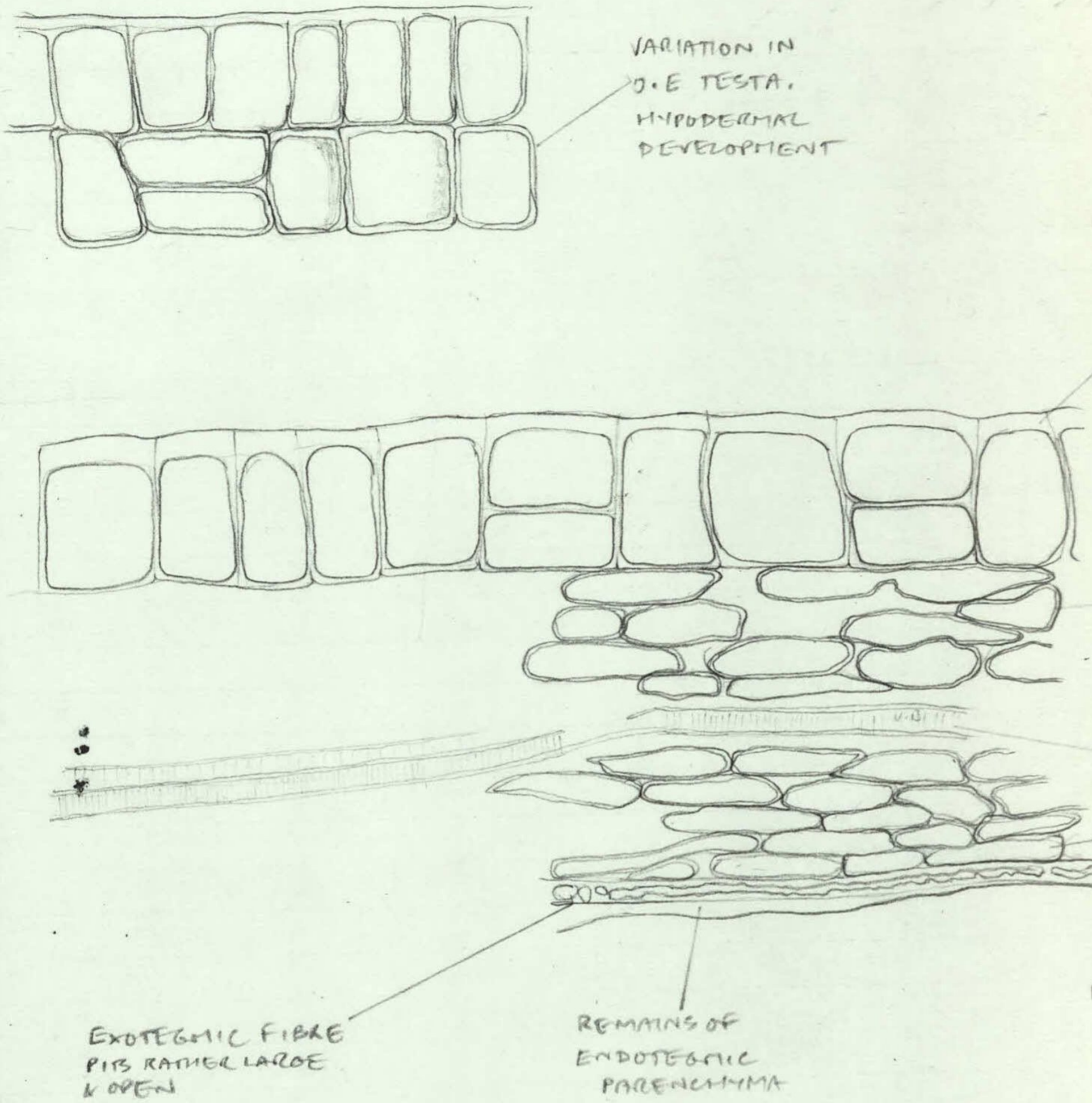


PLATE 117

DYSOXYLUM CAULIFLORUM

ANATOMY OF THE BITEGMIC PART OF THE SEED-COAT. NOTE COLUMNAR TESTAL O.E. (SOMETIMES WITH HYPODERMIS) AND VASCULARIZED, NON-FLESHY TESTAL MESOPHYLL. TEGMEN HIGHLY REDUCED, FIBRES THIN-WALLED AND OF SMALL DIAMETER.

# PLATE 118

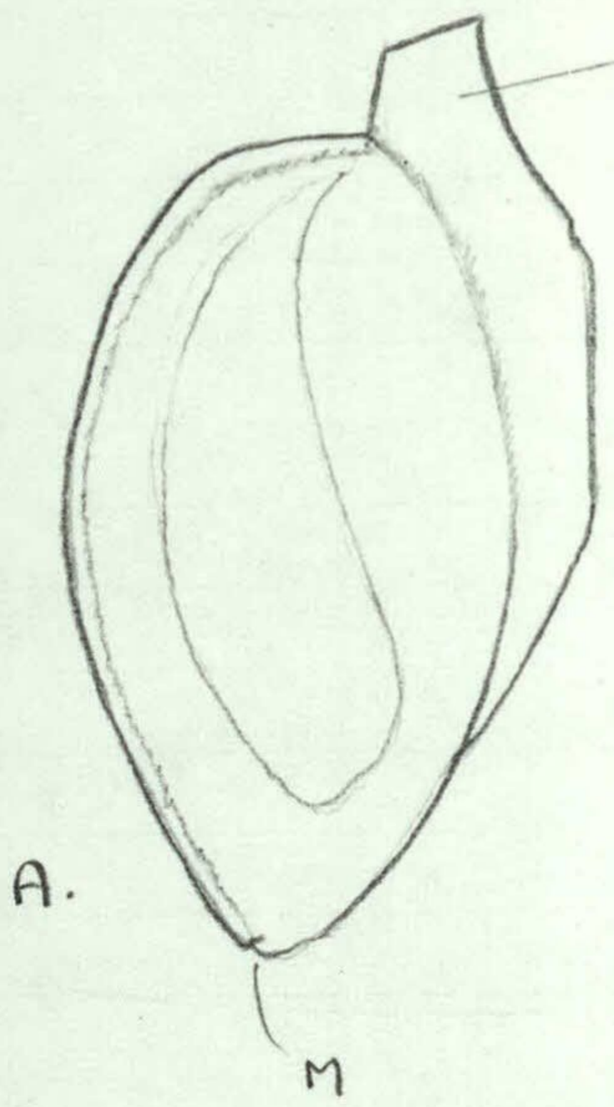
## DYSOXYLUM 'ACUTANGULUM'

A-D SEED STRUCTURE: SARCOTESTAL AND ENTIRELY PACHYCHALAZAL.

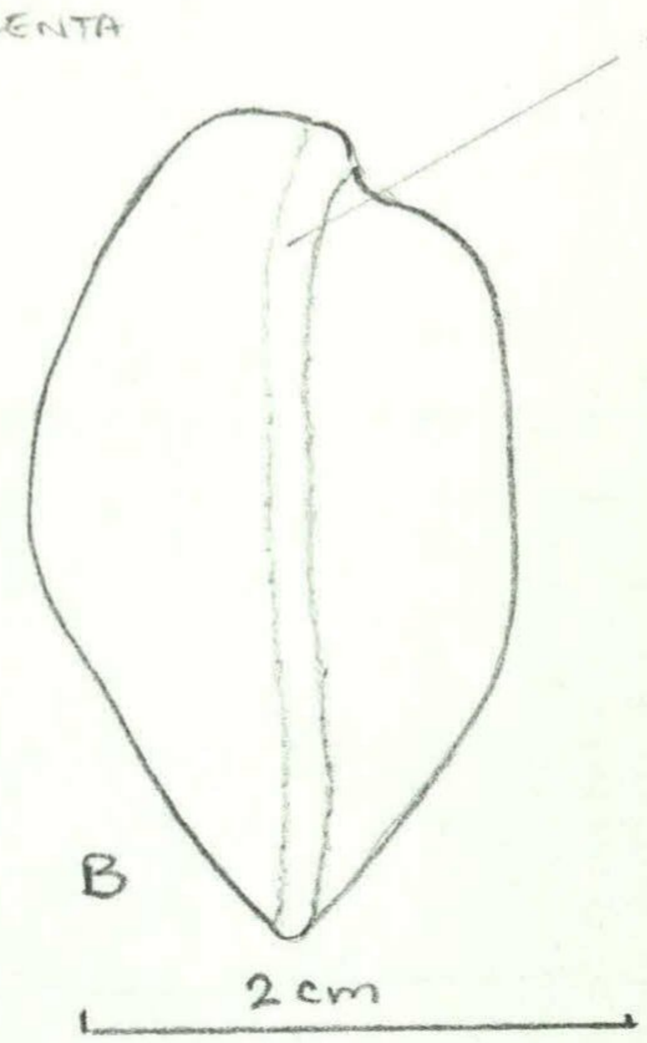
# Dysoxylum 'acutangulum'

SEEDS - SLIGHTLY IMMATURE

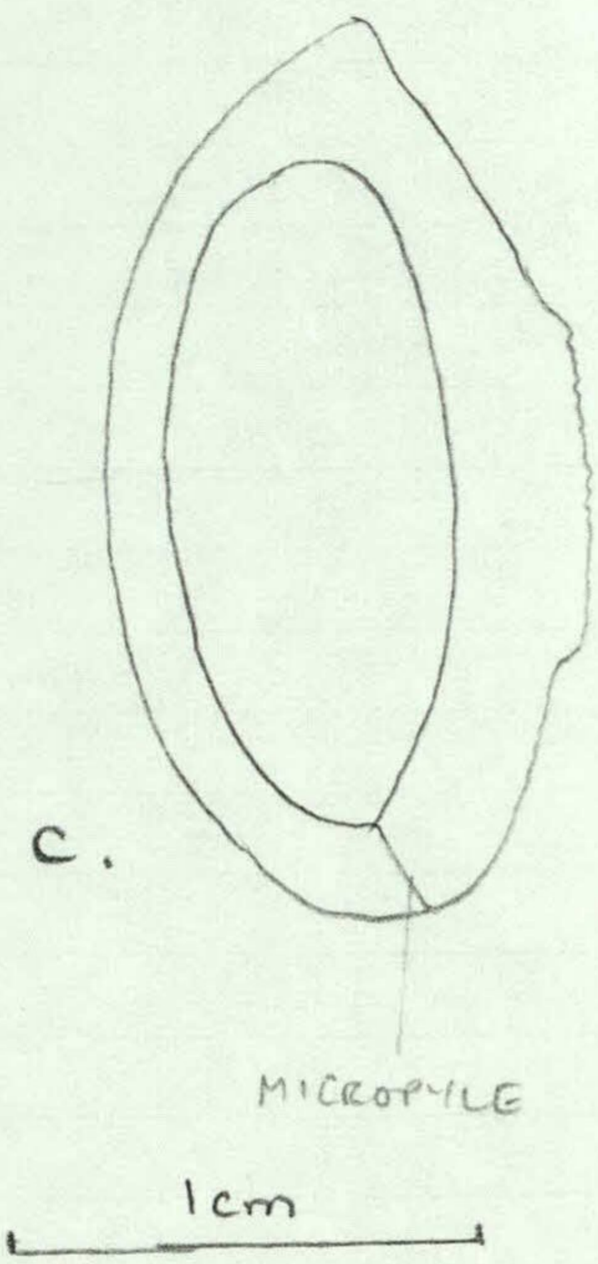
WHOLE. LONGITUDINAL VIEW



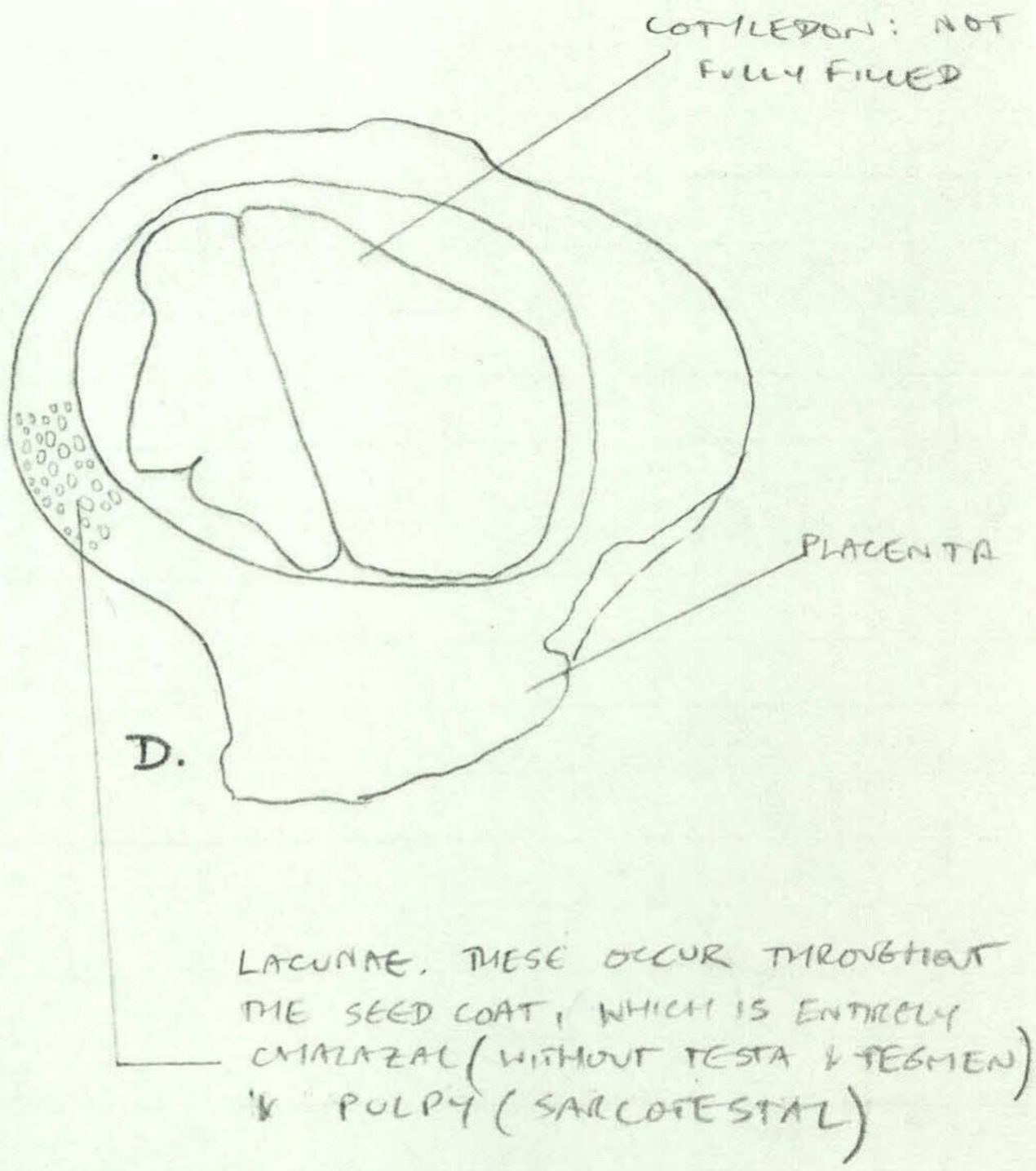

PLAN VIEW




L.S. (EMBRYO REMOVED)




T.S.



# PLATE 119

## DYSOXYLUM ANGUSTIFOLIUM

A-C FRUITS

D. SEED: DETAIL OF CHALAZA.

E-G SEED AND FRUIT: STAGES IN SEED PRESENTATION. SEED HANGS BY BUNDLE (IF DIFFUSE, LESS LIKELY TO 'PULL OUT') AND ORIENTATION OF FRUIT (MUST BE PENDULOUS).

Dysoxylum angustifolium 1991

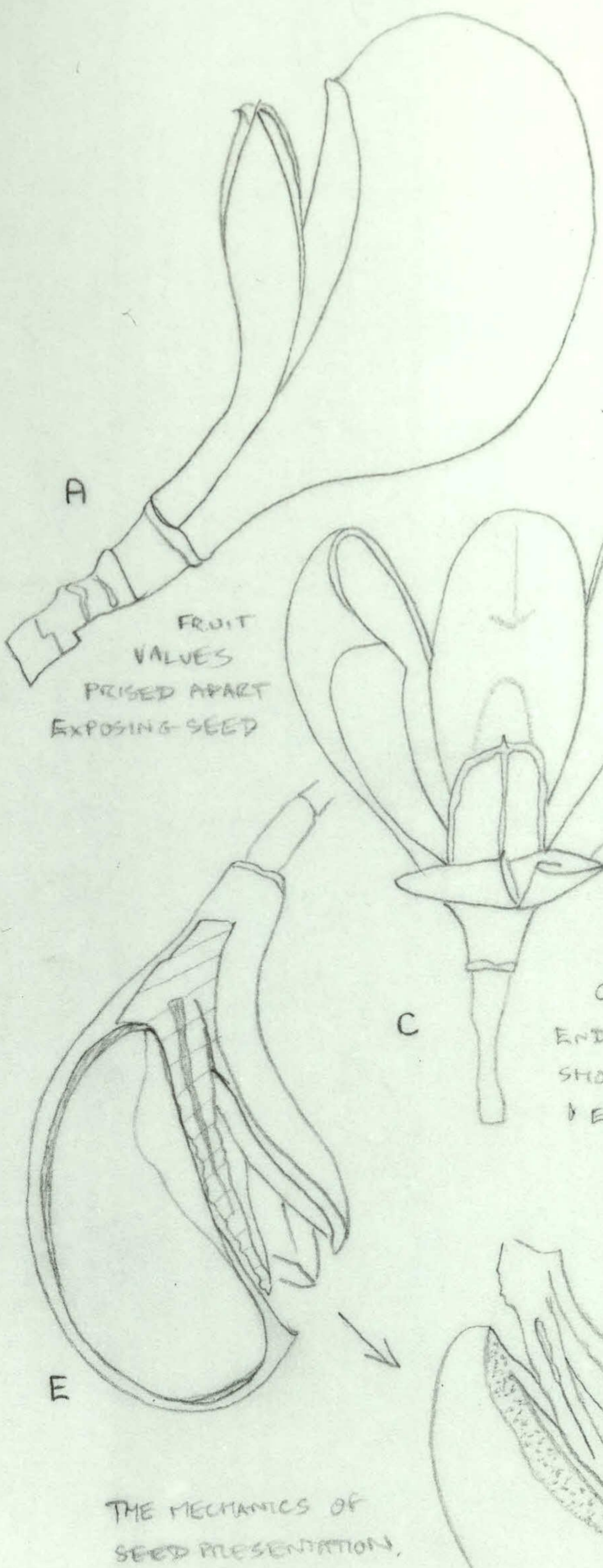


PLATE 120

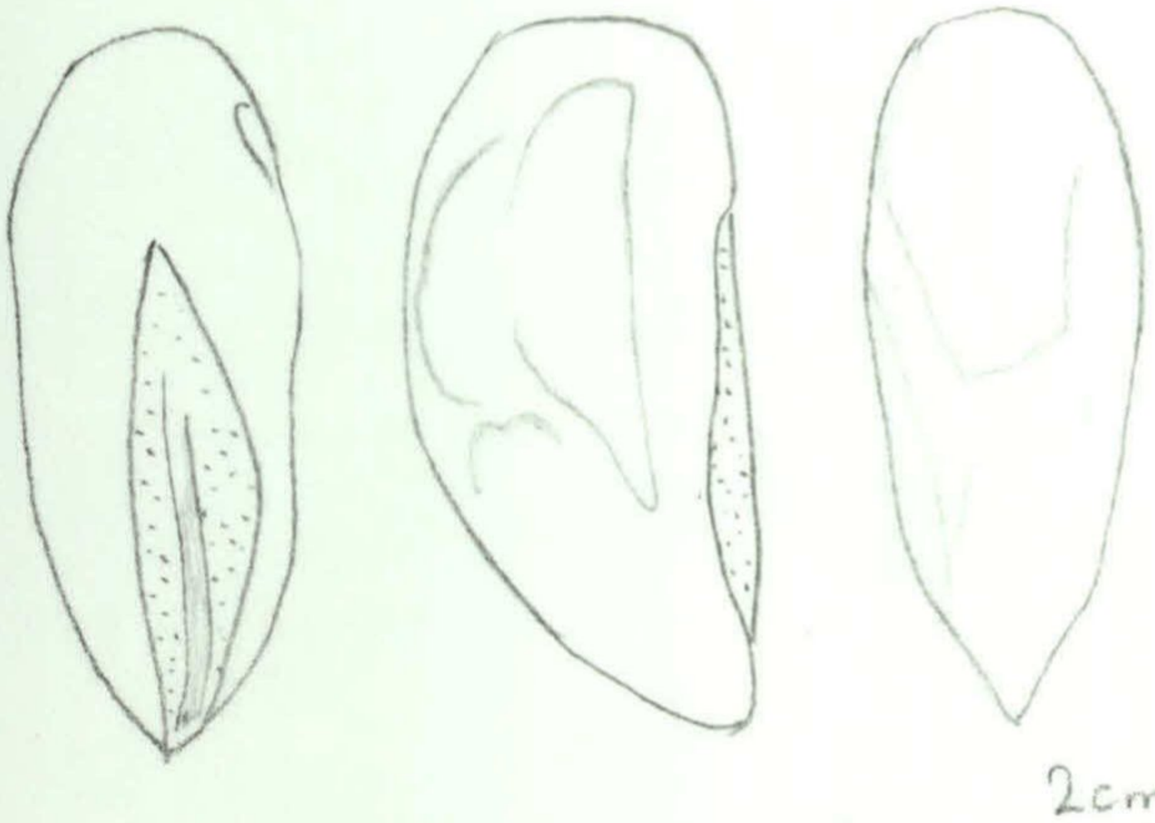
# DYSOXYLUM ANGUSTIFOLIUM

SEEDS: COMPLETELY SARCOTESTAL

Dysoxylum angustifolium 1991

SEEDS

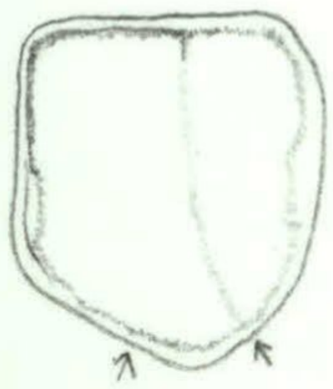
WHOLE




SEED 1

DORSAL RIDGE ABSENT

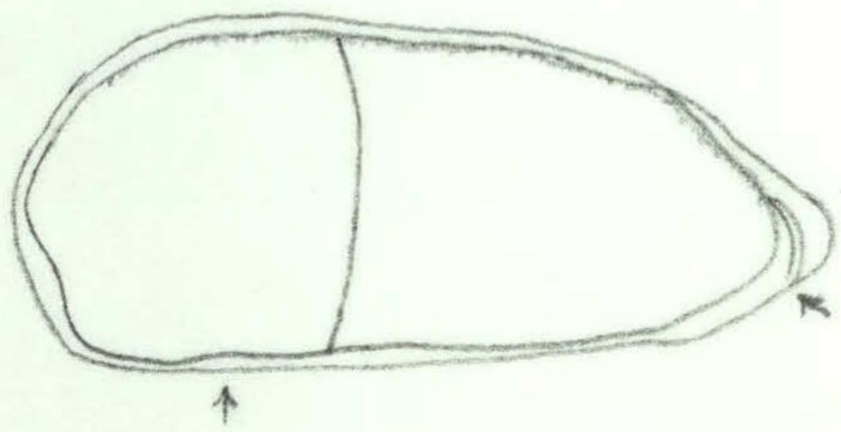
T.S.



SEED 2

ARROWS INDICATE LIMITS OF HILUM

L.S.




SEED 3

NOTE CONTRASTING COTYLEDON ORIENTATION IN SEEDS TWO & THREE.

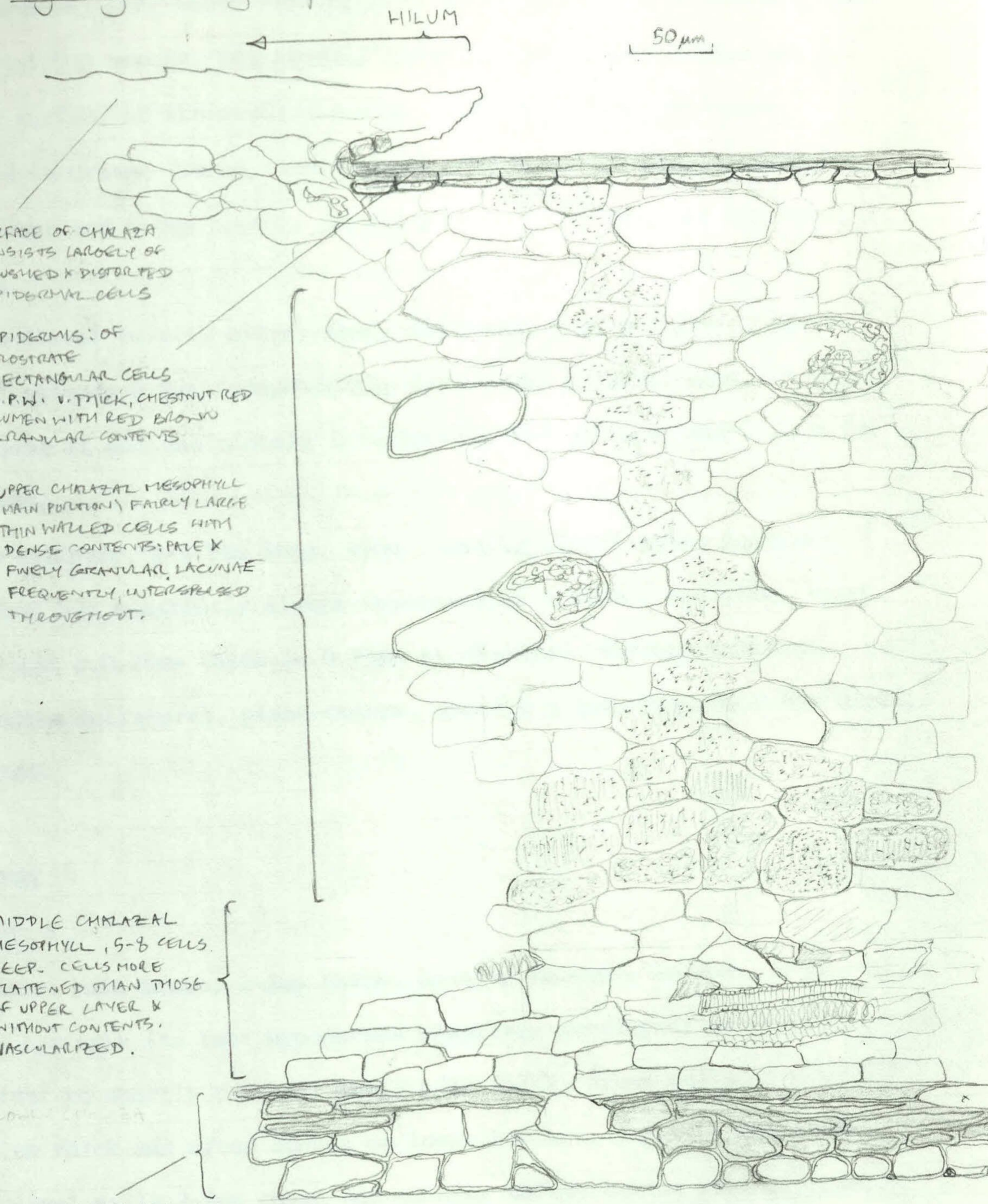
PLATE 121

DYSOXYLUM ANGUSTIFOLIUM

ANATOMY OF THE COMPLETELY UNITEGMIC SEED-COAT. NOTE UPPER LAYER THIN-WALLED PARENCHYMA WITH LACUNAE CONSTITUTING THE SARCOTESTA. LOWER, MECHANICAL LAYERS WITH THICK, DEEPLY STAINED AND THICK-WALLED CELLS INTERGRADE. THIS CONSTRUCTION PROBABLY PACHYCHALAZAL, BUT POSSIBLY UNITEGMIC BY LOSS OF TEGMEN.

# Dysoxylum angustifolium 1919

L.S HILUM BOUNDARY



Chalaza at blunt end, circular transversely elliptic, slightly sunken or flat, dark brown. Micropyle with a prominent boss projecting 0.75-1mm at the pointed end. Raphe running from micropylar boss to chalaza, the scar 0.5-1.5mm across, not usually straight, but bowed around the ventral surface of the seed; vascular bundle exserted, discrete, embedded in orange fleshy tissue which most prolific near micropyle (c.3mm deep and 8-9mm broad), tapering to c.0.5mm deep and wide at the chalaza.

In the distal (w.r.t. hilum) seed, the raphe (and prolific fleshy tissue) extends 6-7mm independently around the proximal seed, partly enveloping it and and closely interlocking (becoming adnate?) with its raphe-aril.

Hilum elliptic, 1-1.5mm long, wide, usually placed close together (<0.25mm) but apparently always separated by a double epidermal layer.

Seed-coat c.0.25mm thick (c.0.75mm at chalaza). Endosperm absent. Cotyledons collateral, plano-convex, radicle c.1mm long, by 0.6mm broad, exserted.

ANATOMY

TESTA

Cuticle: pale brown, 2-3um thick. Locally thicker, to 9um.

O.E. a single (to two: hypodermis sometimes developed) layer of cuboidal to shortly columnar cells with thick, brown walls, o.p.w. 6-7 (-12)um thick and often convex on lower surface, i.p.w. c.4um thick, anticlinal walls 3-4um thick and thinner below. Lumina with diffuse, pale brown contents, sometimes with scattered dark granules. A second epidermal layer derived from thickened mesophyll or periclinal division of the O.E. is sometimes present.

Mesophyll: two to four layers of prostrate elliptic cells 14-30um wide, 10 (-14)um high; walls 1-2um thick, pale brown. Away from the chalaza, often severely crushed or lost.

I.E. a single layer of prostrate, shortly elliptic cells 17-28um wide, 9-18um high, walls pale brown, c.2um thick. Lumina colourless or a dense, pale orange. Endocrystal usually rhombic, to 10um wide.

TEGMEN

Exotegmen a single (to two) layers of fibrous cells 140-560(-665)um long, endwalls rounded or tapered, walls very pale yellow, 3-7(-9)um thick, with fine circular or obliquely transversely elliptic pits up to 4um long, not very conspicuous. In T.S. rounded- columnar to erect elliptic, 35-61um high and 11-20um wide, lumina sometimes with sparse black, granular deposit. Cells of the second, under layer sub-spherical, thinner-walled and of smaller diam. in T.S.

Endotegmen largely crushed, except the uppermost cell layer which is prostrate rectangular 15-30um high and 60-70um wide. Lower layers crushed to an amorphous layer 50-60um thick.

I.E. not differentiated.

?PERISPERM

Two to four layers of longitudinally fibrous cells with thin, colourless walls. In LS, 48-77um wide, anticlinal walls angular to rounded. In T.S., prostrate, shortly elliptic, 17-31um wide, 14um tall.

I.E. a single layer of prostrate, shortly rectangular cells 20-35um wide, c.20um high with black, granular contents (LS and TS), o.p.w. 7-8um thick, colourless. In paradermal view isodiametric, anticlinal walls 3um thick, irregularly sinuate by mutual compression.

?ENDOSPERM

A crushed, amorphous zone, 0-28um thick.

VARIATION

Testal O.E. hypodermal at ventral surface: cells markedly columnar, many with median anticlinal walls.

Testal I.E. crystal expression intermittent near chalaza (dorsal), but larger and more regularly expressed ventrally, near chalaza.

Testal mesophyll layers proliferate at raphe, confluent with flesh of 'aril'. Cells uncrushed, aerenchymatous, prostrate-elliptic 30-50um wide, 24-32um high. Walls 1-2um thick. Lumina and walls pale brown.

Exotegmic fibres occasionally transverse near micropyle.

## DISCUSSION

### Anatomical characters: assessment of taxonomic value

Orthotropous seeds characterize all species of Heckeldora and Chisocheton and also occur in some species of Guarea, otherwise the seeds in this tribe are more or less anatropous (with some verging towards the hemi-anatropous, e.g. Ruagea) and in relation to the placenta, are all descending and epitropous except Synoum (descending but apotropous) and Turraeanthus (epitropous but ascending). As was mentioned in the introduction, bitegmic seeds characterize four genera and unitegmic seeds three genera with both conditions (and intermediates) occurring in Chisocheton and Dysoxylum. Arillate seeds characterize the four genera with bitegmic seeds and sarcotestal seeds the unitegmic genera, whereas both occur in Chisocheton and Dysoxylum. The distinction between arillate and sarcotestal, whilst important at

the generic and infra-generic levels ( e.g. Chisocheton, see Mabberley, 1979) becomes blurred in some cases e.g. Ruagea. In addition, both conditions can be further sub-divided on the basis of anatomy into more or less distinct types, for example two types of sarcotestal seed can convincingly be shown in Chisocheton, and also seem to occur in Dysoxylum and possibly also in Guarea whilst at least three and possibly four arillate seed types occur in Dysoxylum. These different types of aril and sarcotesta show much promise of taxonomic use at the infra-generic level and in inferring phylogeny. They are categorized and named below under Chisocheton and Dysoxylum (those showing the greatest range) and the seeds of the other genera are later brought into line with them.

Integument vascularization occurs in the tegmen of Chisocheton and in the testa of Dysoxylum as well as most of the seed-coat in the genera with unitegmic seed-coats that seem to be of pachychalazal origin. The remaining genera, those with bitegmic seeds, do not seem to have vascularized integuments.

The testal O.E. comprises, in all genera, polygonal, isodiametric cells (paradermal section) which appear more or less cuboidal in L.S.. However, in Chisocheton they are almost always rectangular and usually two to five or more times as wide as high (except in e.g. C. ceramicus (Miq.) C.DC.), whereas, in Dysoxylum, they tend to be slightly columnar, but no more than twice as high as wide. The outer periclinal wall (o.p.w.) is usually characteristically thickened and although, in contrast with all the characters above, seems of little use at the generic level, it may have some use in delimiting species and discerning species affinities. A hypodermis was detected only in Dysoxylum cauliflorum Hiern, and a distinct bi-layered sub-epidermis occurs

sometimes in C. ceramicus. The testal mesophyll varies very greatly in thickness. In the four small bitegmic genera it is from two to five layers thick and usually slightly crushed, proliferating at the raphe to form an aril and is the same in Dysoxylum and Chisocheton (except those in the latter have no raphe) except that where the species is sarcotestal there may be 20-30 layers of larger, thinner-walled cells (e.g. Dysoxylum macrostachyum (Baillon) C.DC. and Chisocheton ceramicus) which form the basis of the succulence. However, most of the bitegmic Dysoxylum species have the thick-layered mesophyll, and only three of those intensively investigated do not, whereas in Chisocheton, the inverse is true, and indeed some species lack mesophyll almost entirely e.g. C. lasiocarpus (Plate 69B). The testal I.E. usually consists of smaller cells than the O.E., lacks the thickened o.p.w. and includes a prismatic crystal. This occurs in all the bitegmic genera (although crystals may be expressed only intermittently in an individual seed-coat as in Pseudocarapa (see plate 103B) except Synoum where the I.E. is closely similar to the O.E. in all respects and in Chisocheton where only C. ceramicus (plate 83B) of the species so far examined seems to have a differentiated I.E. with crystals. As in Synoum, so in Chisocheton the I.E. resembles the O.E. (see e.g. C. schoddei P.F. Stevens plate 74A).

The exotegmen consists of a single layer (sometimes two) of lignified fibres in all genera except Chisocheton where, although often of similar thickness, they can be much thicker. C. lasiocarpus can have up to five cell layers and C. ceramicus nine to twelve. Synoum is unusual in that a layer of fibroid cells appears at the base of the tegmen as an I.E. . The fibres vary very much in length, height, end walls, pitting , wall thickness and colour, and pigmentation of the lumina, particularly in

Chisocheton . These characters seem of great potential there in delimiting species and perhaps will be of use at detecting species affinities. Synoum is distinguished by very weakly developed fibres. These are very short (60-70um X 15um: plate 101 B & C) and thin-walled. Pseudocarapa has highly columnar (about three times as high as broad - see plate 103D) exotegmic fibres in T.S. Those of Ruagea and Cabralea are similar in many respects, suggesting an affinity. Undoubtedly the exotegmen is the single most taxonomically useful part of the seed-coat in this tribe.

The endotegmen is clearly detectable in all the bitegmic genera as eight to ten layers of unspecialized parenchyma cells without any specialized I.E. except in Pseudocarapa (plate 57 B, C & E) where it is plainly distinguishable and similar to the testal I.E. The cells of the endotegmen do vary from one genus to another in length and breadth, but there is an overlap in the range of dimensions and, more importantly, these layers are usually distorted in crushing and so must be considered as of relatively little taxonomic value. They can best be viewed near the chalaza. Dysoxylum is unusual in that the endotegmen is almost entirely absorbed - only a single layer of fibres remaining of the entire tegmen, whereas in Chisocheton the endotegmen is heavily vascularized and not markedly crushed or absorbed, the cells being filled with a hard, dark brown material (assumed to be tannin) and are rigid. The number of tanninized cell layers in the endotegmen (from 3 to 15) seems to be of some use at the species level in this genus.

The chalaza is extremely well defined from the integuments in Chisocheton and was studied and described in some detail for many of the 12 species investigated there, as was the 'transition zone' between these two parts of the seed-coat. The anatomy of the chalaza, whilst

different in many respects from that of the integuments is generally of less taxonomic utility. This is because there are fewer distinct layers, and those, that there are, are not so well defined and tend to vary in number of cell layers over the breadth of the chalaza and, futhermore, are intermingled to a greater degree. Often, great disruption is caused by proximity to the hilum, especially in species with a small chalaza, because the vascular bundles interrupt the stratification. Nevertheless, an assessment of the taxonomic value of this layer is presented here, if only to make the comparison with the integuments.

The O.E. of the chalaza is often indistinguishable from that of the testal O.E. with which it is continuous. However, in some species of Chisocheton (notably those species where the testa is not fleshy), it is distinctly different (e.g. C. schoddei: plate 74, cf. A & D), sometimes strikingly so ( e.g. C. lasiocarpus: cf. plate 69B & 71A) so that the chalazal O.E. is diagnostic of the species whilst the testal O.E. is not. Underneath the epidermis, the chalaza can be divided into two . The upper chalaza (see e.g plate 87A) of succulent tissue, consists of large, thin-walled, aerenchymatous cells, usually interspersed with lacunae (see earlier) which only occur otherwise in confluent parts of the testal mesophyll in the three bitegmic sarcotestal species examined. The number of cell layers in this part is commonly 30-60 at maturity. The cells vary in dimensions according to stratification. At first, they increase in size with distance away from the epidermis and then become smaller and less aerenchymatous as the lower chalaza is reached. The difficulty in using this tissue as a source of taxonomic characters is that it seems to vary enormously according to the stage of seed development in the size and number of layers of cells: as one might expect with succulent tissue. The lower part of the chalaza (see e.g.

plate 87B) is less variable in this respect but more subject to disruption by vascular bundles. It closely resembles the endotegmen with which it is confluent, but tends to be less darkly pigmented and have slightly greater numbers of cell layers. Occasionally, pockets of sclerotic cells occur in the chalaza which correspond with the exotegmic fibres but are always much shorter and thinner-walled and more randomly arranged. In C. ceramicus these exotegmoid cells make up the entire lower chalaza and the normal endotegmoid cells are not developed.

The endosperm and perisperm were also investigated as a source of taxonomic characters in Chisocheton, but they present difficulties in that in some species they are entirely absorbed and there are difficulties in establishing homologies. This is not the case with the embryo where the origin can readily be established by tracing cell layers from the suture between the two hemispherical cotyledons. The tissue of the outer cotyledon is far from uniform. Below the epidermis, three zones, here numbered arbitrarily #1, #2, and #3 from the inside out, can usually be recognized. Zone #2, the most distinctive, consists of sclereid bundles. The size of the radially elongate (columnar) to isodiametric sclereids, their shape, wall thickness, the number in each cluster, the spacing of these clusters and whether or not they are accompanied by crystalline idioblasts all seem to be reasonably constant within species (more than one collection was examined of C. cumingianus (C.DC.) Harms, C. sarawakanus (C.DC) Harms and C. ceramicus) and to vary considerably between species. Some species have no sclereids at all (e.g. C. ceramicus & C. medusae Airy Shaw) whereas in others they form a thick, uninterrupted layer (C. sarawakanus). Generally they form discrete, evenly-sized clusters a set number of cell layers below the cotyledon epidermis, but in C. cumingianus (see plate 81B) smaller

clusters are thinly scattered in the layers above. Whilst the sclereids of the latter species are small (30-50um diam.), isodiametric, thick-walled (16um) and accompanied by crystalline idioblasts. Those of other species (e.g. C. granatum) are always larger, columnar (c. 100um X 30um) with thin (4um ) walls and be totally without accompanying crystalline idioblasts. This part of the cotyledon seems to have considerable potential as a source of taxonomic characters at the species level in Chisocheton. Sclereid clusters were not detected in the embryo of any other genus.

Zone #3 (above #2) and zone #1 (below) both consist of layers of parenchyma cells. Zone #1 is the most uniform across the genus consisting of more-or-less isodiametric cells with finely granular grey contents and being tightly packed, often with apparently collenchymatous corner thickenings. Those of zone #3 seem to have more potential as taxonomic characters. In some species the cells are smaller, more rounded, less closely packed with more air-spaces (see e.g. plate 81B): C. cumingianus), in others they are tightly packed, large, highly polygonal, columnar and thick-walled (see e.g. plate 90: C. granatum). But the cells in zone #3 are often a mixture of both, the constituents varying from one part of the cotyledon to another (for example, often differing under the chalaza) and seem far less reliable as a source of taxonomic characters than does zone #2.

Large lacunae occur prominently in the outer embryos of some species e.g. C. schoddei but, although they are probably latex cells (immature cotyledons are reported as exuding white latex when cut in some species), they are possibly resin canals as reported for Trichilia emetica by Vaughan (1970) or a mixture of both. They are not apparent in

all species (perhaps they are lost at maturity in some) but are possible sources of characters.

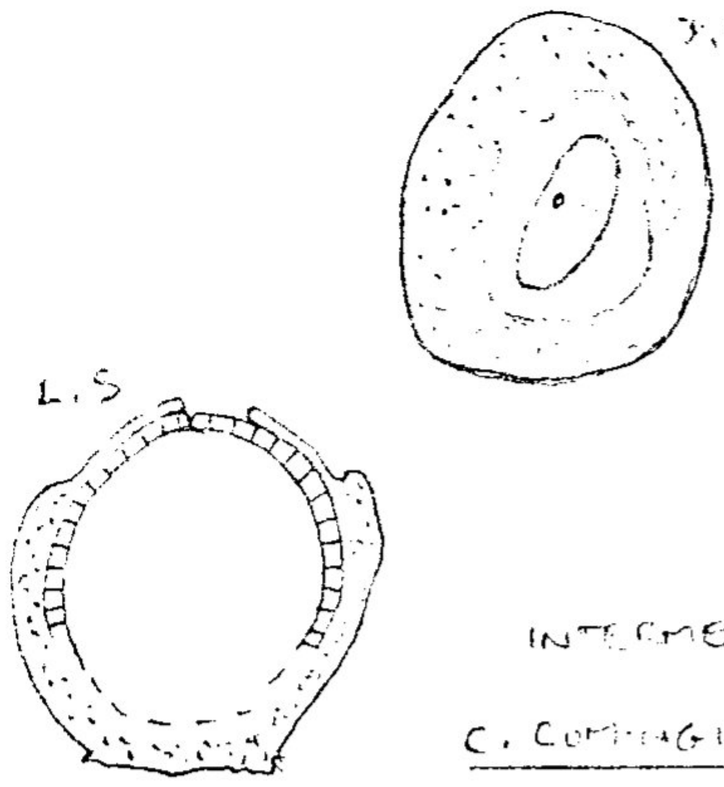
## THE GENERA: VARIATION, DELIMITATION AND AFFINITIES.

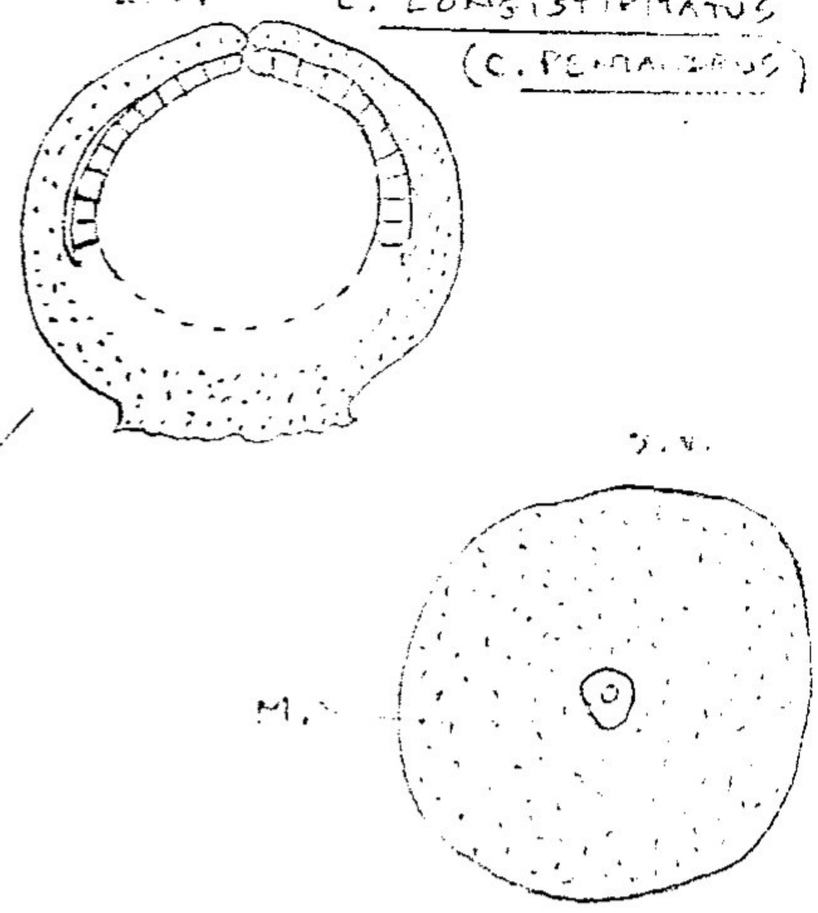
### Chisocheton

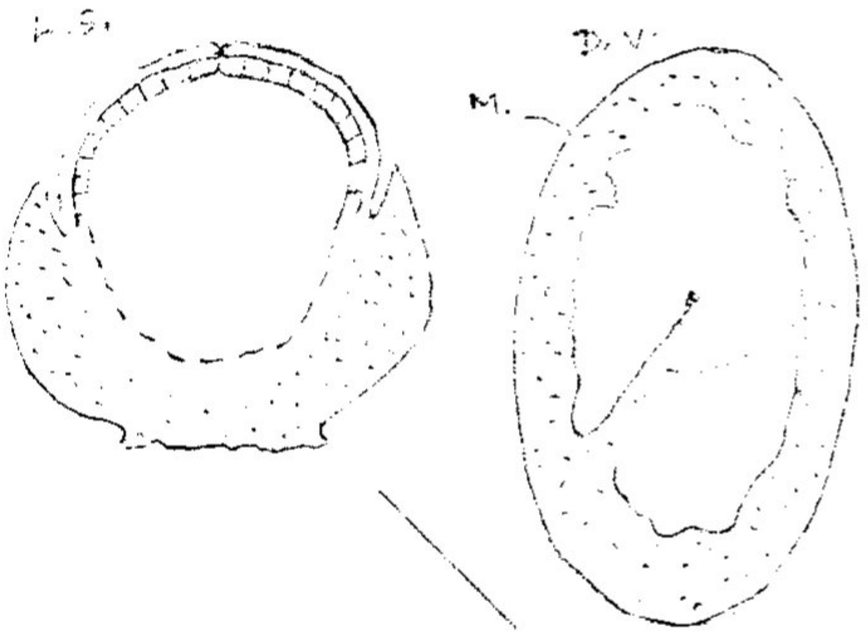
This genus is alone in the family in having locellate anthers (but not all species have them). It is closely related to Guarea which like it also has dormant leaf buds in most species, but generally differs in its capitate (versus discoid) style-head and a longer and narrower staminal tube (Pennington and Styles, 1975).

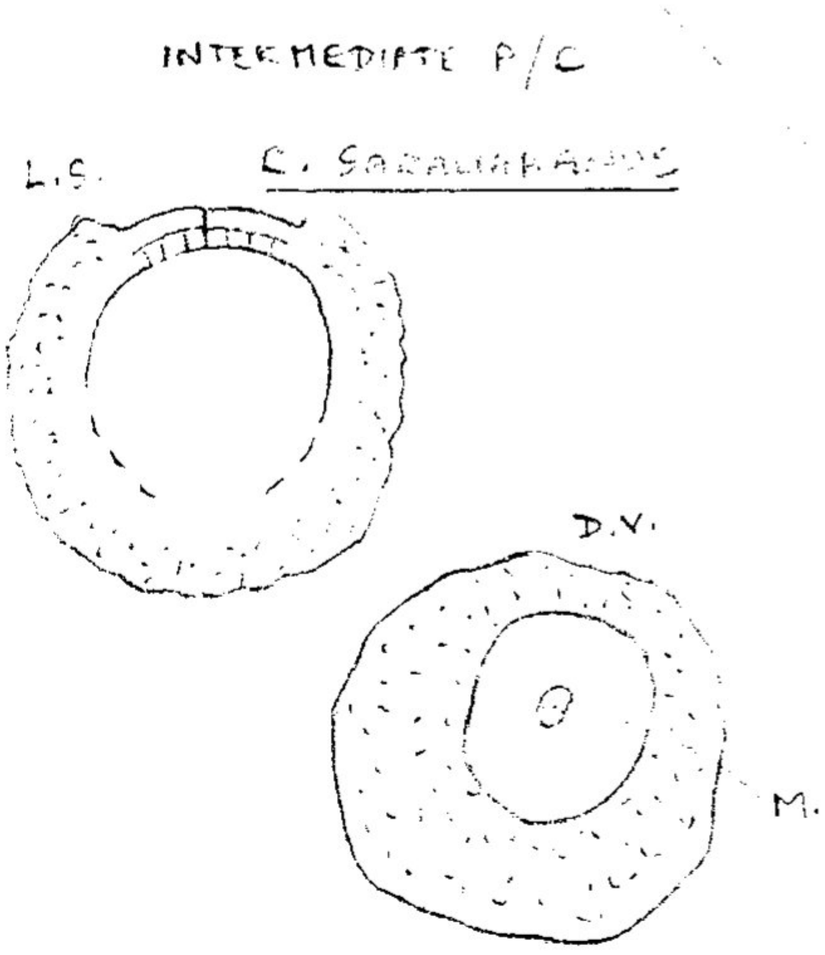
Chisocheton is well-defined on seed structure in being the only orthotropous genus with two integuments in the tribe. It is also alone in having a vascularized tegmen and having a predominantly chalazal aril. Its affinities seem to lie with Guarea and Heckeldora which are also orthotropous. Unfortunately, all the material investigated of those genera appears unitegmic and it is not possible to make a good seed anatomical comparison with them because this type of seed-coat is so poor in taxonomic characters (see discussion in the introduction and under Trichilieae). Although Dysoxylum shows a broadly similar range of variation in seed structure, its anatomy is entirely different (see there).

As a genus, Chisocheton is also unusual in that all of its species seem to have a large chalaza, taking up at least 25-35% of the surface area of the seed (in most other genera in the family, c.10% is usual), so that to some extent all species are pachychalazal. The entire chalazal surface always seems to be fleshy whereas the testa surface is not usually so. Hence, where the chalaza forms only 25-35% of the



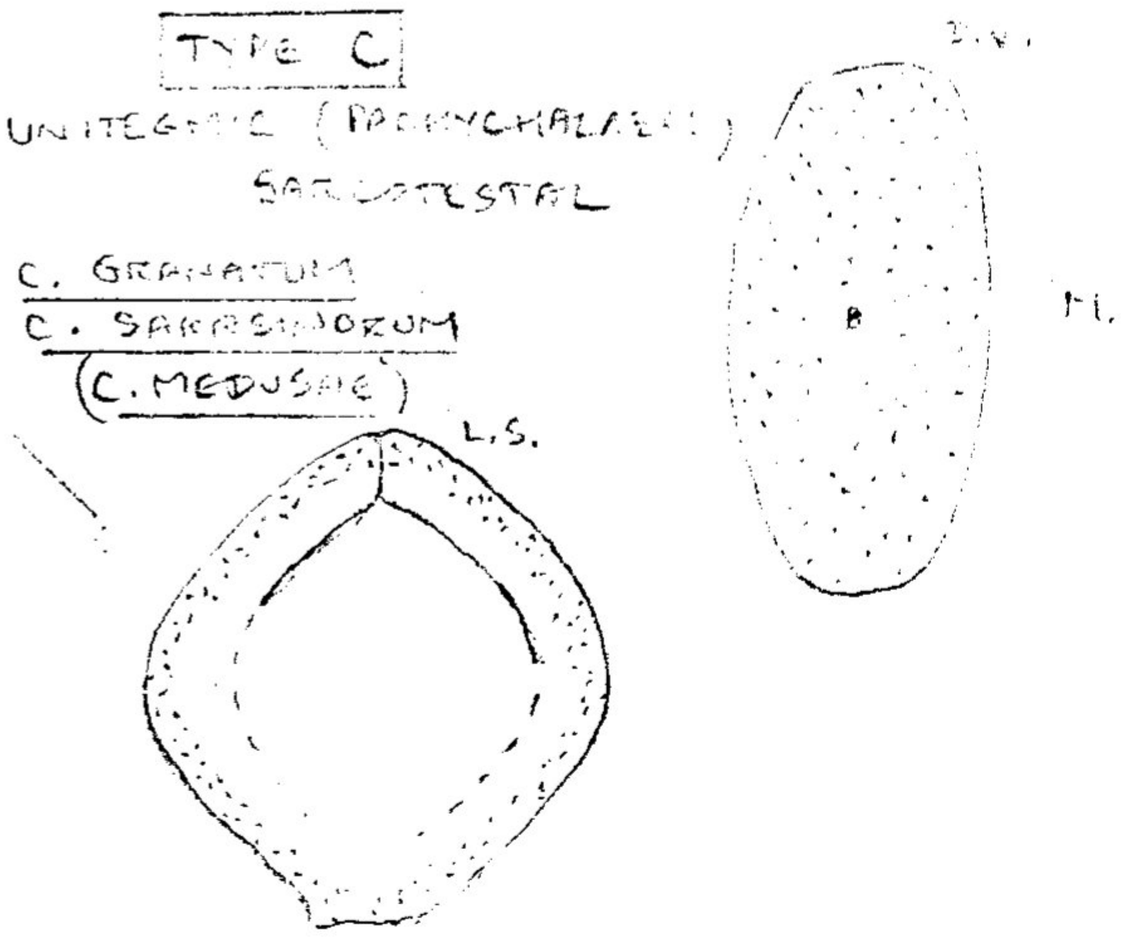




FIG. 8 SEED ORGANIZATION TYPES IN CHISOCHETON

FLESHY TISSUE.

TEGMEN (IF SHOWN; IMPLIES TESTA ABOVE)

D.V. - DORSAL VIEW
L.S. - LONGIT. SECTION
M. - MICROPYLE

POSSIBLE EVOLUTIONARY RELATIONSHIPS

seed-coat surface, as it does in most species, the seed-coat appears 'arillate' in the way that this is usually perceived, i.e. that the main body of the seed is partly enclosed in what appears to be a flap of brightly coloured succulent tissue derived from somewhere near the site of attachment of the seed. Actually this flap extends only a few millimetres over the hard, testal part of the seed-coat, the remainder of the aril representing the succulent chalazal surface. Whilst the hilum is large, often nearly the size of the chalaza, the fleshy tissue is associated with the chalaza and not the hilum/funicle. For the purpose of this discussion, it has been decided to term this appendage type a 'chalazal-aril' (see fig. 8,C; e.g. C. polyandrus Merr.: plate 66) but it might equally justifiably be called a 'chalazal-sarcotesta'.

Fully sarcotestal seeds in Chisocheton are of two very different types. In some species (see fig. 8, C) the chalaza forms the entire seed-coat and no vestigial testa or tegmen are left, so that the entire seed surface is fleshy. These are described here as unitegmic (pachychalazal) sarcotestal. C. sarawakanus represents an intermediate between type A and type C in that the chalaza forms 80-90% of the seed-coat. The second type of 'sarcotestal-ness'in Chisocheton is where, as in type A, the chalaza occupies only 25-35% of the seed-coat, but instead of the remaining part of the testa being hard, it is fleshy and indistinguishable superficially from the chalaza. This type of seed is here called 'bitegmic sarcotestal' (see fig.8, B). An intermediate between type B and type A occurs in C. cumingianus where the part of the testa proximal to the chalaza is thick and fleshy (as in type B), whereas that which is distal is thin and hard (as in type A).

It might reasonably be considered that type C is merely type B after loss of the inner integument and that it may not be pachychalazal at

all. But examination of the anatomy shows this to be extremely unlikely. Firstly, the putatively pachychalazal integument of type C species has all the characteristics of the proven pachychalazal (by presence of testa and tegmen distally ) part of the seed-coat of e.g. C. sarawakanus, that is, an upper fleshy aerenchymatous part intergrading with a lower, apparently tanniniferous part and being heavily vascularized. Secondly, it is shown by the fact that the testa of all other Chisocheton species does not contain vascular bundles or tanniniferous type cells.

It is useful to compare the groupings of species suggested by these fleshy appendage types and other seed anatomical characters with the existing classification in the genus (Mabberley, 1979). On the basis of fleshy appendage type, there is fairly close agreement at the sectional level in that the species with type B seeds occur only in sections Dasycoleum (C. ceramicus and C.pentandrus) and Rhetinosperma (C. longistipitatus). Similarly, all but one of the species with type 'A' seeds occur in section Chisocheton and none in sections Dasycoleum or Rhetinosperma. The difficulty is caused by the three species with type C seeds which occupy three different sections. The occurrence of one of these species, C. medusae in section Clemensia together with C. macranthus Merr. Airy Shaw a type 'A', is accounted for by Mabberley (1979) who shows that despite the variation in fruit morphology in this section, all members share a distinctive and primitive flower type, suggesting that this section 'represents the relics of the proto-Chisocheton stock which gave rise to the two major lines in the genus'. Indeed, despite the differences in fleshy appendage type, both species share the unusual absence of cotyledon sclereids: they are

readily confused in other characters and perhaps they are linked in seed features as well.

The other two type C species, C. sarasinorum Harms and C. granatum both not only have cotyledon sclereids, but are very similar in the structure and arrangement of these sclereids. Both have strongly columnar sclereids (80-100um X 25-35um) with thin walls (3-5um thick) and are grouped in blocks of 9-12 cell layers thick and 13-40 cells wide. Prismatic crystal idioblasts are not associated with the sclereid clusters. In those species with type A seeds which do have cotyledonary sclereids, they are always in smaller groups (though in one collection of C. cumingianus, these groups do link up) and the sclereids are isodiametric and smaller (30-50um diam.), with walls more than twice as thick (8-16um diam.) and the sclereids are associated with prismatic crystal idioblasts.

The seed anatomical evidence suggests that, these two species seem to be more closely related to each other than to to any of the above mentioned groups. The only linking species of those examined is C. sarawakanus, which has a similar chalazal anatomy (though this as was seen in the Trichilieae, is relatively featureless and poor in taxonomic characters) and, more importantly, shows links in the cotyledon sclereid structure, the sclereids being isodiametric to columnar (24-65um X 23-42um) and similarly thin-walled (4um) and free of prismatic crystals. They are also grouped in large blocks, though only six to seven cell layers thick.

It would be interesting to carry this analysis further and use additional anatomical characters to compile a classification based purely on seed anatomical characters and then to compare it with the existing one based on conventional macro-morphological ones. There are

certainly enough characters in these seed-coats to do so. The difficulty is that although spirit material was available of 12 species, three of these were of immature, undehisced material (C. longistipitatus, C. macranthus and C.schoddei) which had clearly not finished development of mature exotegmic fibres (see plates 74A & 77, then cf. e.g. 83B), the single richest source of seed anatomical characters. The remaining nine species are relatively thinly scattered through this genus of 51 species and consequently it is difficult to examine relationships any further. It is possible to point out for example that C. lasiocarpus and C. sarawakanus (same section and series) share exotegmic fibres which are both columnar in cross-section and also have pigmented lumina (both not seen in any other species examined of the genus), although they are clearly different in other seed anatomical characteristics. The potential exists, but more material is needed if it is to be realised.

Dysoxylum

This genus usually differs from Guarea and Chisocheton in lacking a dormant leaf bud and in having a cyathiform or tubular nectary (versus a stipitate or patelliform one). In seed anatomy it is clearly different from Chisocheton in its anatropous/hemi-anatropous (versus orthotropous) seeds with a vascularized testa, but pachychalazal seeds of Guarea are less easily distinguished from similar seeds in Dysoxylum. Bitegmic species of Dysoxylum have rather similar seed anatomy to species in the four small, bitegmic genera Pseudocarapa, Cabralea, Ruagea, and (but less so) Synoum.

The species of Dysoxylum show an immense amount of variation in seed anatomy (first demonstrated by Corner (1976,1:188)), more so than any other genus I have investigated in the family. Perhaps this variation

D.V.

PLACENTAL-FUNICULAR-RAPHE-ARILLATE

D. PACHYPHYLLUM

T.S.

R.

3

D.V.

FUNICULAR-RAPHE-ARILLATE

D. SPECTABILE

R.

T.S.

2

D.V.

R.

T.S. RAPHE

R.

L.S.

1

RAPHE-CHALAZAL-ARILLATE

D. MACRANTHUM

D.V.

T.S. RAPHE

L.S.

4

BITEGMIC-SARCOTESTAL

D. PETTIGREWIANUM

D.V.

L.S.

5

BITEGMIC-UNITEGMIC SARCOTESTAL

D. MACROSTACHYUM

D.V.

L.S.

6

UNITEGMIC (-PACHYCHALAZAL?) SARCOTESTAL

D. ANGUSTIFOLIUM

D.V.

L.S.

7

UNITEGMIC (TEGMEN LOST?) SARCOTESTAL

D.V.

L.S.

8

UNITEGMIC (PACHYCHALAZAL?) PSEUDO-ARILLATE

D. ACUTANGULUM SSP. FOVEOLATUM

L.S.

9

UNITEGMIC (PACHYCHALAZAL?) NON-FLESHY

D. COSTULATUM

**FIG. 9 SEED ORGANIZATION TYPES IN DYSOXYLUM**

FLESHY TISSUE

TEGMEN (IF SHOWN; IMPLIES TESTA ABOVE)

D.V. - DORSAL VIEW
L.S. - LONGITUDINAL SECTION
T.S. - TRANSVERSE SECTION

NOTE: VASCULARIZATION NOT SHOWN EXCEPT IN T.S. TO SHOW THE RAPHE.

– – – – – POSSIBLE EVOLUTIONARY RELATIONSHIPS

will be of some use in constructing an infra-generic classification in the genus. Indeed, Corner (1976,1:189) says ' There can be no doubt that all the species of Dysoxylum need full examination of their seeds before there can be an adequate understanding and classification of them'. This variation is largely due to the extent of the development of the chalaza and of the fleshy part of the seed surface (see fig.9). The basic structure of the testa and tegmen is fairly uniform and very different from Chisocheton apart from the ovule orientation and difference in vascularization: the testal O.E. in L.S. is usually cuboidal to slightly columnar (rather than broadly rectangular). The testal mesophyll does vary greatly; it is at least three cell layers thick (rather than 0-2(-3) in Chisocheton unless sarcotestal) and in the sarcotestal species, considerably more. To some extent, the testal mesophyll appears to take on the function of the endotegmen in Chisocheton - its lowest layers holding the vascular supply and even containing tanniniferous cells in some species e.g. D. pettigrewianum F.M. Bailey and at the same time its upper layers may be aerenchymatous and sarcotestal, as in that species. The testal I.E., unlike that of Chisocheton, is always distinct from the O.E. (as is usual in the family) in being smaller, more rounded, with virtually no o.p.w.. It is usually crystalliferous (unlike Chisocheton). The exotegmic fibres are usually only one layer thick (two in D. gaudichaudianum (A. Juss.) Miq.) and, compared with Chisocheton, rather uniform, usually having thinner walls and a smaller diameter (isodiametric) in T.S. The endotegmen is always completely crushed and often absorbed, quite unlike the tanniniferous multi-layered structure of Chisocheton: usually the thickest part of the seed-coat. A tegmic I.E. was detected in D. pettigrewianum, but is not usually present in the genus.

In Chisocheton, the relationship of fleshy tissue to the integuments seems relatively fixed and only three basic types of seed organization occur. This is not so in Dysoxylum where it is additionally complicated by the presence of a raphe and lack of a large chalaza and where nine different types of seed organization can be recognized.

The closest approximation to the chalazal-aril condition seen in most species of Chisocheton covered here, is the pattern seen in species such as D. macranthum C.DC. (plates 112-114) and D. cauliflorum (plates 115-117). Here an 'aril' is developed in the neighbourhood of the chalaza, much as in Chisocheton, but extends along the adaxial side of the seed broadly along the raphe (i.e. it is broadly raphe-chalazal-arillate). Anatomical investigation shows that there is no strictly aril-correlated expanded chalaza here as in Chisocheton (where it occupies a minimum of 25-35% of the seed-coat surface). Rather, the 'aril' in these species usually extends beyond the chalaza into the proximal part of the testa (rather as in the exceptional C. cumingianus: see plates 78-81), but leaving most of the testa mechanical, not fleshy.

Similarly, in these species, not just the raphe, but a large part of the testa near the raphe is fleshy. In a sense, the seed-coat can just as easily be labelled 'partly sarcotestal' as arillate. Within this group of species, the surface area of the chalaza (loosely correlated with the surface area of the aril) varies: in D. gaudichaudianum it is only about 10%, in D. cauliflorum 30%, in D. macranthum 40-50%- so that this type is much more heterogeneous than the Chisocheton 'chalazal-arillate group' where the chalaza is usually c.25-45%. D. mollissimum Blume seems to fall into this category, but the chalazal area has not been assessed.

A second and very different type of seed organization is represented by D. spectabile Hook. f. Here the chalaza, (c. 10% of the seed-coat) hardly seems to be fleshy at all- the aril issues almost completely from a narrow strip of testa along the raphe towards the funicle (i.e. it is a funicular-raphe-aril). Here seems to belong (from his figure) Corner's 'Dysoxylum sp. (Corner, 14 Nov. 1937)'.

A third type of seed organization is represented by D. pachyphyllum Hemsl. (plates 105-107). Superficially this resembles the previous two types, in that there is a fleshy adaxial 'aril' which is largest over the chalaza. Close examination of two different spirit collections from Lord Howe Island reveals that this fleshy tissue is mainly placental (and contains the placental vascular bundle) which has detached from the fruit with the seed. Underneath is a weakly-developed raphe-aril, like that of D. spectabile, but in proportion, less than half the size. The chalaza in this species covers 10-20% of the seed surface and is not fleshy. This species could be termed placental-funicular-raphe-arillate.

A fourth type of seed organization is represented by D. pettigrewianum F.M. Bailey and seems usual in the species of Dysoxylum from New Caledonia (e.g. D.bijugum (Lab.) Seem., D.canalense (Baill.)C.DC., excepting D. macrostachyum). Here, the chalaza occupies only c.10% of the seed-coat, and is fleshy as in species of the 'macranthum' type, but is different in that the entire seed-coat is sarcotestal: superficially the chalaza cannot be detected as it can in D. spectabile and D. pachyphyllum. These species might be termed bitegmic sarcotestal. A fifth type of seed-coat is that of D. macrostachyum (plates 108-111). This is superficially identical with the last, in that the entire seed-coat is sarcotestal, but its chalaza in contrast covers almost 50%

of the seed-coat. It might be termed bitegmic/unitegmic (pachychalazal) sarcotestal. If intermediate species with perhaps 20% or 30% chalaza are found, this type might be amalgamated with the 'pettigrewianum' type.

It is fortunate in species of the 'pettigrewianum' type that the chalaza and integuments can be clearly differentiated from each other by the presence of distinctive exotegmic fibres and a crystalline testal I.E. in the innermost part of the bitegmic portion. The upper nine-tenths of the seed-coat is much the same in both chalazal and bitegmic parts of the seed-coat: aerenchymatous parenchyma mixed with vascular bundles, though the latter less frequent in the testa. In D. macrostachyum however, the essential distinguishing characters are partly lost, the I.E. is not crystalliferous and so is not so clearly differentiated. If the exotegmic fibres were also lost and the I.E. perhaps crushed, how would one distinguish the bitegmic derived sarcotestal portion of the seed-coat? One can generally tell the difference, because the chalazal portion often has irregularly distributed patches of sclereids and tanniniferous cells in its lower cell layers, and is far more chaotically vascularized (as was explained in Chisocheton and Trichilieae) and usually has Chisocheton chalazal type 'lacunae'(see e.g.D. macrostachyum: cf. plate 110 (sarcotestal chalaza) and plate 111 (sarcotestal testa)). But, as sclereids may not always be present in the chalaza in this genus, and tanniniferous cells and vascular bundles do occur in the testa, e.g. D. pettigrewianum (well demarcated by I.E. crystals and exotegmic fibres), one cannot be entirely sure of making the distinction in the absence of the 'markers ' referred to above. Thus, in other sarcotestal species without the 'markers', it is difficult to be completely sure how much of the seed-coat is chalazal and how much of bitegmic origin. Into this sixth

category fall unitegmic (presumed pachychalazal) sarcotestal species known here as the 'angustifolium' type such as D. angustifolium King (plates 103B, 119-121), 'D.acutangulum' (plate 118), D.peerisiae Kosterm. and apparently, Corner's D. sp. Sing. F. 32212, 34930: one cannot be completely sure of whether the unitegmic condition is derived from loss of the tegmen or by the seeds being largely pachychalazal. From the anatomy, they appear to be pachychalazal, but unlike Chisocheton (q.v.), one cannot be sure. However, Corner (1976,1:188-189) who has evidently investigated some of these species in more detail than has been possible here, concurs: D. acutangulum Miq. .... 'greater part appearing to be pachychalazal'. and for Dysoxylum sp. Sing. F. No. 32212, 34930 '...covered by an orange pachychalazal sarcotesta 1-2mm thick'. The possibility must not be overlooked that, in this category, some species might be included of another and non-homologous seed organization which would constitute a seventh type, that which is also unitegmic sarcotestal but of immediate bitegmic origin (i.e. most similar to the pettigrewianum type). Thus far, it is surprising that no species have been identified of this type, but should they be discovered, perhaps they should be known simply as 'unitegmic sarcotestal'.

An eighth type of seed organization may be represented by D. arborescens (Blume)Miq. wherein, although anatomically seemingly pachychalazal (but according to Corner (1976,1:189) possibly of bitegmic origin), only the ventral part of the seed-coat is swollen and fleshy, the remainder being relatively hard. Thus the whole seed appears superficially to be arillate. In one spirit collection of Dysoxylum, possibly of the same species, from N. Australia (Dunlop s.n.) this pattern is more or less inverted and again the entire seed-coat seems

to be pachychalazal. Seeds of this sort might be known as unitegmic (pachychalazal?) pseudo-arillate'.D. parasiticum (Osbeck) Kosterm.(plate 103A) may also belong here.

A ninth type of seed-organization seems to be shown by Corner's 'D. costulatum Miq. (Sing. F. No. 36415; Singapore, Bukit Timah Forest as tree 334)'for which he describes the seed-coat 'as D. acutangulum [i.e. the 'angustifolium' type - unitegmic (pachychalazal?) sarcotestal] but the seed larger with a thin testa and without an aril' and also by his 'Dysoxylum sp. (Sing. F. No. 32810, Pahang, Cameron Highlands'. He brackets these together as being 'exarillate with blackish brown testa': a condition not seen in the material I have examined, but resembling that seen in the picture of D. grande Hiern reproduced in plate 103C.

Cabralea (plates 54 & 55).

Pennington and Styles (1975) point out that Cabralea is very close both morphologically and in wood anatomy to Ruagea and that Harms (1896, 1940) considered it to be closely related to Didymocheton (which they place in Dysoxylum) on morphology, especially in its cyathiform nectary. They show however, that Cabralea is distinct from the second in that its petals are free from the staminal tube, from the first by the absence of a stipitate nectary and from both by the pellucid lines and dots in its leaves.

In terms of gross seed structure, the monotypic Cabralea is different from all species of Dysoxylum seen in that the two seeds in each locule (itself unusual in Dysoxylum) are held tightly together by their entwined arils. The seed organization in Cabralea seems the same as the 'spectabile' type in Dysoxylum, i.e. it is funicular-raphe-arillate and

bitegmic, the chalaza only c. 10% of the seed surface (but quite different from the raphe-chalazal-arillate/partly sarcotestal Ruagea q.v.). The seed-coat anatomy of Cabralea is strikingly similar to that seen in those species of Dysoxylum such as D. spectabile, D.pachyphyllum and to some extent those of the 'macranthum' type: the testal I.E. is more or less cuboidal in L.S., the mesophyll has only four or five layers of aerenchymatous parenchyma (D. pachyphyllum has as few as three) and lacks vascular tissue; the testal I.E. is well-differentiated from the O.E., the cells smaller and sporadically with crystals; the exotegmen has two layers of fibres (unusual in Dysoxylum, but seen in D. gaudichaudianum). The fibres have narrow scalariform pits (as in D. pachyphyllum). However, they are larger in diameter than in any species of Dysoxylum and it is still possible to detect individual cells in the endotegmen despite its being crushed, whereas, in Dysoxylum, there is usually no trace at all of this tissue beyond an amorphous, thin grey layer. In terms of seed anatomy and overall structure, there are also similarities between Cabralea and Pseudocarapa, and to a lesser extent Ruagea and Synoum (see there).

Ruagea (plates 56 & 57).

Pennington and Styles (1975) imply that Ruagea is most likely to be confused with Guarea but show that it is separable by two diagnostic characters: the imbricate (not open) calyx lobes and the 'peculiar, greatly swollen basal sarcotesta which is quite unlike that of Guarea or Chisocheton'.

It was only possible to examine one of the five species (Pennington and Styles, 1981) of the genus and so the following remarks are based only on Ruagea glabra Tr. & Pl. In seed structure it is completely

different from Guarea which always seems to be completely sarcotestal, and in the three species considered here, essentially unitegmic. Ruagea has markedly bitegmic seeds. In seed organization they are similar to the raphe-chalazal-arillate species of Dysoxylum of the 'macranthum' type. Like the latter, the fleshy tissue is only loosely correlated with the raphe but differs in being highly associated with the chalaza. The seed-coat anatomy of Ruagea is also very similar in general pattern to that seen in these species of Dysoxylum, and also those of D. spectabile, D. pachyphyllum and that of Cabralea. The similarities are those listed for Cabralea (see there) with Dysoxylum, as are the differences, but in addition, the exotegmic fibres of Ruagea are strongly columnar (c.3:1) in T.S. (isodiametric in most Dysoxylum and isodiametric to slightly columnar in Cabralea) and the endotegmen is even less crushed, and a distinct tegmic I.E. remains.

Pseudocarapa (plates 102 & 103)

Although this genus has been recently restored to its monotypic state (Mabberley, 1985) it is assumed the remarks made by Pennington and Styles (1975) are still valid. They point out that the genus is most closely related to Dysoxylum from which it differs in having an annular or patelliform nectary (versus tubular or cyathiform) and suggest that it is also related to Guarea, Synoum and Anthocarapa. They say it is different from all genera in the Meliaceae in having pollen shed in tetrads.

The seed structure of Pseudocarapa championii (Hook. f. & Thoms. ex Thwaites) Hemsl. is indeed remarkably similar to that of some species of Dysoxylum excepting that, like Cabralea it differs in that the two seeds in a locule are united by entwined arils. It shares the same type of

seed organization as D. spectabile, i.e. it is funicular-raphe-arillate and largely bitegmic. Its chalaza is less than 10% of the seed-coat area. In seed-coat anatomy, the overall structure is again remarkably similar to that of Dysoxylum, indeed, to the same species and in the same characters as were Cabralea and Ruagea. Like Ruagea, it differs from Dysoxylum in the robust and well developed layer of exotegmic fibres and well preserved endotegmen, but also in having strongly columnar (>3:1) exotegmic fibres in T.S. Anatomically, the resemblance with Ruagea, especially that of the exotegmic fibres, is quite striking. There is also a strong similarity with Cabralea, apart from the fact that the two seeds in a locule are united by their arils. Indeed, one cannot but conclude from this study of seed structure that all three genera, although separable, are closely related first to each other and then to species of Dysoxylum of the 'spectabile' type.

Synoum (plates 100 & 101).

Pennington and Styles (1975) consider the monotypic Synoum closely related to Guarea and Dysoxylum, but they distinguish it 'by the presence of the arillode which unites the two seeds of each locule, a situation unknown elsewhere in the family'. Synoum further differs from Guarea by lacking a dormant leaf bud and a stipitate nectary and in the pollen and wood anatomy. It further differs from Dysoxylum in lacking a cyathiform or tubular nectary but is similar in pollen and wood anatomy.

The seeds of Guarea investigated here are totally unlike those of Synoum being unitegmic and sarcotestal. The seeds of Dysoxylum, especially that of the 'spectabile' type (and those of Cabralea and Pseudocarapa) have much more in common with those of Synoum: they are

all raphe-funicular-arillate and largely bitegmic with a chalaza composing 10% or less of the seed-coat. There are also similarities in the seed anatomy: they share a more-or-less cuboidal testal O.E. and a few cell-layered testal mesophyll. But there the similarities end. The testal I.E. of Synoum lacks crystals and is very similar to the O.E. ; unknown in all bitegmic genera of this tribe except Chisocheton (where this condition occurs in most species). Further, the tegmic fibres are very weakly formed (50um long and 5um high) and sometimes occur as an I.E. (see plate 101C); neither characters occur elsewhere in the tribe. Most striking of all, however, is that the seeds of this genus are apotropous and descending rather than epitropous (in relation to the placenta) and that the seeds are united by their arils, not as in Cabralea and Pseudocarapa by the arils entwining, but so that they form a common, single structure (see phylogenetic speculation, fig.10) rather like Siamese twins. The two raphe bundles remain quite separate but connect to the placenta through a common hilum. The arils are united almost up to the chalaza. Apotropy and this type of 'common aril' are not seen elsewhere in the family.

Guarea (plates 61-65)

Guarea seems most closely related to Chisocheton (see there) and there are no absolutely diagnostic characters that can be used to distinguish the two (Pennington and Styles, 1975).

Three species of Guarea were studied. The American G. guidonia (L.) Sleumer from Corner's description (1976,1:189-190) and the African Guarea glomerulata Harms and G. mayombensis Pellegr. The last species was transferred to a separate genus, Leplaea, by Vermoesen and maintained there by Harms (1940) on the basis of its indehiscent fruit.

Pennington and Styles (1975), after examining mature fruit preserved in spirit, found that although they had not dehisced, the inner surface of the pericarp was split along the centre of each loculus and 'it is clear that this fruit would dehisce into four valves on falling to the ground, if not before'. Recent field observations (Kigezi, Uganda, 1975) have shown that a proportion of fallen fruits do indeed eventually dehisce on the ground (see plate 63C), but only old fruits, by which time the thick, yellow-orange sarcotesta (plate 63 A & B) has decomposed. Indehiscent or tardily dehiscent fruits may also occur in American Guarea (Pennington and Styles, 1981). The seed anatomy of G. mayombensis comprises an outer epidermis of slightly rectangular cells in L.S. (isodiametric in paradermal section) intermediate between that seen in Dysoxylum and Chisocheton, and below, an upper zone of more than 30 layers of thin walled aerenchymatous cells with orange contents that form the bulk of the sarcotesta. Vascular bundles penetrate the lowest layers which intermingle with the lower zone. This consists of ten layers of variously shaped sclerotic cells of which the upper layers tend to be the most fibrous. The innermost part of the lower zone of the seed-coat consists of crushed cells. This is broadly similar to the seed-coat anatomy of Guarea guidonia as described by Corner, although that species has much smaller seeds only 12mm long (70-80mm long in G. mayombensis) and proportionately fewer cell layers - only four to six layers in the upper zone - and these further differ in having yellow oil drops (not seen in G. mayombensis). The lower zone in G. guidonia differs from that of G. mayombensis in being thicker than the upper zone and in having only two to three layers of 'tracheid-like' cells. Like that of G. mayombensis, the upper layers are longitudinally fibriform,

the lower layers smaller and cuboidal and an innermost layer of crushed cells exists.

This type of seed-coat is similar to the unitegmic and presumed pachychalazal seed-coats seen in Dysoxylum species of the 'angustifolium' type and in Chisocheton (also Turraeanthus and Heckeldora: discussed there). However, these latter genera usually have tannin-filled cells associated with the sclerotic cells in the lower zone but those are not seen here. The chalazal part of the seed-coat of C. ceramicus is closest to Guarea in that it lacks tannin cells and just has sclerotic cells.

Guarea glomerulata (plates 61 and 62) is different from the previous two species of Guarea in that it lacks a lower zone of sclereids (or tannin cells) so that the entire seed-coat is composed of aerenchymatous cells with a few vascular bundles. Very weakly developed and sporadic longitudinal fibres do occur in the lowest layer (in two collections: see plate 62C and D) and it is possible that this unitegmic seed-coat is not of pachychalazal origin at all, but is derived by loss of the tegmen, i.e. rather like the bitegmic part of the seed-coat of Dysoxylum macrostachyum (plate 111) but with the lowest layer lost in addition, hence perhaps the 'seventh' type of seed organization referred to there. The absence of sclerotic and tannin cells (rarely seen in the testa) is in keeping with this hypothesis, but study of earlier stages is needed to be certain.

The organization of the seed varies markedly from species to species in Guarea. In Guarea guidonia, the hilum is superior and ventral and the embryo orientated so that the radicle is also superior (i.e. at the distal end of the fruit) so the seed appears anatropous as in most Dysoxylum. However, in seeds of G. mayombensis, the radicle is lateral

(see plate 63B) so that the seed verges on the orthotropous. Finally, in some seeds of G. thompsonii Sprague and Hutchinson and G. ramiflora Vent. with the same embryo orientation, the hilum is ventral but lateral, not superior, so that the seed appears completely orthotropous; as in Chisocheton and Heckeldora. In this genus then, seed structure seems of little use in giving absolute generic delimitation. This is partly due to the variability in ovule orientation, and partly due to the lower character content (and hence ambiguous nature) inherent in the unitegmic seed-coats that seem to characterize the genus.

Turraeanthus (plates 58-60)

This genus is closely related to both Guarea and Chisocheton, differing from both in that the corolla is united to the staminal tube for most of its length and in that the leaves lack a dormant terminal bud. Species of Turraeanthus lack the stipitate nectary that characterizes most species of Guarea and the locellate anthers that characterize most species of Chisocheton.

Two species were investigated: Turraeanthus mannii Baill. (in depth) and T. africanus (Welw. ex C.DC.) Pellegr. (only superficially). Both have unitegmic (probably pachychalazal) seed-coats which are sarcotestal, thus resembling the species investigated of Chisocheton 'type C', Dysoxylum 'angustifolium' type and all Guarea. The structure of the seed-coat follows a similar pattern to these species: an O.E. of isodiametric (paradermal section), more or less cuboidal (L.S.) cells above the upper zone of the seed-coat consisting of 10-20 layers of large aerenchymatous cells that comprise the sarcotesta, the lower layers being highly vascularized. The lower zone consists of five to ten layers of isodiametric to shortly longitudinally extended lignified

cells with further layers of crushed cells underneath. Inasmuch as there are no tannin cells, the anatomy is closer to that of Guarea than Chisocheton or Dysoxylum, but Turraeanthus mannii is different from all, including the former, in that the lignified cells have spiral to scalariform thickenings and not simple pits.

Unlike in the species of the above genera, the seed is affixed to the proximal end of the fruit (see plate 58C) i.e. the hilum of Turraeanthus is inferior. In addition, the embryo is directed laterally, but centripetally, the radicle directed towards the central axis of the fruit, the fruit being ascending and epitropous rather than descending as in the above genera. T. africanus seems to show the same type of organization. As in Guarea both indehiscent fruits (T. mannii- not hitherto noted) and indehiscent-fruited species (T. africanus) occur.

Heckeldora (plates 51-53)

Although the monotypic Heckeldora is included in Guarea by Harms (1940), Pennington and Styles (1975) maintain it as a distinct genus because it has a unilocular ovary with parietal placentas. They say it also differs from Guarea in the indehiscence of its fruit and the embryo with collateral cotyledons and superior radicle, though the latter does occur rarely in Guarea. Heckeldora also differs in pollen structure from the several species of Guarea examined by Pennington and Styles.

The seed is sarcotestal, unitegmic (apparently pachychalazal) and the seed-coat is divided into an upper fleshy zone of aerenchymatous parenchyma and a lower zone of sclereids underlain by crushed cells just as in most species of Guarea and as in Turraeanthus, Chisocheton type 'C' and Dysoxylum species of the 'angustifolium' type. From most species

of the latter two groups it differs in lacking tannin cells. The numbers of cell layers and overall appearance of the seeds of this monotypic genus are particularly close to those of Turraeanthus mannii, though anatomically it differs in sclereid wall-thickenings. In terms of seed-coat anatomy it is undoubtedly closest to Guarea, differing from G. mayombensis only in quantitative characters. In the final analysis, seed anatomical data add no new evidence to support this genus. The gross structure of the seed shows some unusual characters, not previously noted. Firstly, the micropyle is usually adnate to the pericarp, and at the point where the seed joins the placenta, one or two swellings are detectable. In addition, the seed appears orthotropous. Although the latter state has been noted in species of Guarea, the former two have not.

## TRIBAL DELIMITATION

Unlike the Turraeeae, it is very difficult to define the Guareeae on seed characters. The similarities with the Trichilieae are particularly marked, but, unlike that tribe where most (seven out of ten) of the 'satellite' genera have indehiscent fruits and most (five out of seven) of these have a lignified endocarp, the Guareeae include only one (monotypic) genus which is completely indehiscent, though some degree of indehiscence occurs in two other genera; none however has a lignified endocarp as is so common in the Trichilieae. Another difference between these two tribes is the incidence of the sarcotestal condition. In the Trichilieae, only a small proportion of the species of the 'core' genus, Trichilia are sarcotestal, and extremely few (two?) are completely sarcotestal, whereas, in the Guareeae, completely sarcotestal seeds

occur in many or most species of five genera, three of these with all their species sarcotestal.

In seed orientation the genera of the Trichilieae are all more-or-less anatropous and epitropous and descending with respect to the placenta, Astrotrichilia (orthotropous) being the exception. However, in the Guareeae three genera are completely (Chisocheton and Heckeldora) or partly (Guarea) orthotropous and two others (Synoum and Turraeanthus) appear to depart from the epitropous and descending arrangement.

In the anatomy of the seed-coat, pre-raphe vascular bundles, which occur in some Trichilieae, were not detected in Guareeae, but columnar (T.S.) exotegmic fibres, which seem characteristic of that tribe, occur in at least four genera of Guareeae - Chisocheton, Cabralea, Ruagea and Pseudocarapa - and are particularly marked in the latter two.

Despite the differences set out above, the resemblance between the two tribes is striking if one compares the seeds of the primitive (as considered here) species of Trichilia with those of seeds of Cabralea and Pseudocarapa. They seem almost to show less variation as a group than is found within either Dysoxylum or Trichilia!

## PHYLOGENETIC SPECULATION

### Evolution in Chisocheton.

Can seed anatomy be used to trace phylogeny in this genus? It is clear, that of the three seed types illustrated in fig.8, the unitegmic (pachychalazal) sarcotestal species (type C) must be the most derived (see 'unitegmic seed-coats', Chapter 3). But what are they most immediately derived from - the chalazal-aril (type A) or the bitegmic sarcotestal (type B) condition? The chalazal-aril condition seems the more likely candidate at the moment, because C. sarawakanus, as

described earlier, makes a convincing link between A & C. By most criteria it would be placed in the chalazal-aril group, but it is 80% or so pachychalazal rather than the more usual 25-50% of the rest of the group. In addition, its cotyledon sclereids are much closer to those of C. granatum and C. sarasinorum (unitegmic sarcotestal) than for example C. lasiocarpus. If type C is derived from type A, as seems possible given existing data, how is the bitegmic sarcotestal type B related? If there are no clear links with type C, perhaps it is derived or primitive with respect to type A. This is certainly suggested by the seed organization of C. cumingianus which is directly intermediate between the two groups of species in terms of fleshy appendage type. But this gives no guide as to the 'direction' of evolution. A further pointer is provided if the cotyledon sclereids are considered. These were found in no other genus - so most likely they are derived in Chisocheton. If so, then perhaps their degree of development can be taken as a rough guide of evolutionary 'advancement' in the genus. Certainly the most numerous number of layers (9-12) occur in the 'advanced' pachychalazal species, followed by C. sarawakanus with 6-7 sclereid layers. C. lasiocarpus and C. cumingianus (chalazal -arils) have 2-4(-5) sclereid layers, but the bitegmic sarcotestal species have no sclereids except C. pentandrus (Blanco) Merr., which has, in addition, very thin testal mesophyll and can hardly be considered fleshy: perhaps it is another link between type B and type A. These facts seem to suggest that the bitegmic sarcotestal type is ancestral to the chalazal arillate type. A final clue is provided by two collections of different chalazal-arillate species: Mabberley 1718 (C. macranthus) and Mabberley 1773 (C. schoddei). Occasionally seeds of both show an extension of the fleshy chalazal 'aril' towards the micropyle (this was noted by Mabberley, 1979):

illustrated in Plate 76 D & E. Anatomical investigation shows that this is not an extension of the chalaza to the micropyle as might seem most likely, since the testa and tegmen are perfectly distinct (see plate 75A). What has occurred is that the testa along this strip has become sarcotestal, exactly in the same manner of the bitegmic sarcotestal species. Perhaps this represents a step forward in evolutionary terms, type A evolving again towards type B. But it seems unlikely that this would occur as regularly as our sample would seem to suggest. It is more reasonable to argue that these monstrosities represent 'throw-backs' to a more primitive state. In short, the evidence presented here clearly suggests an evolutionary sequence of B>A>C. This is not incompatible with other evidence. C. ceramicus (type B: here considered the most primitive) has several characters in common with other genera in the tribe which are not seen in the rest of the genus (lack of sclereids, presence of testal I.E. crystals and sub-cuboidal testal O.E.): surely indicative of a closer proximity to the ancestral state. It would be useful to obtain and investigate other species, in order to test the hypotheses presented here.

Seed evolution in Dysoxylum and the bitegmic genera.

The phylogenetic sequence of the 9 seed types described for Dysoxylum is not as clear cut as it seems to be in Chisocheton. However it seems reasonable to say that types 6-9 (see fig.9), being unitegmic are derived (see e.g. Sporne, 1974) from one or several of types 1-5 (bitegmic), but it is far from certain which is derived from which. It seems likely that type 6 is derived from type 5 or a species of type 1 with an already enlarged chalaza e.g. D. macranthum, by further extension of the chalaza, just as in Chisocheton the pachychalazal

sarcotestal type C (see fig.8) seems to have evolved from the chalazal-arillate type A via a species such as C. sarawakanus also by the chalaza increasing further at the expense of the integuments. The pachychalazal but pseudo-arillate 'arborescens' type (8) seems most likely to be derived from the 'angustifolium' type (6) in parallel with the postulated developments in African Trichilia (see fig.5). Perhaps type 9 is a further development from the 'arborescens' type in a trend towards loss of seed fleshiness.

The hypothetical type 7, sarcotestal and unitegmic but by loss of the tegmen, could be derived from bitegmic types 4 or 5, by that transition. Unless a large chalaza is primitive, type 5 ('macrostachyum') is most likely to be derived from type 4 ('pettigrewianum' type) by increase in the chalaza unless it is derived from a species of type 1 ('macranthum') with an already large chalaza, simply by the testa becoming sarcotestal: this would represent a reversal of the state of affairs in Chisocheton where the chalaza-aril 'type A' has been shown to be probably derived from the sarcotestal bitegmic 'type B'.

Of the remaining groups of species, that is seed organization types 1-4, which is the most primitive and is a small chalaza really primitive? Perhaps it is best to answer this by searching for the lowest common denominator in the other genera of the tribe in order to find the basic, primitive seed type. Clearly the unitegmic genera (Guarea, Turraeanthus and Heckeldora) can be ruled out: they are clearly advanced ( see e.g. Sporne, 1974:154) which leaves Cabralea, Ruagea, Pseudocarapa and Synoum. It has already been noted how close the organization type of three (all but Ruagea) of these four diverse genera, (all with a small chalaza of c. 10% of the seed-coat or less) is to the 'spectabile'type (2) of Dysoxylum, i.e. they are funicular-raphe-arillate. It can be

argued that although these monotypic (perhaps relic) genera have differentiated morphologically and (in Synoum in other aspects of seed structure), the basic organization pattern has remained close to the archaic condition. If this is so , and the 'spectabile' type is the most primitive of the Dysoxylum seed organization types, it becomes relatively straightforward to draw out the origin of the bitegmic types from it. It is possible that D. pachyphyllum has been reached from the 'spectabile' type by transference (Corner, 1958) of a large part of the arillar functions to the placenta. Perhaps this is a first step towards an indehiscent berry-like fruit? The raphe-chalazal aril may also be viewed as derived by partial transference of function of the predominantly raphe-aril to the chalaza. Within the 'macranthum' group of species considered here, the closest to the 'spectabile' type is seen in D. gaudichaudianum. Here the fleshy tissue at the raphe extends further across the ventral seed-coat (verging towards the sarcotestal) than it does in the 'spectabile' type, but it is still narrow compared with that seen in e.g. D.cauliflorum. This trend from a raphe-aril towards what could be described as a raphe sarcotesta was also postulated in E.African Trichilia ( see fig.5). In addition, the chalaza in D. gaudichaudianum is at the small end (c.10% of the total seed-coat area: considered primitive here) of the range (upper end 50%) seen in the 'macranthum' type and it has a comparatively well developed tegmen: two layers of thick-walled fibres (rare in Dysoxylum, but found in other bitegmic genera of the tribe and considered primitive here). The 'pettigrewianum' type could be derived directly from the 'spectabile' type in a step where fleshiness is transferred from the funicle-raphe to the chalaza and testa, but it could also be derived, using a smaller step (and thus more likely) from a species such as D. gaudichaudianum of

the 'macranthum' type where the chalaza and ventral part of the testa are already fleshy. Other species of the 'macranthum' type such as D. cauliflorum are less appropriate candidates because they have a larger chalaza than that seen in the 'pettigrewianum' type and a reduction in chalazal size (against the general trend of small to large) is seen here as unlikely. The mechanism by which the testa in the 'pettigrewianum' type becomes fleshy is uncertain. Two possible routes can be envisaged. Firstly, the locally sarcotestal, ventral part of the seed-coat (of raphe derivation) seen in D.gaudichaudianum (and Ruagea glabra) might expand to cover the entire seed-coat. Alternatively the 'chalazal-aril'(which might also be called a partial (chalazal) sarcotesta), might lose its restriction to the chalaza and cover the rest of the seed-coat.

It is curious how different the phylogeny proposed here (although tentative) commencing with the funicular-raphe -arillate state is from that posited in Chisocheton where the argument used strongly favours a sarcotestal origin. Despite the differences, in both Dysoxylum and Chisocheton, the 'sarcotestal' and 'arillate' patterns seem to alternate with each other. In Chisocheton the sequence appears to be sarcotestal>arillate>sarcotestal, whilst in Dysoxylum it may be (in short) arillate>sarcotestal>pseudo-arillate. This explanation for this alternation might lie in the functional significance of the two different states (sarcotestal and arillate) and is considered further under 'Ecological Aspects'.

The position of Synoum.

Whilst Ruagea, Pseudocarapa and Cabralea seem to share close evolutionary origins with Dysoxylum, Synoum does not. Although Synoum

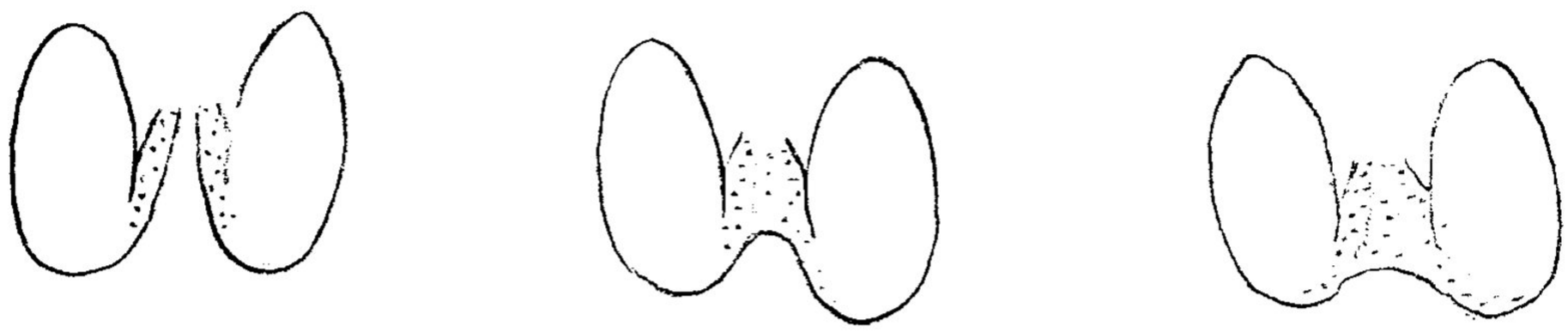
shares with those genera the primitive type of seed organization, its testal I.E. is very different and suggests a link with Chisocheton. However, its very strange tegmen, seen in no other genus in the tribe and the even stranger seed orientation and aril unity seem to mark it out as the genus of most remote evolutionary origin within the tribe. The derivation of the 'Siamese-twinned ' aril from the usual condition might be as in fig.10

Guarea, Heckeldora and Turraeanthus: the link with Chisocheton

The remaining genera of the tribe, Guarea, Heckeldora and Turraeanthus share with Chisocheton a strong tendency towards a unitegmic seed-coat (all Chisocheton seeds, even those considered most primitive, are at least partly pachychalazal, the chalaza forming at least 25% of the seed-coat). In addition, these genera share a tendency towards orthotropy (seen in all except Turraeanthus). Perhaps Guarea represents the link with a primitive anatropous condition: see fig.11

The two principal genera are further linked by the unusual morphological trait of a dormant terminal leaf bud (not seen elsewhere in the family). Seed characters, few though they are for paucity of bitegmic seed-coats, tend to favour recognizing these four genera as a group apart from Dysoxylum and Ruagea, Cabralea and Pseudocarapa. Certainly, where it is possible to draw a meaningful comparison (i.e. with data from bitegmic seed-coats) between the two main genera (Chisocheton and Dysoxylum) of each group, it is immediately apparent that they are as different as they can be whilst remaining in the same family. It would be useful to obtain and investigate the seed-coat anatomy of a bitegmic-seeded species of Guarea (if any exist they are

EVOLUTION ?

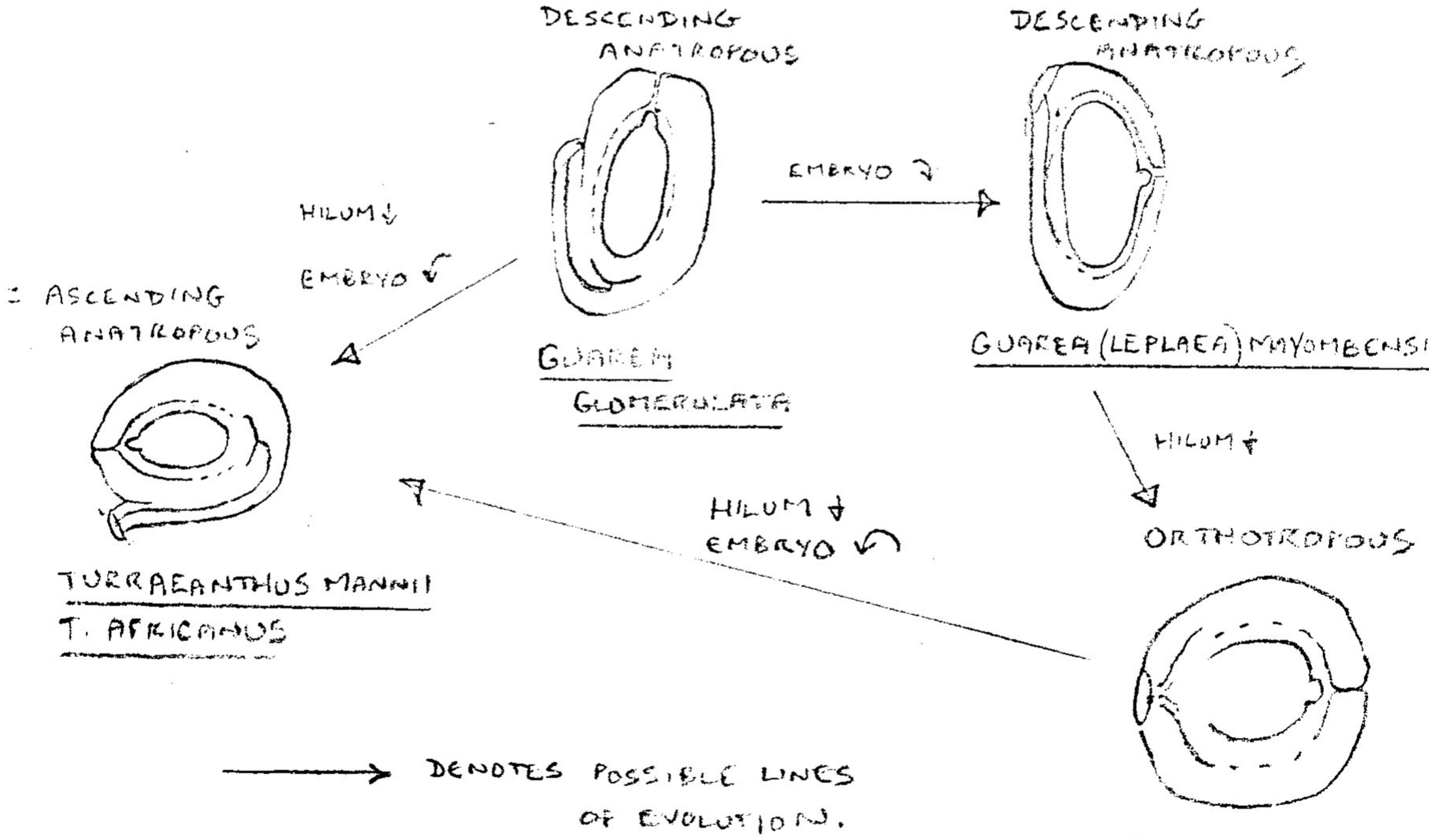


FUNICLES SEPARATE, FLESHY.

FUNICLES UNITE

FUNICLES WEBBED FLESHY.

FIG. 10 PHYLOGENETIC SPECULATION: DERIVATION OF UNITED RAPHE-ARIL IN SYNOUM




→ DENOTES POSSIBLE LINES OF EVOLUTION.

FIG. 11 SEED ORIENTATION IN GUAREA CHISOCHLTOIS & HECKELDORA.

probably American) to see how closely it matches that of Chisocheton. If the affinities are as postulated (admittedly on thin evidence ) above, then that of the bitegmic Guarea should be more similar to that of Chisocheton than Dysoxylum.

## ECOLOGICAL ASPECTS

In contrast to the Trichilieae where fully sarcotestal seeds occur only very rarely, they are almost as common as arillate seeds in both Chisocheton and Dysoxylum (in both genera sarcotestal seeds are of at least two different origins ) and occur in all the investigated species of Guarea, Turraeanthus and the monotypic Heckeldora. Thus it is perhaps more useful to contrast the Aglaia fruit syndromes of Pannell & White (1985) and Pannell & Koziol (1987) here than to do so in the Trichilieae. In brief, the first, bird dispersal, syndrome has dehiscent capsules, brick-red or pink outside and contains seeds with orange-red, lipid-rich arils. The second, primate-dispersed syndrome has indehiscent fruits with an orange, pinkish-orange or brown pericarp and the seed is surrounded by a gelatinous, translucent, sugar-rich 'aril' that firmly adheres to the seed-coat. The fruit is opened by the animal, the seeds extracted and because of the nature of the seed-coat, swallowed whole. The first state is regarded by her as primitive, the second derived.

Seeds corresponding with the second syndrome in that they are indehiscent with an orange or brown pericarp and with the seed covered by an 'aril' that firmly adheres to the seed-coat (i.e. sarcotestal for the most part) are found and have been anatomically investigated in Chisocheton (e.g. C. medusae, indehiscent fide Mabberley, 1979), Guarea (e.g. G. mayombensis) , the monotypic Heckeldora and Turraeanthus (T. manniii). All these species have unitegmic seed-coats that

appear to be pachychalazal, and all have a vascularized sarcotesta. Since the unitegmic condition appears advanced (see e.g. Sporne, 1974:154), this appears to be in accordance with Pannell's views of the second syndrome being derived from the first. Do primates actually disperse these fruits though? Nothing is known of the dispersal agents of any of those species listed above except for G. mayombensis in Kigezi, Uganda, where the local people are adamant that baboons eat the seeds which are covered by a slightly sweet, orange pulp. Supposing that the four species above are all eaten and dispersed by primates, it seems worthwhile examining the functional significance of the seed structure: do these seeds show adaptations to primate dispersal? The sarcotesta, in being less easily detached from the seed-coat than a loosely attached flap of tissue such as an aril, can be construed as an adaptation to primate dispersal (see 'Ecological Notes' under Trichilieae). Similarly, a pachychalazal seed-coat might be more resistant to the hazards of primate gnawing and also allow a larger seed size to be achieved, so favouring seed access to primates (versus birds): see 'Ecological Notes' under Trichilieae. Further information on whether these fruits are really dispersed by primates can be obtained from the painstaking review of the relevant literature (sparse though it is ) made by Pannell and White (1985) from which these references are largely drawn. Crome (1975) records the seeds of an Australian Dysoxylum (species unknown) being taken by Woompoo and Purple Crowned Pigeons; Leighton and Leighton (1983) record the seeds of three species of Chisocheton and 12 of Dysoxylum being eaten by four species of Hornbill in Indonesian Borneo; Howe and De Steven (1979) record seeds of Guarea glabra Vahl being eaten in Panama by 12 resident and seven migrant species of bird, whilst Pennington and Styles (1981:267) note the fruits

of Guarea guidonia in South America as being 'attractive to birds', and Bawa and Bullock (1983) note the seeds of Guarea rhopalocarpa Radlk. as being eaten by 'birds'.

Thus the literature does not yet support primate dispersal in the Guareeae at all- not a single reference has been traced that refers to this. Naturally the works cited above may all refer to arillate-seeded, dehiscent fruits of the first, bird-dispersal syndrome, but at least those three referring to Guarea must be taken to refer to sarcotestal seeds (a generic character) so perhaps sarcotestal and pachychalazal seeds are not so closely tied to primate dispersal after all. Whilst seeds of this construction seem advanced, their functional significance might equally as well be explained by selection for more rapid seed growth (thus reducing the period of vulnerability of the developing seed) and the larger seed size that pachychalazy may facilitate may be of more significance in enhancing establishment success of the seedling than in favouring primates as dispersal agents.

# CHAPTER NINE

# SANDORICEAE

## INTRODUCTION

This tribe was erected by Pennington and Styles (1975) to hold Sandoricum, a small genus of five species (Mabberley, 1985) on the basis that, although placed after Dysoxylum by Harms (1940) on account of its free tubular disk, it has little in common with this genus or any other, being at once identified by its trifoliolate leaves, the ribbed staminal tube, characteristic style-head with divided stigma, the indehiscent drupaceous fruit and the secondary xylem which is unlike that of Dysoxylum or any other genus in the Guareeae. The very heterogeneous ray tissue, non-septate fibres and sparse vasicentric or aliform parenchyma distinguish the genus immediately.

All five species are restricted to western Malesia, but one, S. koetjape (Burm. f.) Merr. which occurs in the wild state eastwards to Papua New Guinea and is widely cultivated as a fruit tree (Mabberley, 1985).

The first and most comprehensive investigation of the seed anatomy of this genus was that of Sandoricum koetjape by Juliano (1934) who traces the development of the seed-coats from the ovule. This is most useful, since, because the usual Meliaceae integument 'markers' are absent, seed-coat homologies would otherwise be uncertain. His description and figure agree broadly with that presented here although he does not mention several features of the mature seed-coat as Corner does (1976,1:191). Nair (1958) also appears to have investigated this species

('S. indicum Cav.') but his study was largely of floral morphology and embryology and he does not give any information on the anatomy of the mature seed-coat.

## RESULTS

Sandoricum koetjape (Burm.f.)Merr.

This description based on Pennington 7819.

Collector's notes: 'Fruit in axils of fallen leaves, fleshy edible; pericarp yellow, thick, containing sticky white latex. Seeds surrounded by white fleshy mass, (edible). Indehiscent. After falling, the 3-4 seeds germinate in the rotting fruit'.

Juliano (1934): 'Usually a single seed is formed in each locule, but two seeds are not uncommonly encountered in it. The seed or seeds become surrounded by a thin stony layer or shell derived from the inner epidermis of the pericarp and this bears the translucent or pale white, edible, acidic or sweetish inner half of the pericarp. The seed bears two distinct coats: namely the testa and the tegmen. The testa is usually tough, thick and brownish in colour while the tegmen is whitish and papery to the touch. The embryo consists of two plano-convex cotyledons between which are the small stubby radicle and the plumule.

The extensive endosperm is however, absorbed completely by the developing embryo and is totally absent in the mature seed.' He goes on to describe developments of these components from the ovule.

Nair (1958): 'Of the two integuments the inner arises first and forms the micropyle. The outer and inner integuments are two and three layered respectively. The vascular supply of the ovule terminates at the chalaza'.

PLATE 122

SANDORICUM KOETJAPE

A-B FRUITS: INDEHISCENT AND FLESHY.

C. PYRENE: COVERED IN TIGHTLY ATTACHED FLESHY MESOCARP.

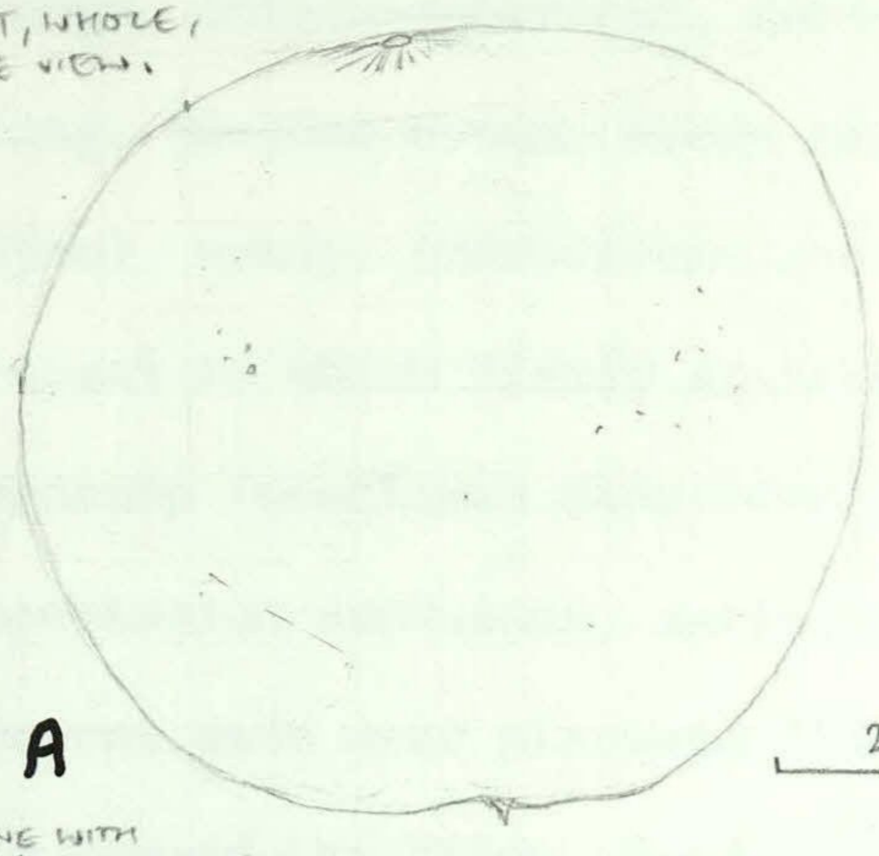
D. PYRENE.

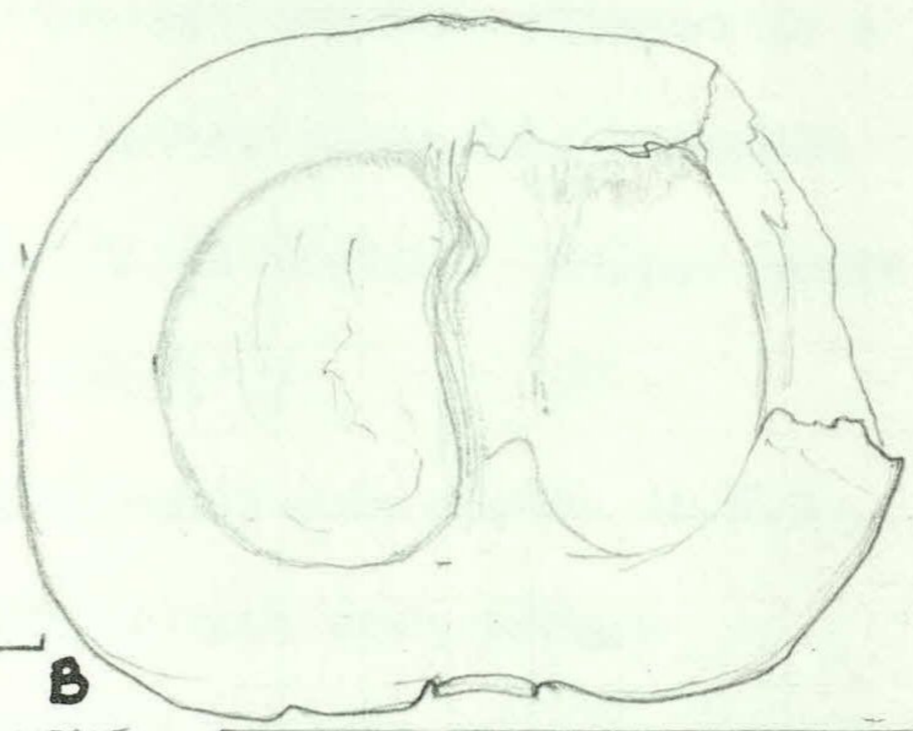
E-J SEED: WHOLE AND IN SECTION. NOTE LACK OF FLESHINESS AND THAT 50% OF THE SEED IS PACHYCHALAZAL (J).

K. SEED-COAT ANATOMY (HOMOLOGIES ESTABLISHED BY JULIANO, 1934). CRUSHED AND REDUCED TEGMEN BUT COMPLICATED TESTA: I.E. WITHOUT CRYSTALS AND LOWER MESOPHYLL TANNINIFEROUS AS SOME DYSOXYLUM. NOTE UNUSUAL, SPONGY AND PITTED UPPER AERENCHYMA.

# SANDORICUM KOETJAPE (Burm.f.) Merrill.



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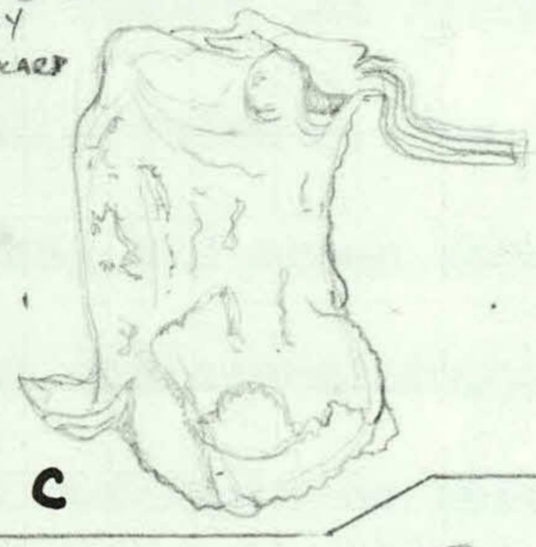
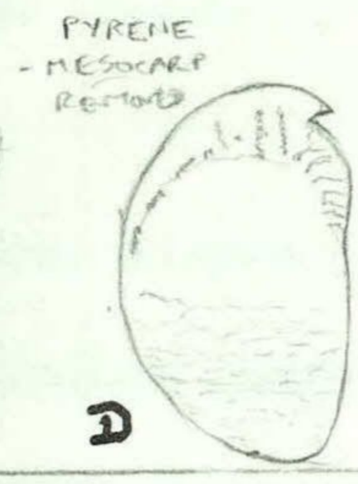
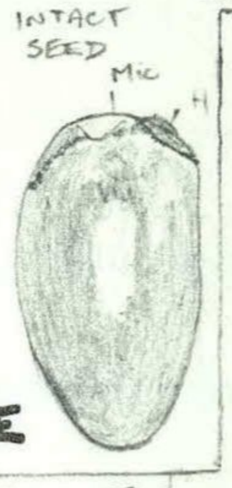
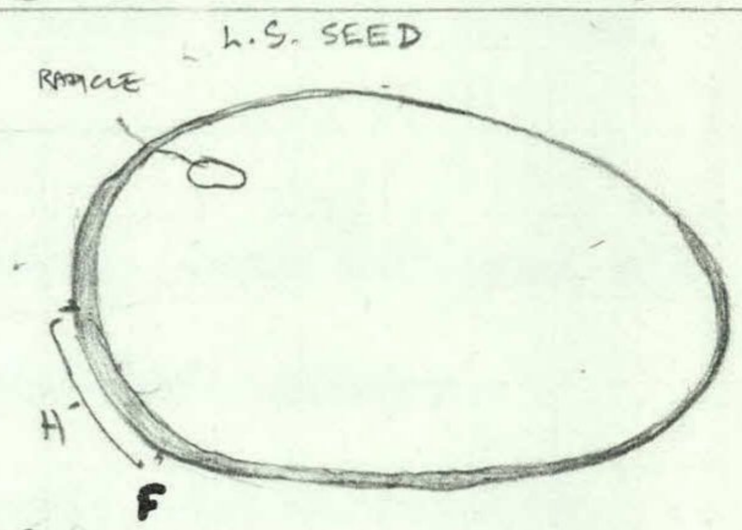


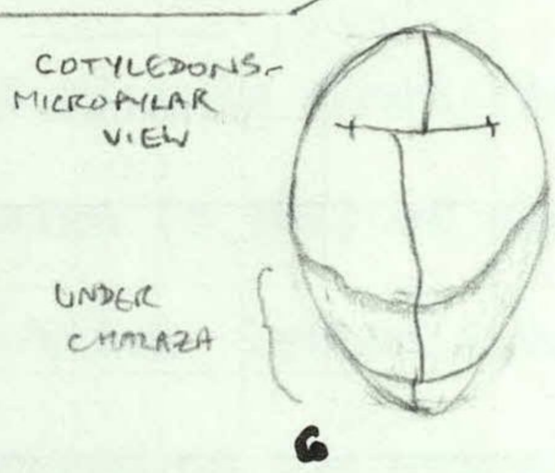



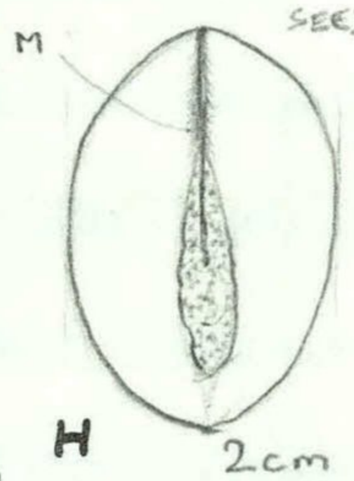




END VIEW OF SEED

T.S PYRENE

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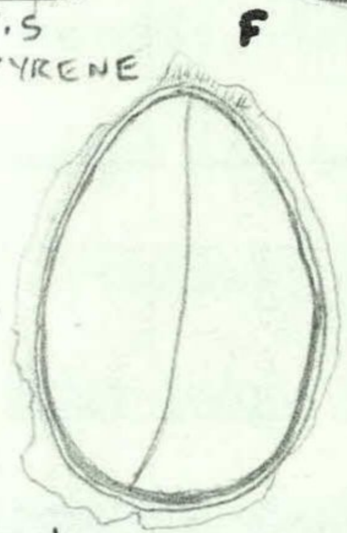
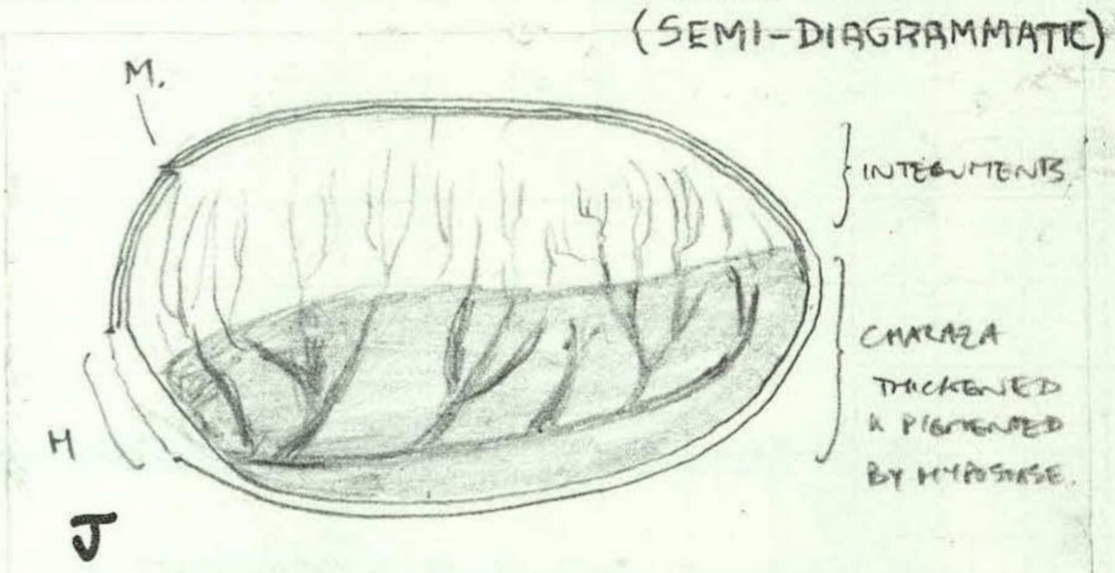
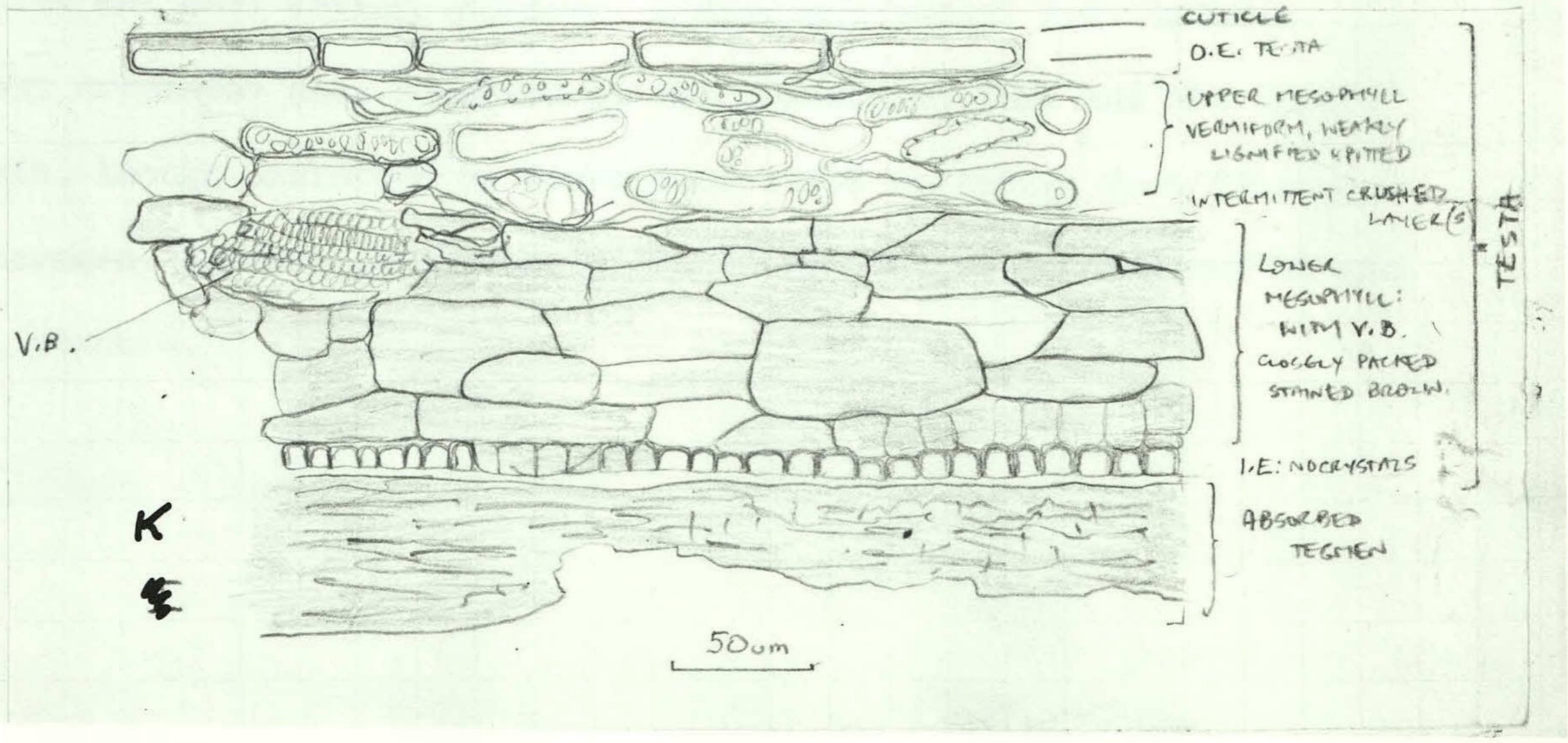



L.S. SEEDCOAT -TISSUE PLAN (SEMI-DIAGRAMMATIC)




L.S. DORSAL SEEDCOAT



GROSS MORPHOLOGY

Fruits large, oblate-spherical, sub-glabrous, indehiscent, baccate, 42-65mm long, 50-70mm broad. Seeds one to two per locule, encased in a thin (0.25mm), woody, indehiscent endocarp (latter sometimes mistaken for seed-coat) to which firmly attached the thick (c.1cm), pulpy, white edible mesocarp (sometimes described as an 'aril'.)

Seed placentation pendulous, axile; shape roughly ellipsoid. In T.S., ovate, ventral side near placenta flattened, dorsal side ridged especially toward the hilum. Seeds 21-24mm long, radial breadth c.10mm, tangential breadth c.15mm.

Testa glossy mid-brown above, almost black in section, thin (<0.1mm) but thicker at chalaza-micropyle(c.0.25mm); tegmen very thin, papery. Endosperm and nucellus absent. Cotyledons collateral, hemi-ellipsoid. Radicle and plumule short (together about 3-4x2mm), not exserted.

Chalaza large (c.50%) of seed-coat), elliptic, ventral, coinciding with sub-apical hilum; latter narrowly elliptic (c.10mm long, 2.5mm wide), slightly raised on the apical-dorsal ridge. Micropyle inconspicuous, sub-apical, 5-10mm from hilum.

ANATOMY

In the absence of the Meliaceae characteristic crystalline testal I.E. and strongly developed exotegmic fibres, the boundary between tegmen and testa is not well marked. However, a distinct testal I.E. (albeit without crystals) does commence at the transition zone and the layers beneath, though distorted by comparison, look as though once fibrous. Furthermore, Juliano (1934) who followed the entire development of the seed, concurs.

TESTA

Cuticle fairly even, colourless, 1-2(-5)um thick.

O.E. a single layer of prostrate, distinctly narrowly quadrangular cells (T.S. and L.S.), predominantly 35-40um in T.S. and 65-75um wide in L.S. In paradermal section, range from isodiametric (40um x 40um) to highly extended polygonal (25um x 140um), but largely extended polygonal, orientated along seed length. Height 15-25um. Walls grey-amber, slightly darker than cell contents, o.p.w. 3-5um, anticlinals and i.p.w. 2um.

Mesophyll divisible into an upper part (4-6 layers, 55-65um thick) of weakly lignified, tangentially orientated vermiform aerenchyma with colourless contents and faint scalariform pitting; a lower part (c.8 layers, 80-90um thick) of prostrate quadrangular cells (T.S. and L.S.; isodiametric in paradermal view) closely packed and with walls and contents uniformly medium-brown (probably tannin). In between the two parts, remains of cell layers crushed.

Upper part: cells 42-63um long (tangentially), 10-18um broad (radially); walls 2-2.5um thick, straw coloured.

Lower part: cells 84-120um wide, 28-60um high.

I.E. of sub-cuboidal cells, 1-2 layers thick. Cells c.24um high and 31-34um wide. Walls brown-colourless. Contents completely colourless, layer then strongly contrasts with mesophyll, or mid-brown when easily confused with layers above.

TEGMEN

Highly crushed and partly absorbed: individual cells indistinguishable. Layer about 50um thick.

ENDOSPERM

None detected.

DISCUSSION

On seed anatomical evidence, this species seems to be most closely related to the Guareeae of those tribes investigated here, in particular the genus Dysoxylum, although the relationship is probably rather distant.

A vascularized testa and a very weakly developed tegmen is characteristic of Dysoxylum and in at least one of the sarcotestal species of that genus ( D. pettigrewianum), tannin-filled cells occur in the lower testal mesophyll. Lack of testal I.E. crystals occurs in several bitegmic Dysoxylum species (e.g. D. macrostachyum) though it is not characteristic of the genus. The highly pachychalazal seed-coat (c. 50% of the surface area (c. 50% of the surface area) is a common tendency in the Guareeae though does not occur in the most 'primitive' Dysoxylum species as it does in Guarea, Chisocheton, Turraeanthus and Heckeldora. The aerenchymatous, 'armed' spongy cells of the upper testa, noted by Corner (1976, 1:191) are very unusual in being weakly pitted and lignified. The latter two traits also occur in the testal mesophyll of Trichilia capitata, but the two taxa are otherwise very different in seed structure and gross morphology so this character has probably arisen independently in each. Non-fleshy seeds in indehiscent endocarpic fruits such as that of Sandoricum are particularly common in the Trichilieae, but since the testal anatomy of their seeds, especially of the bitegmic species, is very different from that of Sandoricum (no

tannin or vascular bundles in the testal mesophyll, testal I.E. with crystals, exotegmic fibres present) this is probably a result of convergent evolution. The correlation of indehiscent fruits with unitegmic seeds (as is the case with Sandoricum) is discussed in Trichilieae above.

ECOLOGICAL ASPECTS

Although widely cultivated on account of the edible flesh of its mesocarp, no account of animals eating the fruit has been discovered in the course of this study. This fruit would fall into Pannell and White's (1985,1988) primate syndrome, but the protective function of the seed-coat seems to have been transferred (see Corner, 1958) to the leathery-woody endocarp and the attractive function of the sarcotesta to the mesocarp.

## SWIETENIOIDEAE

This, the other major sub-family of the Meliaceae, contains 13 genera placed in three tribes, the Cedreleae, the Swietenieae and the Xylocarpeae. It is completely distinct from the Melioideae morphologically and anatomically (see Pennington and Styles, 1975). For example, its species have septicidally dehiscent fruits, numerous ovules per loculus, imparipinnate leaves and buds with scales. Their seeds differ from those of the Melioideae in being dry and winged or corky (versus fleshy and unwinged), but Corner (1976,1:185-192), who has investigated the anatomy of a representative of each tribe, shows that

the same basic bitegmic Meliaceae seed anatomy, with a crystalline testal I.E. and lignified longitudinal exotegmic fibres obtains in the alate, perichalazal Swietenia macrophylla King (Swietenieae). However the testal mesophyll of that species shows modifications for lightness compatible with a wind-dispersed seed and is thinly lignified and pitted as is the testal O.E. which has frequent stomata. Whilst all of these characters occur in the Melioideae (except the wingedness), they are always rare and largely in different tribes, perichalazy occurring in Aglaieae, pitted testal mesophyll in Trichilieae and Sandoriceae and stomata in Trichilieae. I have investigated this genus briefly, and found the structure as Corner states it to be. Khaya and Neobeguea which I have also looked at cursorily are similar in anatomy, the largest amount of taxonomically useful variation occurring in the shape of the testal mesophyll cells. Corner also investigated Carapa guianensis Aubl. ( as 'Carapa guyanensis' from Ceylon and Singapore) of the Xylocarpeae, a tribe unusual in the sub-family in that the seeds are not winged, but corky and apparently distributed by water. He reports that it is almost completely pachychalazal, but with a vestigial bitegmic area around the micropyle. The largest part of the seed-coat consists of a mesophyll of aerenchymatous, sub-stellate cells, the inner layers vascularized, the O.E. with a highly convex o.p.w., all becoming lignified and slightly pitted. The bitegmic part consists of a multi-layered (40-50 cells thick) testa of unspecialized cells and a multi-layered tegmen of c. 30 cell layers, also unspecialized apart from the fibrous exotegmen (one layer). I investigated, but did not describe material of Xylocarpus granatum Koen. from Kenya and found that it largely matched Corner's description of Carapa guianensis, apart from the lack of the vestigial testa and tegmen and in having tanniniferous cells. In the Cedreleae

(distinct from all other tribes in the free stamens, lacking appendages), Corner investigated a species of Toona, possibly T.ciliata M. Roemer (as 'Cedrela toona Roxb.', the material from Peradeniya, Ceylon) and describes its anatomy as being unlike that of Swietenia, the cells of both the testa (four to five cells thick) and tegmen (four to five cells thick) being unspecialized and unlignified, lacking the usual Meliaceous features of a crystalline I.E. and a fibrous exotegmen and being very poor in taxonomic characters. Several members of the tribe were investigated, in both genera (i.e. Toona and Cedrela) and detailed descriptions and plates prepared of two. The anatomy is broadly as Corner describes, rather featureless and apparently unrelated to either of the other two tribes, but the distribution of the wings in relation to the vascular bundles , especially in the species of Toona, is much more interesting and offers considerable scope for phylogenetic interpretation. It is hoped to publish these data as a separate paper in the near future. Lack of time precludes inclusion here.

It is clear from the foregoing that each of the three tribes appears to have distinct seed anatomy- but it remains to be seen whether these remain as distinct when material of other genera is examined.

## QUIVISIANTHOIDEAE

With a single genus, restricted to Madagascar, this sub-family has loculicidal capsules, naked buds and two-ovulate locules as in the Melioideae, but has a dry fruit and a dry, winged seed as in the Swietenioideae (Pennington and Styles, 1975).No anatomical investigation has been published of the seeds, but a description and illustrations have been prepared of Q. papinae Baill., which has bitegmic seeds like

those of the winged Swietenioideae, but differing in organization. Lack of time precludes the inclusion of the data here.

## CAPURONIANTHOIDEAE

With a single genus, restricted to Madagascar, this sub-family has dry fruits with septifragal dehiscence and corky seeds as in the Swietenioideae but with only two seeds per loculus, naked buds and floral structure as in the Melioideae. Its wood anatomy is also intermediate between these two sub-families (Pennington and Styles, 1975).

No account of seed anatomy has been published. I have investigated, described and illustrated the seed anatomy of C. mahafalensis Leroy, but hope to publish the information separately: as with Quivisianthe, time does not permit its inclusion here and in any case, the taxonomic significance of its anatomical characters will only be properly appreciated when more is known of the seed anatomy of the Swietenioideae. The seed-coat is about 60% pachychalazal, the remainder bitegmic, matching most closely that described by Corner for the bitegmic part of Carapa, but differing in that here the cells are more differentiated, and a crystalline testal I.E. is present.

## NEOMANGENOTIOIDEAE

With a single genus, restricted to Madagascar, this sub-family was described recently by Leroy (1981). It is very unusual in its fruit (a septicidal drupe) and flowers (perigynous) and is known from only a single, fragmentary collection. Seed material was not available for

study. It is hoped to collect further material of this plant in November of this year.

# CHAPTER TEN

## CONCLUSION

Seed characters in this family do seem to have considerable taxonomic use (insofar as can be judged from the limited amount of material investigated here), as Corner (1976,1:186-188) foresaw. They seem to to be especially useful in questions of generic delimitation as has been seen here for example in Naregamia, Pseudobersama, Heynea and Humbertioturraea, bringing a wealth of additional characters to bear on each case. Seed characters also show great potential at the infra-generic level, as has been shown in Chisocheton, Dysoxylum, Trichilia and Turraea, seeming relatively constant at the species level, but showing great variation between species. It is to be hoped that in generic monographs in the family where 'the variety in fruits and seeds far outweighs in complexity the floral details which are the basis of classification' (Corner, 1976,1:185) and in those cases where an over-reliance on floral characters seems to have been misleading (see Pennington's comments in Pennington and Styles, 1975 on earlier attempts to fragment Turraea ) that subsequent authors of monographs will avail themselves of the opportunities presented by seed anatomy to form improved classifications for such genera. At the tribal level, seed-characters seem to be of less use in delimitation, than do morphological and wood anatomical characters for example, in distinguishing the Trichilieae and Guareeae, but, nevertheless, as in the Sandoriceae, they do seem to give an indication of affinities with other tribes, and in some cases, of generic groupings within tribes (e.g. Guareeae ).

The single most taxonomically useful layer of the seed-coat in the majority of Meliaceous genera is the exotegmen. Not only are the dimensions (length, breadth, height and end-walls) of these longitudinally orientated fibres a useful source of characters, but also wall characters : thickness, nature of pitting, colour and occasionally lumen colour. Number of cell layers can also be important. Lower layers of the exotegmen can be of markedly different shape (e.g. Turraea heterophylla and Trichilia capitata ) or orientation (e.g. Munronia pinnata & Walsura pinnata ) from the uppermost layer.

The epidermis of the testa is probably the next single most useful layer, varying from columnar to rectangular in T.S./L.S., this character sometimes being important at the generic level (as in Dysoxylum versus Chisocheton). In paradermal view, most species and most genera are isodiametric and polygonal, but some genera (e.g. Humbertioturraea) and species groups (e.g. in Trichilia) are partly defined by elongated testa cells. The outer periclinal wall curvature is an important character in some taxa in the Turraeeae, but is usually secondary in importance to the extent and nature of the o.p.w. (less frequently the i.p.w.) thickening- an important species character in many genera, e.g. Turraea and Dysoxylum. More infra-specific variation is seen in all of these characters than those of the exotegmen: perhaps being at the surface rather than removed from it, it is to be expected that the epidermis will be less conservative since it is more likely to be subject to environmental influence. Multiple epidermises or hypodermises characterize some species but are only important in generic delimitation in the Turraeeae.

The testal mesophyll is a relatively poor source of characters, although it may show great variation in the number of cell layers and

cell dimensions. This is because these cells are often thin-walled and consequently crushed to a greater or lesser extent (cells being deformed in shape and whole cell layers disappearing), apparently depending on the precise state of maturity or nature of preservation of the material: older and dried seeds having fewest (or no) cell layers or intact cells. Consequently, seeds from the same species or even the same plant may show great variation in these characters as was seen in Turraea heterophylla. Although paucity of characters is generally the case in the testal mesophyll, it is by no means always so. In the Trichilieae, the 'East African group' is distinguished by rigid, uncrushed thick-walled and sometimes pitted testal mesophyll, that of Nymania is tanniniferous, uncrushed, with huge lacunae and contains the only seed anatomical characters that are absolutely diagnostic for the genus. Apart from the labile nature of the testal mesophyll, its cells are relatively plastic in shape (again, see Turraea heterophylla ) sometimes varying considerably in shape, size and wall thickness within a few cell diameters. This is particularly marked in those species with fleshy appendages, since it is usually the testal mesophyll which proliferates in these structures to form their bulk, the cells changing by becoming larger and thinner walled. The distribution of such tissue, an important taxonomic character, is considered later.

The tegmic mesophyll or endotegmen has far fewer characters to offer than the testal mesophyll, is even more prone to crushing during development, and so is one of the parts of the seed-coat of least taxonomic importance. In some large genera (e.g. Dysoxylum) it is completely crushed and usually entirely absent. In most, it is absent from the majority of species, but present in a few (see e.g Turraea). The only case where the endotegmen offers characters useful at generic

delimitation and at the species level, is Chisocheton, which is distinct in its tanniniferous, uncrushed endotegmen. The number of endotegmen cell layers seems to vary from one species to another.

The inner epidermis of the testa, each cell normally characterized by containing a single prismatic crystal of calcium oxalate, is very important in establishing the homologies of the seed-coat strata, but less so as a source of taxonomic characters. Some genera (e.g. Calodecaryia) are characterized by the absence of crystals, others in addition have an I.E. closely similar to their O.E. (Synoum and Chisocheton) or undifferentiated (e.g. Heynea). But this layer is usually useful at the species level on the basis of presence or absence of crystals. Size of crystal may be important at the species level, but this hypothesis was not tested rigorously. Presence of tannin (e.g. in Dysoxylum) can be useful at the species level as can unusual wall thickenings. The latter may be important at the generic level in Azadirachta.

A tegmic I.E. is even more rarely uncrushed in mature seeds than the endotegmen and although, when present, the walls seem characteristically thickened, they are of little use for comparative purposes.

Vascularization of the seed can be very important at the generic level, whether of integuments (Chisocheton versus Dysoxylum) or pre-raphe (Walsura and Heynea versus Trichilia).

Unitegmic seed-coats are, in contrast to bitegmic ones, of greatly reduced taxonomic value, whether they arise by pachychalazy or by loss of the tegmen. The O.E. and upper parenchymic part found in most unitegmic seed-coats seem comparable in taxonomic value in Chisocheton for example, to the testal O.E and mesophyll respectively, but the lower part of a pachychalazal seed-coat is of far less value than the

exotegmen: where sclerotic cells occur, they are of irregular occurrence and seem much less characteristic (if at all) of species in their structure than do cells of the exotegmen.

An interesting result of this study is the discovery that adjoining tissues of the chalazal and bitegmic parts of the same seed-coat can be totally different in character. This emphasizes the need to distinguish and identify chalazal and bitegmic parts of the seed-coat before making comparative studies. It is not enough simply to cut sections from the same place of a seed-coat in such a study to be sure of comparing like with like, since in doing this one might unknowingly compare the chalazal part of the seed-coat in one species with the bitegmic part of the seed-coat in another. Even if one cuts near the micropyle, the difficulty is not resolved. The only solution is to discover the chalazal:bitegmic boundary in the entire seed. This is often possible via the dissecting microscope in some genera (e.g. Turraea) but in others (e.g. Chisocheton and Dysoxylum ) sections must be taken before the boundary can be reliably ascertained.

Other, but non-seed-coat, seed structural characters found to be of taxonomic use in this study were, embryo sclereids- important at the species level in Chisocheton; seed orientation- useful in delimiting Synoum and Turraeanthus; radicle exsertion, embryo curvature, cotyledon shape and presence of endosperm- all the latter have been used by Pennington and Styles (1975) at the generic or tribal level.

The various sorts of fleshy seed appendages are generally very useful as taxonomic characters, once their anatomical basis, especially their relationship to the chalaza and raphe has been established. Some genera are characterized by one appendage type (e.g. Guarea: sarcotestal and

unitegmic, Turraea funicular-raphe-arillate, bitegmic) whereas others, for example Trichilia and Dysoxylum, show a large range. Here seed appendage/organization type seems very useful in discerning species groups, in the latter genus probably more so than any other seed-coat character since the exotegmen is reduced and poorly developed and the testal O.E. (compared with Turraea ) is relatively uniform. With respect to the nomenclature of fleshy seed types, none of the existing 'rigid' classifications (e.g. van der Pijl 1969; see literature review) seemed practicable in compartmentalizing the variation in structure shown here. Whilst seed types are relatively rigidly organized into different types in some genera (e.g. Chisocheton), in others (e.g. Dysoxylum or Trichilia) the distinctions are less marked. Even the distinction between 'sarcotestal' and 'arillate' proves not to be an unbridgeable one as Pennington and Styles (1975) suspected. It has seemed best here to define a classification for each genus on a 'type-species' basis (see e.g. figs. eight and nine) and to bear in mind that those of different genera (e.g. Dysoxylum and Chisocheton) may not be directly comparable. Where it is desired to refer to a particular seed organization type in general discussion, it seems best to use the word arillate or sarcotestal with a prefix to define the part of the seed from which it is derived, e.g. 'chalazal-arillate' or 'funicular-raphe-arillate'.

The investigation here of genera such as Chisocheton (12 of 51 species), Dysoxylum (19 of c.75 species) and Trichilia (9 of c. 86 species) has shown that seed characters can offer much material for phylogenetic speculation. The number of seed structural characters and the relative ease with which they can be polarized are both useful assets in this respect.

On the basis of this study, taking the most 'primitive' members of each tribe and looking for the lowest common denominators, it seems possible to conjecture that the ancestral Meliaceous seed was bitegmic, with a small chalaza (c. 10% of seed surface area) . It was comparatively (to temperate seeds for example) large, 8-16mm long (Turraea seeds are regarded here as reduced) with a funicular-raphe-aril. The radicle was exserted from the cotyledons and some endosperm persisted in the mature seed. The seed-coat consisted of a single layered O.E. with isodiametric cells over a testal mesophyll of three to five layers of thin-walled parenchyma which proliferates at the raphe to form the aril. The cells of the testal I.E. were smaller and much more thinly-walled than the O.E. and each had a single trapezoid crystal of calcium oxalate. The tegmen had a single layer of shortly longitudinally extended, sclerotic cells. The endotegmen was five to ten layers thick, of larger parenchymatous cells than the testal mesophyll and thick-walled and rectangular in L.S.

In several genera (e.g. Trichilia and Dysoxylum) it seems possible to trace a link from bitegmic and funicular-raphe-arillate seeds to the unitegmic and sarcotestal state and then to unitegmic 'pseudo-arillate' conditions: the aril re-evolves. If any explanation at all exists, it must surely lie in the functional significance of the seed characters. The transition from the loosely attached raphe-aril towards more closely attached structures such as the sarcotesta, can be viewed as a mechanism for reducing 'aril predation'; the increase in pachychalazy as a selective advantage allowing development of larger seeds (better establishment potential in rain forest since they have a larger food-reserve) with stronger seed-coats or of allowing more rapid development, thus reducing exposure to seed predation during this

period. But this is all speculation. No evidence exists, though it is plain that all the largest seeds are unitegmic and many of the largest of these (e.g. Chisocheton spp., Trichilia grandifolia to 100mm long) have been shown beyond doubt to be pachychalazal. Despite the (much vaunted) conservative nature of seed characters, there does seem to be an indication that some seed-coat characters and not just epidermal ones may be of functional significance in seed dispersal in the family. Pannell's (1985, 1987) syndromes of primate- and bird-dispersed fruits provide useful models here. Putatively primate-dispersed species (i.e. those which fit Pannell's syndrome on morphological grounds) do indeed seem to have mechanically stronger seed-coats with firmly attached surface fleshy tissue (arrived at by various anatomical pathways), completely compatible with Pannell's data on primate dispersal: see 'ecological aspects' in chapters eight and seven. The difficulty is that there appear to be very few field observations, that establish whether these species are primate- or bird-dispersed.

The anatomical features which characterize the Meliaceous seed, namely the longitudinal, pitted exotegmic fibres and the presence of calcium oxalate crystals in the testal I.E., are not unique to the Meliaceae. Corner (1976,1:15) lists them as occurring in 18 other families of flowering plant, and is inclined to attribute this to a monophyletic origin, although contemporary classifications of dicotyledonous families do not reflect this, but place these families in widely different orders. Another group of families are also exotegmic, but their sclerotic cells are not fibrous, but radially elongate ('palisade'). Corner (1976) evaluates the evidence that suggests that this may be the state from which the fibrous exotegmen is derived. There is evidence

that seems to support this hypothesis in the Meliaceae: it is reviewed at the end of chapters five and seven.

The main limitation to seed anatomy as a source of taxonomic characters in tropical families is that imposed by the requirement for spirit material if a proper anatomical investigation is to be made, especially if the seed is fleshy and the genus has not been investigated previously. Here, better education of collectors is necessary to secure available material of the missing genera, especially those of the fleshy-seeded Melioideae: Anthocarapa, Sphaerosacme and Reinwardtiodendron and from genera which are still poorly represented, such as Turraea and African Guarea. Even in those relatively well-collected genera such as Chisocheton, only slightly more than 20% of species have been investigated, and would be well served by additional collections. Much remains to be done with species already represented by fruiting spirit material- many collections of South American Trichilia and Guarea remain uninvestigated. An important priority for further work is the investigation of the origin of unitegmy, especially in the Guineo-Congolian Trichilia and the more 'advanced' species of Dysoxylum where the absence of relictual bitegmic seed-coats makes the diagnosis of pachychalazal unitegmy equivocal. The Aglaieae and Swietenioideae must not be forgotten. Their seed anatomy remains largely a closed book and until more is known, an overall view of the picture of the family will be partly obscured.

In view of the numerous characters afforded by seed structure, many of which seem to be easily polarized as compared with those of conventional morphological characters, it would now be useful to employ cladistic analysis in investigating the phylogeny of the Meliaceae. A preliminary analysis, using the cladistic package P.A.U.P. (Phylogeny Applied Using

Parsimony) of the Turraeeae was made and seemed very promising but was hampered by the lack of an infra-generic classification in the 'core' genus, Turraea and so is not included in this thesis.

In the future, it is hoped that the lengthy descriptions and illustrations presented here will serve as a basis for pursuing these goals with further comparative work.

With the conclusion of the work presented here, the Meliaceae must now be the most intensively explored medium sized tropical family in terms of systematic seed anatomy. As is indicated above, there is great scope to build further on this work. It remains a most interesting family to work on from the seed anatomical point of view because of the diversity, within a basic common model, of the seed structure. For example there is a range from fully bitegmic to fully pachychalazal and from raphe-arillate to fully sarcotestal seed-coats. Between these extremes, a wide range of intermediates and elaborations exist, which facilitate evolutionary interpretation. As far as can be judged from Corner's (1976) work, most nearly related families, even large ones such as the Sapindaceae, do not show such a large range of variation and tend to be more canalized in their seed structure.

# REFERENCES


Anon. (1978) Corner, E.J.H. The seeds of the dicotyledons (Review). Taxon 27 (1):103-105.

Bentham, G. & Hooker, J.D. (1862) Genera Plantarum. 1(1): 327- 340. Lovell Reeve, London.

Baillon, H. (1874) Sur l`origin du macis de la muscade et des arilles en générale. Adansonia 11: 329-340.

------- (1875) Meliacées. Histoire des Plantes. Paris, 5: 497.

Balkwill et al. (1986) Taxonomic studies in the Acanthaceae: testa microsculpturing in southern African species of Peristrophe. S. Afr. J. Bot. 52: 513-520.

Beehler, B. (1983) Frugivory and polygamy in birds of paradise. The Auk 100: 1-12.

Bentvelzen, P. A. J. (1962) Reduction of the genus Heynea Roxb. ex Sims to Trichilia P.Br. (Meliaceae). Acta. Bot. Neerl. 11: 11-20.

Barthlott, W. & Ehler, N. (1977) Räster-Elektronmikroskopie der Epidermis-Oberflachen von Spermatophyten. Trop. u. Subtrop. Pflanzenwelten 19: 1-175.

*
Boesewinkel, F.D. (1981) Development of the seed of Trichilia grandifolia Oliv. (Meliaceae). Acta Bot. Neerl. 30(5/6): 459-464.

---------- (1985) Development of ovule and seed-coat in Averrhoa (Oxalidaceae) with notes on some related genera. Acta. Bot. Neerl.

* Bawa, K. W. & Bullock, S.H. (1983) Guerea rhopalocarpa in D.H. Nickerson Janzen (Ed.), Costa Rican Natural History, University of Chicago Press, Chicago, London: 246.

34(4): 413-424.

---------- (1987) Ovules and seeds of Trigoniaceae. Acta Bot. Neerl. 36 (1): 81-91.

---------- (1988) The seed structure and taxonomic relations of Hypseocharis Remy. Acta Bot. Neerl. 37 (1): 111-120.

Boesewinkel, F. D. & Bouman, F. (1984): The seed: structure, in Johri, B.M. (Ed.) Embryology of the Angiosperms. Springer-Verlag, Berlin: 567-610.

Boucher, D. H. (1981) The real disperser of Swartzia cubensis. Reproductive Botany (supplement to Biotropica 13(2)): 77-78.

Bouman, F. (1984) The Ovule, in Johri, B.M. (Ed.) Embryology of the Angiosperms. Springer-Verlag, Berlin: 123-157.

--------- & J. I. M. Chalis (1977) Integumentary shifting - a third way to unitegmy. Ber. Deutsch. Bot. Ges. 90: 15-28.

Breytenbach, G. J. (1986) Dispersal: the case of the missing ant and the introduced mouse. S. Afr. J. Bot. 52: 463-466.

Brown, R. (1818) On some remarkable deviations from the usual structure of seeds and fruits. Trans. Linn. Soc. London 12(1): 143-151.

------- (1826) Character & description of Kingia etc. in King, P.P., Narrative of a survey of the intertropical & western coasts of Australia... London. 2:534-565.

de Candolle, A. (1824) Prodromus Systematis Naturalis Regni Vegetabilis 1: 619-626. Paris.

de Candolle, C. (1878) Monograph Phanerogamarum 1: 399-758. Paris.

Carlquist, S. (1962) Comparative Plant Anatomy. Holt, Rinehart and Winston, New York.

Cheek, M. (1983). Seed and Fruit Anatomy of Sapindaceae. Univ. of

Reading. Unpubl. M.Sc. Thesis. (Univ. of Reading library).

--------- (1989a) New combinations in Malagasy Meliaceae. Kew Bull. 44(2)(in press).

--------- (1989b) A new species of Turraea (Meliaceae) from Tanzania. Kew Bull. 44(2)(in press).

---------- (1989c) A new Trichilia (Meliaceae) from Tanzania and its relationship with Pseudobersama. Kew Bull. 44(2)(in press).

Chuang, T. I. & Heckard, L. R. (1983) Systematic significance of seed-surface features in Orthocarpus (Scrophulariaeae - subtribe Castillejinae). Amer. J. Bot. 70(6): 877-890.

Corner, E.J.H. (1949) The Annonaceous seed and its four integuments. New Phytol. 48 (3): 332-364.

------------ (1951) The leguminous seed. Phytomorphology 1(1): 117-150.

------------ (1958) Transference of function. J. Linn. Soc. Bot. 56: 33-40.

------------ (1976) Seeds of the Dicotyledons. 2 vol. C.U.P., Cambridge.

Crome, F.H.J. (1975) The ecology of fruit pigeons in tropical northern Queensland. Australian Wildlife Research 2: 155-185.

Cutler, D.F.(1978) Applied Plant Taxonomy. Longman, London.

Davis, P. H. & Heywood, V. H. (1963) Principles of Angiosperm Taxonomy. Oliver & Boyd, Edinburgh.

Earle Smith, C. (1960) A revision of Cedrela (Meliaceae). Fieldiana, Botany 29 (5): 295-341.

Foster, M. & McDiarmid, R.W. (1983) Nutritional value of the aril of Trichilia cuneata, a bird-dispersed fruit. Biotropica 15(1): 26-31.

Gaertner, J. (1788) Fructibus et Seminibus Plantarum. Stuttgart.

Geesink, R., Leeuwenberg, A. J. M., Ridsdale, C. E. & Veldkamp, J. F., (1981) Thonner's Analytical Key to the Families of Flowering Plants. Leiden U. P., The Hague.

Ghosh, R. B. (1972) Studies in the embryology of the family Meliaceae-IV. Fertilization, endosperm and embryogeny of Aphanamixis polystachya (Wall.) Parker - A medicinal plant with a discussion on its taxonomic status and horticulture. Anales Estacion Experimental Aula Dei (Zaragoza) 11, 3-4 396-403.

Grew, N. (1671) The Anatomy of Vegetables Begun.... . London.

----- (1682) The Anatomy of Plants. W. Rawlins, London.

Harms, H. (1896) Meliaceae in A. Engler & K. Prantl. Die Natürlichen Pflanzenfamilien 3(4): 258-308.

---------- (1940) Meliaceae in A. Engler & K. Prantl, op. cit., 2 ed., 19bI: 1-183.

Herrera, C. M. (1984) Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of Berberis hispanica. Oikos 42: 166-170.

Heywood, V.H. (1968) Plant Taxonomy today in V.H. Heywood (Ed.), Modern Methods of Plant Taxonomy. Academic Press, London: 3-12.

---------- (1976) Plant Taxonomy. Arnold, London.

Hoffman, G.F. (1814) Genera Plantarum Umbelliferarum. Stuttgart.

Holmgren, P.K. et al. (1983) Index Herbariorum (7th Edition). Junk, The Hague and Boston.

Howe, H. F. & Primack, R.B. (1975) Differential seed dispersal by birds of the tree Casearia nitida (Flacourtiaceae). Biotropica 7(4): 278-283.

-------- & D. De Steven (1979) Fruit production, migrant bird visitation and seed dispersal of Guarea glabra in Panama. Oecologia 39: 185-196.

Janzen, D. H. (1981) Digestive seed predation by a Costa Rican Baird's tapir. Reproductive Botany (Supplement to Biotropica 13(2)): 59-63.

Juliano, J. B. (1934) Studies on the morphology of the Meliaceae: I Sandoricum koetjape (Burm. f.) Merrill. Philippine Agriculturalist 23 (1): 11-35.

de Jussieu, A. (1789) Genera Plantarum. Paris.

de Jussieu, A-L. (1832) Mémoire sur le groupe des Meliacées. Mém. Mus. Hist. Nat. Paris. 19: 153-304.

Kapil, R. N., Bor, J. and Bouman, F. (1980) Seed appendages in Angiosperms. Bot. Jahrb. Syst. 101 (4): 555-573.

Keay, R. W. J. (1958) Meliaceae, in Hutchinson, J. and Dalziel, J. M.,Flora of West Tropical Africa. Crown Agents. London:697-709.

Khosla, P. K. & Styles, B. T. (1975) Karyological studies and chromosomal evolution in Meliaceae. Silvae Genetica 24 (2-3): 73-83.

Kribs, D.A. (1930) Comparative anatomy of the wood of the Meliaceae. Amer. J. Bot. 17: 724-738.

Kurz, S. (1875) Contributions towards a knowledge of the Burmese flora. J. Asiatic Soc. Beng. 44: 128-190.

de Lanesson, J. (1876) in H. Baillon, Dictionnaire Botanique. Paris, 1:258.

Leck, C. F. (1969) Observations of birds exploiting a Central American fruit tree. Wilson Bull. 81: 264-269.

*Leroy, J.F. (1958a) Sur un genre africano-malgache : le Lepidotrichilia (Harms) J. F. Leroy. J. Agr. Trop. Bot. Appl. 10: 673-675.

---------- (1958b) Un genre nouveau endémique à Madagascar: le Capuronianthus. J. Agr. Bot. Appl. 11: 762-764.

* Leighton, M. & Leighton, D.R. (1983) Vertebrate responses to fruiting seasonality within a Borneon rain forest. In S.L. Sutton, Whitmore, T.C. & Chadwick, A.C. (Eds.), Tropical Rainforest: Ecology & Management, Blackwell, Oxford: 181 - 196.

---------- (1958c) Sur un genre endémique de Madagascar: l' Astrotrichilia (Harms) J.F. Leroy. J. Agr. Bot. Appl. n.s. 12: 861-862.

-------- (1960) Recherches sur les Meliaceae: un interessant genre de Turraeeae, le Calodecaryia J.F.Leroy (deux espèces) endémique a Madagascar. J. Agr. Trop. Bot. Appl. 7(6) 379-382.

---------- (1964) Recherches sur les Meliaceae: le Malleastrum (Baill.) J. F. Leroy, genre nouveau endémique de la Grand Ile et des Comores. J. Agr. Bot. Appl. 11: 127-149.

---------- (1969) Recherches sur l`évolution: divergence évolutive de l`organization ovarienne dans la tribu des Turraeeae (Meliaceae-Melioideae). Compte Rendu Acad. Sci. Paris. Ser. D. 269:2319-2322.

---------- (1981) Essais de Taxonomie Syncretique. Étude sur les Meliaceae de Madagascar. Adansonia, ser. 2, 16 (2): 167-203.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M.(1979) Seed dispersal by baboons in the Shai Hills, Ghana. Ecology 60(1): 65-75.

Mabberley, D.J. (1979) The species of Chisocheton (Meliaceae). Bull. Br. Mus. nat. Hist. (Bot.) 6(4): 301-386.

---------- (1983) Tropical Rain Forest Ecology. Blackie, Glasgow and New York.

---------- (1984) A monograph of Melia in Asia and the Pacific: the history of White Cedar and Persian Lilac. Gard. Bull. Sing. 37: 49-64

---------- (1985) Flora Malesianae Praecursores LXVII Meliaceae (Divers Genera). Blumea 31: 129-152.

---------- (1987) The Plant-Book. C.U.P., Cambridge.

---------- (1988) Meliacées in C. Tirel (Ed.) Flore de la Nouvelle-Calédonie et Dépendances. 15: 17-89.

Malpighi, M. (1675) Anatome Plantarum etc. 2 vol., London.

Manders, P.T. (1986) Seed dispersal and seedling recruitment in Protea laurifolia. S. Afr. J. Bot. 52(5): 421-424.

Martin, A.C. (1947) The comparative internal morphology of seeds. Amer. Midl. Nat. 36:513.

Mathew, B. (1986) Helleborus vesicarius. The Plantsman 8(3): 167.

McKey, D. (1975) The ecology of coevolved seed dispersal systems in L.E. Gilbert & P.H.Raven (Eds.), Coevolution of Animals and Plants. Univ. of Texas Press: 159-191.

Metcalfe, C.R. & Chalk, L. (1950) Anatomy of the Dicotyledons. 2 vol. O.U.P. Oxford.

Nair, N.C. (1958) Studies on Meliaceae. III. Floral Morphology and embryology of Sandoricum indicum Cav. Phyton 10(2): 141-151.

---------- (1959a) Studies on Meliaceae II. Floral morphology and embryology of Melia azedarach Linn. - a reinvestigation. J.Ind. Bot. Soc. 38: 367-378.

--------- (1959b) Floral Morphology and Embryology of Naregamia alata W.& A. J.Ind. Bot. Soc. 38: 353-366.

Nair, N. C. & Kanta (1961) Studies in Meliaceae IV. Floral morphology and embryology of Azadirachta indica A. Juss.- a reinvestigation. J. Ind. Bot. Soc. 40: 382-396.

Narayana, L.L. (1958) Floral anatomy and embryology of Cipadessa baccifera Miq., J. Ind . Bot. Soc. 38: 147-154.

Netolitzky, F. (1926) Angiospermum Samen, in Linsbauer, Handbuch der Pflanzen Anatomie. X (1): 181-182.

Oatley (1972) The Electron Microscope. C. U. P.

Palmer, E. & Pitman, N. (1973) Trees of South Africa, 2:1052-1077. Cape Town.

Panigrahi, S.G. (1986) Seed morphology of Rotala L., Ammania L., Nesaea Kunth and Hionanthera Fernandes & Diniz (Lythraceae). Bot. J. Linn. Soc. 93: 389-403.

Pannell, C. M. & Koziol, M.J.(1987) Ecological and phytochemical diversity of arillate seeds in Aglaia (Meliaceae): a study of vertebrate dispersal in tropical trees. Philos. Trans. R. Soc. London, Ser. B, 316: 303-333.

Pannell, C.M. & White, F. (1985). Bird dispersal & some derived evolutionary trends in a tropical plant family the Meliaceae. Notes from the Forest Herbarium, University of Oxford No. 3. Unpublished.

---------- (1988) Patterns of speciation in Africa, Madagascar, and the tropical far East: regional faunas and cryptic evolution in vertebrate-dispersed plants. Monogr. Syst. Bot. Miss. Bot. Gard. 25: 639-659.

Peacock (1975) Elementary Microtechnique. London.

Pellegrin, F. (1939) Les Guarea (Meliacées) africains. Bull. Soc. Bot. France. 86: 146-154.

Pennington, T.D. (1969) Materials for a generic monograph of the Meliaceae: a review of the genus Vavaea. Blumea 17: 351-366.

Pennington T.D. and Styles, B.T. (1975) A generic monograph of the Meliaceae. Blumea 22(3): 419-540.

---------- (1981) Meliaceae. Flora Neotropica 28. New York.

Periasamy, K. (1962) The ruminate endosperm: development and types of rumination. In P. Maheshwari (ed.), Plant Embryology, a Symposium. C. S. I. R., New Delhi.

Pfeiffer, A. (1891) De Arillargebilde der Planzensamen. Bot. Jahrb. 13: 492-540.

Phillips, J. F. V. (1927) Ekebergia capensis Sparrm. in the Knysna region. S. Afr. J. Sci. 24: 216-224.

van der Pijl, L. (1955) Sarcotesta, aril, pulpa and the evolution of the angiosperm fruit. I. Proc. K. Ned. Akad. Wet. C. 59:154-161 & 307-312.

---------- (1956) Classification of the leguminous fruits according to their ecological and morphological properties. Proc. K. Ned. Akad. Wet. C. 59: 301-313.

---------- (1957) On the arilloids of Nephelium, Euphoria, Litchi and Aesculus, and the seeds of Sapindaceae in general. Acta Bot. Neerl. 6:618-641.

---------- (1969) Evolutionary action of tropical animals on the reproduction of plants. Biol. J. Linn. Soc. 1: 85-96.

Planchon, M. J.-E. (1845) Developpements et caractères des vrais et des faux arilles. Anal. Sci. Nat. Sér. 3, 3. Bot.: 275-311.

Prakash, N., Lim, A. L. & Manurung, R. (1977) Embryology of Duku and Langsat varieties of Lansium domesticum. Phytomorphology 27(1):50-59.

Radford, A.E. et al. (1979) Vascular Plant Systematics. Harper & Row, New York and London.

Radlkofer, L. (1933) Sapindaceae, Das Pflanzenreich (heft 98A), IV, 165. Band 1. Leipzig.

Robbrecht, E. & Puff, C. (1986) A survey of the Gardenieae and related tribes (Rubiaceae). Bot. Jahrb. Syst. 108(1): 63-137.

Schmid, R. (1986) On Cornerian and other terminology of angiospermous and gymnospermous seed coats: historical perspective and terminological recommendations. Taxon 35 (3): 471-491.

Sernander, R. (1906) Entwurf einer Monographie der europaischen Myrmekochoren. K. Svensk. Vet. Hand. 41(7).

Sporne, K. R. (1948) Correlation and classification in the angiosperms. Proc. Linn. Soc. Lond. 160: 40.

---------- (1974) The Morphology of the Angiosperms. Hutchinson, London.

Stace, C. A. (1980) Plant Taxonomy & Biosystematics. Arnold, London.

Staner, P. & Gilbert, G. (1958) Meliaceae in Flore du Congo Belge et du Ruanda-Burundi. 7: 147-213.

Stevens, P. F. (1975) Review of Chisocheton (Meliaceae) in Papuasia. Contr. Herb. Austr. 11: 1- 55.

Stork, A. L. & Wuest, J. (1978) S E M studies of seed-coats in Malcolmia (Cruciferae). Arch. Sci. Genève. 31 (3):229-237.

Styles, B.T. (1972) The flower biology of the Meliaceae and its bearing on tree breeding. Silvae Genetica 21(5): 149-204.

Taylor, P. (1989) A monograph of Utricularia (Lentibulariaceae). R.B.G. Kew, London (in press).

von Teichman, I., Robbertse, P.J. & Schoonraad, E. (1988) The structure of the seed of Mangifera indica L. and notes on seed characters of the tribe Mangifera (Anacardiaceae). S. Afr. Tydskr. Plantk. 54 (5): 472-476.

Vaughan, J.G. (1970) The Structure & Utilization of Oil Seeds. Chapman & Hall, London: 155-161.

Vaughan, J. G. and Whitehouse, J. M. (1971) Seed structure and the taxonomy of the Cruciferae. Bot. J. Linn. Soc. 64: 383-409.

Waterman, P. G. & Grundon, M.F.(eds, 1983). Chemistry and chemical taxonomy of the Rutales. Academic Press. London & New York.

Wheelwright, N. T., Haber, W. A., Murray, K. G. and Guindon, C.(1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica 16 (3): 173-192.

White, F. (1986) The taxonomy, chorology and reproductive biology of Southern African Meliaceae & Ptaeroxylaceae. Bothalia 16(2): 143-168.

---------- & Styles, B. T. (1963) Meliaceae in A. W. Exell, A. Fernandes and H. Wild (eds), Flora Zambesiaca 2 (1): 285-319.

de Wilde, J.J.F.E., (1968) A revision of the species of Trichilia P. Browne (Meliaceae) on the African Continent.Meded. Landbou. Wageningen 68 (2):1-207.

# APPENDIX

## LIST OF MATERIALS STUDIED

All materials are spirit collections at FHO unless otherwise cited. Abbreviations of herbaria follow Holmgren et al. (1983).

Collections illustrated in plates are marked '*'.

TURRAEEAE

Turraea heterophylla Sm., Cheek s.n., (live, voucher FHO), Oxford Botanic Garden *.

T.leroyana Cheek ined., Cheek 2-27-1, Madagascar*.

T.robusta Guerke, Cheek 998, Uganda *.

T.cornucopia Styles & White ined., Cheek 1155, Kenya*.

T.sericea Sm., Cheek 1160 , Madagascar*.

T.floribunda Hochst., Kerfoot 2193 (dried, K), Kenya.

T.nilotica Kotschy & Peyr., Magogo and Glover 205 (dried, K), Kenya.

T.obtusifolia Hochst. collection data unavailable, photo. only*.

T.mombassana Hiern, Cheek s.n., ( dried, FHO), Kenya.

Calodecaryia crassifolia Leroy, Mc Whirter 159, Madagascar*.

Munronia pinnata(Wall.) Theob., Gee s.n., (spirit, K) Assam*.

M.delavayi Franch., Forrest 13572, Yunnan.

M.unifoliolata Oliv., Henry 4198, Hupeh.

M.pumila Wight, Worthington 7084, Ceylon.

Nymania capensis (Thunb.)Lindb., D.A.H.Taylor s.n. (dried, FHO), S.Africa*.

---------- living material, Dept. Plant Sci., Oxford.

Naregamia alata Wight & Arnott, Sethi, Negi et al. 25904 , India*.

Humbertioturraea malifolia (Baker)Cheek ined., Cheek 2-20-1 Madagascar*.

H. sp. Leandri 2945 (dried, FHO), Madagascar*.

MELIEAE

Melia azedarach L., Cheek et al. 994, Beni, Zaire*.

'Melia dubia Cav.', Cheek 1561, Entebbe, Uganda*.

Melia volkensii Guerke, Hughes 239, Kenya, (spirit, K)*.

Azadirachta indica A.Juss., Cheek 3-13-1 Madagascar*.

TRICHILIEAE

Trichilia emetica Vahl, Cheek 1609A, Mrima Hill, Kenya*.

T.dregeana Sond., Cheek 1576, Uganda.

T.monadelpha (Thonn.)J.J.De Wilde, Keay s.n., Nigeria.

T.pallida Sw., Prance et al. 2341, (K, spirit)

T.sp.1, Cheek B1315, Madagascar, (spirit, K)*.

T.sp.2, Cheek s.n., Madagascar, (spirit, K).

T.capitata Klotzch, T.D.Chapman 6338, (dried material), Malawi*.

T.lovettii Cheek ined., Lovett 8546 (dried, K), Uzungwa, Tanzania.

Pseudobersama mossambicensis (Sim)Verdc., Cheek et al. 1603, (spirit, FHO,K), Kwale, Kenya*.

Pterorhachis zenkeri Harms, Letouzey s.n. ex cult. Wageningen*.

Heynea trijuga Roxb. ex Sims, T.D.Pennington 7927,7877, Borneo*.

Walsura pinnata Hassk., T.D.Pennington 7815, Borneo*.

W.chrysogyne (Miq.)Bakh.f., T.D.Pennington 7831, Borneo.

W.rhomboidea T.Clark ined., T. Clark 79, Borneo.

Lepidotrichilia volkensii (Harms)Leroy, Cheek et al. 1657, Aberdare Mts.,Kenya*.

---------- Cheek B1508, Ngong Hills, Kenya (colour photo)*.

Malleastrum gracile Leroy, Cheek et al. 2-21-3, Madagascar*.

M. mandenense Leroy, Cheek et al. 3-17-1, Madagascar*.

M. isalense Leroy, Cheek et al. 3-26-5, Madagascar*.

M. psammophilum Leroy, Cheek et al. 2-27-7, Madagascar*.

Astrotrichilia asterotricha (Radlk.)Cheek ined., Cheek et al. 2-25-2, Madagascar*.

Astrotrichilia sp.1 Thouvenot s.n. (K, dried material), Madagascar.

Ekebergia capensis Sparrm., Cheek 1055, Mau Escarpment, Kenya*.

Cipadessa sp., cult. Hort.Bot. Munich*.

Owenia venosa F. Muell., J.H.McWhirter 7, Australia*.

GUAREEAE

Heckeldora latifolia Pierre, Thomas s.n., 1985, Cameroun*.

----------Thomas, s.n.,1986, Cameroun.

---------- Onochie, s.n., Nigeria.

Cabralea canjerana (Vell.) Mart., T.D.P. & Budowski, 10105, Costa Rica, (spirit K)*.

Cabralea sp. source unknown*.

Turraeanthus mannii Baill., Cheek et al. 948, Cameroun*.

---------- , D. Thomas s.n., Cameroun*.

Turraeanthus africanus (Welw. ex C.DC.)Pellegr., Hawthorne & Gyaker s.n., Ghana*.

Guarea glomerulata Harms, D. Thomas 4429, Cameroun*.

---------- D. Thomas 4236, Cameroun.

Guarea ramiflora Vent., Nevling & Howard 5527, Puerto Rico (spirit, K).

Guarea thompsonii Sprague ex Hutch., Léonard 85.

Chisocheton lasiocarpus (Miq.) Valeton, D.J.M. 1754, New Guinea*.

Chisocheton schoddei P.F. Stevens, D.J.M. 1773, New Guinea*.

C. macranthus (Merr.)Airy Shaw, D.J.M. 1718, Borneo*.

C. cumingianus (C.DC.)Harms, T.D.P.8052, New Guinea*.

----------, T.D.P. 8084, New Guinea.

C. ceramicus (Miq.)C.DC., T.D.P. 7917, Sandakan, Borneo*.

---------- , D.J.M. 1720, Morobe, New Guinea.

C. longistipitatus (F.M.Bailey)L.S.Smith, T.D.P. 8077, New Guinea.

C. pentandrus (Blanco)Merr. ssp. paucijugus (Miq.)Mabberley, T.D.P. 7865, Borneo.

C. sarawakanus (C.DC) Harms, T.D.P. 7882, Borneo*.

C. granatum Mabberley, T.D.P. 7941, Borneo*.

C. sarasinorum Harms, T.D.P. 7910, Sabah, Borneo*.

C. medusae Airy Shaw, T.D.P. 8002, Borneo*.

---------- , T.D.P. 7913, Borneo.

---------- , T.D.P. 7912, Borneo.

C. polyandrus Merr., D.J.M. 1688 (photo only) Borneo*.

Synoum glandulosum (Smith) A.Juss.,Symons 1491, Australia*.

----------,'Coll. F.R.I. Canberra, Woolgoolga, 10.10.71', Australia.

----------, '10.2.64'.

Pseudocarapa championii (Hook.f. & Thoms. ex Thwaites) Hemsl., C.V.S. Gunatilleke s.n., Sri Lanka*.

Dysoxylum pachyphyllum Hemsl., Game s.n., , Lord Howe Island*.

---------- , Green s.n., Lord Howe Island.

D. macrostachyum C.DC., T.D.P. 8134, New Caledonia*.

D. macranthum C.DC., MacKee 21130, New Caledonia (dried, FHO)*.

D. macranthum C.DC., MacKee 38394, New Caledonia (dried, FHO).

---------- , D.J.M. 2022, New Caledonia*.

D. cauliflorum Hiern, D.J.M. 1692, Sabah, Borneo*.

----------, D.J.M. 1702, Sabah, Borneo.

D.'acutangulum','2062', source unknown*.

D. angustifolium King, D.J.M. 1991, Peninsular Malaysia*.

D. spectabile Hook. f., Meebold 4786, New Zealand.

D. kouiriense Virot, D.J.M. 2029, New Caledonia.

D. bijugum (Labill.) Seem. D.J.M. 2039, New Caledonia.

D. parasiticum (Osbeck) Kosterm. D.J.M. 2159, Java (photo)*.

----------, T.D.P. 8105, New Britain.

D. peerisiae Kosterm., Gunatilleke s.n., Sri Lanka.

D. gaudichaudianum (A. Juss.) Miq. T.D.P. 8037, New Guinea.

D. pettigrewianum F.M.Bailey, T.D.P. 8078, New Guinea.

D. brevipaniculatum C.DC., D.J.M. 1744, New Guinea.

D. brachybotrys Merr., T.D.P. 7975, Sarawak.

D. cyrtobotryum Miq., S.F.N. 29427.

D. mollissimum Biume ssp. molle (Miq.) Mabb. ined., T.D.P. 8044, New Guinea.

D. acutangulum Miq. ssp. foveolatum (Radlk.) Mabberley ined., Dunlop s.n., Australia

D. arborescens (Bl.) Miq., D.J.M. 1735, New Guinea.

SANDORICEAE

Sandoricum koetjape (Burm. f.) Merr., T.D.P. 7819, Borneo*.