A TAXONOMIC STUDY OF THE EBENACEAE WITH SPECIAL REFERENCE TO MALESIA

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A taxonomic study of the Ebenaceae with special reference to Malesia.

ABSTRACT

The Ebenaceae is a family of woody, mostly tropical plants consisting of about 500 species, some of which produce the ebony of commerce, and a few others produce the edible fruits known as persimmons. About 300 species occur in the Indo-Pacific area, with the greatest concentration, of 150 - 200 species, within the tropical rain forest region known as Malesia, which includes the political units Malaysia, Indonesia and the Philippines.

This study is based primarily on herbarium material of Malesian species but whenever it has been necessary to ignore the Malesian boundary in the interests of acquiring a better understanding of the plants, I have done so. Hence all species in the Indo-Pacific area have been examined, at least casually, but some in considerable detail. A few critical examples from Africa have also been included.

The last comprehensive monograph on the family was written almost a century ago, by Hiern (1873), when only 262 species were recognised. Hiern's monograph is now completely out of date at species, sectional and generic levels. For Malesia, the standard regional monograph was completed by Bakhuizen in 1941. This work too, is out of date because much more new material has been collected, especially from areas formerly difficult to reach and consequently under-explored.

The present study is divided into four parts. The first part consists of a series of investigations into form and

structure within the family, covering carpel and seed morphology, seedling behaviour, pollen morphology, wood anatomy, various features of the epidermis especially trichomes and stomata, and karyotype.

It was found that the Ebenaceous gynoecium is composed of 2 - 8 bi-ovulate carpels "fused" to form a multilocular ovary. However, false septa are developed in all except 11 species. These false septa have usually not been recognised for what they are, and for this reason, descriptions of carpel morphology and the use of carpel characters in previous taxonomic treatments of the family have betrayed a considerable amount of confusion which the present research has cleared up.

Pollen morphology and woody anatomy is remarkably constant throughout the family. Chromosome number is very stable. A single euploid series 2n = 30, 60, 90 applies right through the family.

Epidermal structures are, on the other hand, more variable than might have been expected, e.g. there are simple, branched, tufted, glandular and peltate trichomes; stomata may be anomocytic or have subsidiary cells of various forms.

Seedling behaviour during germination is variable, some species being neither hypogeal nor epigeal and have to be described by considering the behaviour of the hypocotyl and the cotyledons separately.

The second part is an investigation into the limits of the family. This consists of a series of critical comparisons between Ebenaceae and the families Sapotaceae, Sarcospermataceae, Styracaceae, Symplocaceae and Lissocarpaceae. A large number of

characters were examined, in the process of which several important points emerged.

Carpel structure has been consistantly misinterpreted especially in the system of Engler (1964). Contrary to the claim that the Sapotaceous ovary is completely partitioned into locules, by which it differs from the partially "open" condition in Ebenaceae, Styracaceae and Symplocaceae, it was found that the locules in every Sapotaceous ovary examined, are in connection with each other by means of a compitum of varying size. In fact, all the six families involved in this survey are eu-syncarpous (Carr & Carr 1961).

Trichome characters are unreliable as markers for the various families. Popular association of branched hairs with Sapotaceae and simple hairs with Ebenaceae and Symplocaceae turn out to be oversimplifications of the truth.

In previously published definitions of these six families, the boundaries between them appear to be fuzzy. It was found that such fuzziness merely reflects bad choice of characters and misunderstanding of certain structures and of their extent of variation. The families are in fact either very sharply defined from each other or not clearly definable at all. Sarcospermataceae is a bad family, quite indistinct from Sapotaceae. All the other families are sharply defined from each other by several to many characters, and there are no problems of intermediate taxa. Lissocarpaceae, sometimes thought to be intermediate between Ebenaceae and Styracaceae, is a distinct family but probably the most closely related to Ebenaceae of all the families considered. Sapotaceae, usually thought of as the closest family to Ebenaceae, is in fact most different. The naturalness of the Order Ebenales is put in doubt.

In the third part, Bakhuizen's classification of Malesian Ebenaceae (actually Diospyros since this is the only genus in Malesia), is put to the test using a taximetric procedure of character analysis. The results support the maintainance of Hierniodendron and Brachycylix as infra-generic taxa worthy of recognition. Support for the other sub-genera and sections was feeble to nil. The genus Diospyros is probably best considered to consist of one very large variable section (Sect. Diospyros) and a small number of little ones.

Problems of species delimitation do not loom very large in this study, but in the fourth part, three species-complexes were analysed for morphological variation over their entire range. In one of these analyses, involving Diospyros sylvatica, D. ehreticoides, D. hermaphrodica and D. fasciculosa, an interesting pattern of allopatry emerged, which suggested that some of these taxa could be regarded as geographical subspecies. The other two analyses were carried out on D. kaki, D. lotus and their relatives. These species produce edible persimmons. Problems of their origin and spread are consequently of wider than taxonomic interest, but the taxonomic approach adopted here serves to sharply outline various hypotheses that others may be able to test by cytotaxonomic and other means. It is suggested that D. kaki originated from D. roxburghii, which is now found wild in the forests of Assam, Burma, Thailand, Yunnan and Indo China. The controversial problem of the role of man in the distribution of D. lotus is reviewed and summarised.

INTRODUCTION

The Ebenaceae is a world-wide family of about 500 woody species, found mostly in the tropics, but with a few representatives in temperate regions. About 300 species occur in the Indo-Pacific area (India to Hawaii, Japan to Australia). Within this region, the greatest concentration is found within Malesia (sensu Flora Malesiana, van Steenis 1948) with 150 - 200 species.

The family was last monographed comprehensively in 1873, by W.P. Hiern. He divided the family into five genera and recognised 262 species, which is roughly half the total number recognised today.

As for the affinities of the family, Hiern suggested that the families closest to Ebenaceae were Oleaceae, Styracaceae, Annonaceae, Ternstroemiaceae, Sapotaceae and Ilicineae. But in all the currently popular systems of classification (Bentham & Hooker 1873 - 1876, Engler 1964, Hutchinson 1959, Cronquist 1968, Takhtajan 1969), the family most constantly associated with Ebenaceae is Sapotaceae. Styracaceae is also deemed to be a close associate by all the above authors except Hutchinson.

After Hiern, all taxonomic work on the Ebenaceae has been on a regional basis, mostly country by country, but the most ambitious of these was a revision of "Malayan" Ebenaceae undertaken by R.C. Bakhuizen van den Brink, a Dutch botanist in Boger, Java, in the period between the two world wars. By "Malayan", Bakhuizen meant the whole of the Malay Archipelago including what is now Malaysia, Philippines and Indonesia. For good measure, he also included Australia and Oceania. In all, he recognised 190 species, merged the genus Maba into Diospyros,

and divided *Diospyros* into five sub-genera with many small sections. The main body of Bakhuizen's work was completed by 1933 as indicated by a precursory paper published that year in the Garden's Bulletin, in Singapore. The complete work was published in Bogor between 1936 and 1941. It contains a comprehensive bibliography and citations of all specimens available at the time, hence it forms a very valuable basis for further work on the family.

My own interest in the *Ebenaceae* is connected with the Tree Flora of Malaya project (Editor T.C. Whitmore), which has been running since 1965, and for which I had, by 1968, completed revisions of the Malayan *Sapotaceae* and *Sarcospermataceae*. With *Ebenaceae* next in line for treatment, I was able to obtain leave to look at the problem from a monographic and more fundamental point of view rather than on a purely floristic basis. My supervisor at Oxford, Mr. F. White, has specialised in the family *Ebenaceae* for many years. Until recently, he and his students have concentrated on the species in Africa and the Americas, but a new world monograph of the family will, it is hoped, eventuate from this school. My own efforts are to be seen as a contribution towards this eventuality.

The need for a new comprehensive monographic work on the *Ebenaceae* has been felt for several decades now. One by one, all but one (*Euclea*) of Hiern's generic limits have been tested by workers in different parts of the world, and been found wanting. His sectional limits have fared equally badly. The result is that Hiern's monograph no longer serves as a useful basis for floristic work. We are left with a number of regional treatments in different parts of the world, of varying quality, with different concepts of sub-genera, sections and species, that badly need to be tested and fitted together before a new overall understanding

of the family can emerge.

One of the objects of the present project was to test Bakhuizen's classification, making use of modern techniques of handling data and taking advantage of the vast amount of new material that has been collected since 1941. However, it was realised from the beginning that the chances of substantially improving the classification of the Ebenaceae are dependent not only on improved methods of data handling and increased amounts of herbarium material, but also on extension of data beyond external morphology. With this in mind, a series of investigations were carried out on pollen, secondary xylem, karyotype, epidermal structures and seedling behaviour. In addition, some 100 bottles of flowers and fruits preserved in alcohol, collected by members of the Forest Research Institute, Kepong (some by myself) and by Dr. T.D. Pennington, formed the basis for a detailed study of gynoecial and seed structure which could not have been carried out adequately on dried herbarium material.

As a result of these investigations, presented in Part I, I was able to show that carpel morphology has been badly misinterpreted in the past, that some structures such as pollen and secondary xylem are remarkably constant throughout the family, and that others, such as the epidermis, are far more variable than expected.

Misinterpretations of form and structure, and faulty appreciation of variability and constancy, have, as might be expected, contributed in the past to imprecision in the definition of the family Ebenaceae as well as to errors in infra-family classification.

Regarding the limits of the family, a critical reappraisal

based on original observations on a broad range of material has probably not been carried out since Bentham and Hooker grouped the Ebenaceae, Sapotaceae and Styracaceae together in the Ebenales. In Part 2, I carried out such a reappraisal, and was able to demonstrate more clearly, where the limits of Ebenaceae, and to some extent, of the other families of the Ebenales, lie.

Part 3 is a taximetric exercise in which Bakhuizen's infra-generic classification of Diospyros was put to the test using a recently developed technique of character analysis. I have, during the course of this whole project, been familiarising myself with Bakhuizen's classification at all levels. I think I can safely claim to understand most of the species as he defined them although I would have defined some of them differently myself. At sectional and sub-generic level, however, I am dissatisfied with his system as a whole. It is true that some groupings such as subgenus Hierniodendron are quite distinct and easy to characterise. Others are distinct as defined by single characters only e.g. subgenus Maba by its trimerous flowers. Modern taxonomy is distrustful of taxa defined by single characters, for the good reason that such taxa have nearly always proved to be artificial. Elsewhere in Bakhuizen's system, e.g. sections 7 - 31 of subgenus Eudiospyros, the limits between sections are virtually invisible. However, I am very conscious of the fact that no two taxonomists perceive taxonomic groupings in exactly the same way. This problem is likely to remain as long as concepts of similarity and difference remain informal and vary from person to person. The rapid development of taximetrics in recent years has at least in part been due to the demand for more objectivity in the construction of taxonomic hierachies. At the time when I began this study, Dr F.A. Bisby, who was another student of Mr. F. White's, was in the middle of

an investigation on the applicability of various taximetric methods to angiosperm taxonomy. Among these methods was the taximetric procedure "character analysis" the usefulness of which Bisby (1970) convincingly demonstrated with an example from the classification of Crotalaria. I decided to apply this method to Diospyros.

The problems of specific delimitation have not bothered me unduly. I have, as earlier stated, familiarised myself with the species as Bakhuizen defined them. I have accepted them as the operational taxonomic units on which I carried out the investigations of Parts 1, 2, and especially Part 3. Nevertheless, it can be easily demonstrated that with the material available before 1941, Bakhuizen could have had only a very imperfect idea of specific and infraspecific limits. With the amount of material vastly increased since the war, and especially from some areas previously under-collected, we are in a much better position to define specific limits. I present in Part 4, detailed analyses of three species-complexes to demonstrate the kind of approach that can be very fruitful in taxonomy at the species level.

Material for this entire study consisted of the rich collections in the herbaria of Kew (K), Oxford (FHO and OXF) and the British Museum (BM), supplemented by loans of material from Singapore (SING), Kepong (KEP) and Leiden (L). Small loans were also obtained from Bangkok (BKF) and Rangoon (RAF). I thank the Directors and Curators of the above herbaria for kindly allowing me the use of their material.

....

I am very grateful to Mr. F. White for supervising this work and suggesting the various problems that I might investigate.

Secondly I thank the staff of the Forest Herbarium Oxford

for help with various aspects of the work; in particular Dr B.T. Styles for translating German and French papers, and Mrs Anita Caveney for many valuable discussions comparing Malesian with African Ebenaceae. Mrs E. Woodley mounted the numerous photographs and Dr T.D. Pennington introduced me to the technique of making pollen preparations.

Dr F.A. Bisby, now of the University of Southampton, advised me on character analysis, and read my account of it. Mrs S. Hockey of the Atlas Computer Laboratory, Chilton, helped me to operate the programme.

I received much encouragement and advice especially in the early stages, from Professor C.G.G.J. van Steenis, Dr M. Jacobs and Dr Ding Hou, all of the Rijksherbarium, Leiden, whose kindness and hospitality I enjoyed during a short stay in Leiden prior to my arrival at Oxford.

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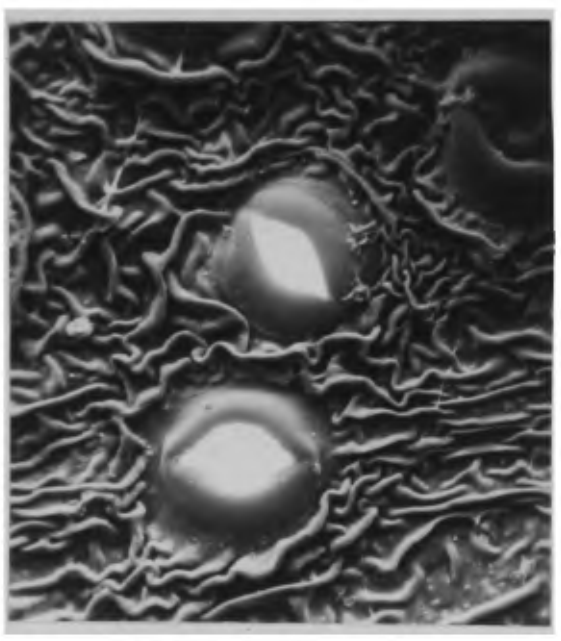


Stomata and cuticular ridges in Diospyros wallichii; scanning electron microscope 300x.

PART 1 : MORPHOLOGY, ANATOMY and CYTOLOGY

Introduction

Sexual polymorphism

Gynoecium, fruit and seed

Seedlings and germination

Pollen

Secondary xylem

Epidermis

Chromosome numbers

Summary : a family description and discussion

Introduction

The taxonomic characters upon which plant classification has traditionally been based are those easily observable by the unaided eye or by low-power microscope and simple dissecting techniques. Practically all revisions of the Ebenaceae, whether on a world-wide or regional scale, have been based on such characters. There is no reason why easily accessible characters should or should not reveal natural relationships clearly enough for a stable classification to be constructed. Some infra-family hierachies defined on such characters have been remarkably stable, but unfortunately not in Ebenaceae. Here, generic and sectional limits have always been very fluid. Perhaps previous methods of handling data have been faulty. Or perhaps the traditional characters simply do not, in Ebenaceae, provide enough clues to natural relationships within the family.

It was partly with the intention of extending the range of data upon which a modern revision at all levels from family to species, can be based, that I undertook a series of investigations on carpel structure, pollen, secondary xylem, and other organs and structures not normally associated with classical phytography and taxonomy.

Another, equally urgent intention was that of critically testing Bakhuizen's (1936 - 1941) revision of Malesian Ebenaceae, which is important not only for its size (190 spp.), but also for the large number of proposals he made at generic, sub-generic and sectional level. If Bakhuizen's classification is a natural one, it should have high predictive value; new characters unknown to Bakhuizen should be well correlated with those characters upon which he based his classification.

A body of information on pollen, wood-anatomy, embryology etc. of Ebenaceae already exists in standard reference works

on these topics. However, such reference works, useful as they are for giving a bird's-eye view of variation from family to family, are often deficient for more critical taxonomic purposes. "Family" accounts in such works may be based on very small samples of species. Geographical representation may be very uneven. Problematical species of great taxonomic interest may be missed. The specialist on any taxon is generally obliged to fill in vast gaps of information before he can use such data with any confidence.

But although desirable, it is impracticable to make more than a limited number of microscope preparations, because all such preparations are excessively time-consuming. A taxonomist can never hope to prepare, for example, a pollen slide for each herbarium sheet of any particular taxon. One preparation per species would be an ideal minimum but even this would mean making about 200 preparations for pollen, another 200 for secondary xylem, and so on, for Malesian species alone, which is an impossible task even if the raw material was available. For the purpose of testing Bakhuizen's classification, in which sections are small, relatively homogeneous, and often appearing to merge into one-another, I have aimed at making preparations from different and contrasting parts of his classification as an initial survey to detect significant patterns of variation, followed by more detailed work on those parts of the classification which showed promise.

The following accounts are based therefore primarily on Malesian material but with a liberal representation from the rest of the Indo-Pacific region. I have also included critical examples from Africa whenever my attention has been drawn to them by my supervisor Mr. F. White or his assistant Mrs A.N. Caveney. The next section, however, on sexual polymorphism, differs from the others in being a review of a conventional topic of classical taxonomy. I have had to do this to prepare the background for the subsequent sections.

Sexual polymorphism

Nearly all flowers in Indo-Pacific Ebenaceae are unmistakably male or female. What appear to be hermaphrodite flowers occur only sporadically.

The male flower and male inflorescence.

Male flowers bear stamens, but instead of pistils, they have pistillodes consisting usually of small lumps of tissue lacking ovules and styles. In some species, even such pistillodes are suppressed, leaving only an empty space in the centre of the flower (e.g. D. maingayi). The stamens are variously arranged; D. lotus is representative of most species : here the stamens occur in two whorls; the members of the outer whorl are twice as numerous as the corolla lobes and occupy positions both opposite and alternate to them; the members of the inner whorl are shorter but as numerous as those of the outer whorl and are opposite them. The stamens therefore occur in radial pairs. The filaments of such pairs are adnate to each other and the outer one is also basally adnate to the corolla. Minor departures from the D. lotus condition involve (i) variation in numbers of stamens in either or both whorls, associated with (ii) irregularities in adnation. With the symmetry of the staminal whorls upset by loss or addition of stamens, the various members may occur as singles, pairs, triads, etc., the adnation of filament-bases depending on how close they arise to each other. It must be emphasized that although some species are more constant than others, the number and precise arrangement of stamens tends to vary a little from flower to flower.

Major departures from the D. lotus condition are represented

(fig. 1.1) by D. latisepala with only one whorl of stamens, (b) D. toposioides with stamens proliferated (up to 100) to fill up the whole of the receptacle area enclosed by the corolla (c) D. maingayi with all filaments fused into a cylinder and (d) D. clavigera with only the inner whorl of filaments fused into a cylinder but the outer stamens free (except perhaps basally) and distinctly shorter.

Male flowers are typically borne on exclusively male inflorescences of three or more flowers. The inflorescences are determinate and bracteate. The terminal flower is developmentally more advanced than those immediately behind, hence a three-flowered inflorescence appears as a typical dichasium. Very rarly, the male flower is solitary and terminates a bracteate stalk. The latter situation may be interpreted as having arisen by suppression of lateral flower-buds. A more comprehensive discussion of inflorescences is reserved for Part II later.

The female flower and the female inflorescence.

Female flowers have fully-formed pistils with swollen syncarpous ovaries and two or more free or basally-united to fully-united styles. Stamens are reduced to a single whorl of epipetalous staminodes. In structure, such staminodes range from small triangular flat lobes bearing little resemblance to stamens, to stamen-like structures which however, do not produce viable pollen. Rarely, even staminodes are absent (D. buxifolia, D. confusa, D. ferrea and D. kajangensis).

Female flowers are typically borne on exclusively female inflorescences. Usually, such inflorescences are fewer-flowered than the corresponding male. Reduction to a single terminal flower on a short bracteate peduncle is of very common occurrence.

Sexual differentiation also extends to the corolla and calyx. In Indo-Pacific species, female flowers are always larger than male flowers. This is correlated with the fact that the female inflorescences are fewer-flowered. The size difference can be resolved into three components. Firstly the female flower has a larger receptacle area, to accomodate the swollen sessile ovary. Secondly the corolla tube is wider. Thirdly, the calyx is larger, often very much so. The enlargement of the corolla and calyx is a consequence of the larger receptacle area, but not entirely. The female calyx, especially, is often greatly exaggerated in size. It is persistent in fruit and we may deduce that it has a role to play in protection or dispersal of the fruit. In some species there are also pronounced differences in structure between male and female calyces. One of the most extreme examples occur in D. toposioides, in which the female calyx has prominent spreading lobes whereas the male calyx is an unlobed globular bag which at antheasis, is forcibly split open by the expansion of the corolla and stamens contained within.

Notwithstanding the differences in male and female flowers, it is not difficult to put the corresponding male and female specimens together in herbarium studies, because the leaves show no sexual dimorphism and are generally distinct enough between species, to be used in identification.

The hermaphrodite flower.

In a family like Ebenaceae in which unisexuality of flowers is the general rule, the occurrence of hermaphrodites generates a considerable amount of interest. Hiern (1873) was sufficiently impressed to distinguish Royena from other genera on the grounds "hermaphrodite or rarely sub-dioecious" versus "dioecious or rarely polygamous", following the lead of A. de Candolle (1844).

The first person to dissent from this view was Wright (1904), who in an intensive study of the genus Diospyros in Ceylon, found that in addition to male and female flowers, hermaphrodite flowers were also produced by eight species out of the twenty he examined. Describing one of them, D. sylvatica, in detail, he wrote that such hermaphrodite flowers bore stamens and pistils, the latter developing into fruits possessing "seeds which in the characters of the testa and embryo exactly agree with those from known female trees." Also, "the whole of the anatomy and development of seedlings of D. sylvatica ..... was first worked out from seeds obtained from a tree which has for many years been labelled as a 'male' and from which material for sketching 'male' inflorescences has been derived".

There are two points in Wright's observations that are of interest. Firstly, hermaphrodite flowers do occur in Diospyros. This is of taxonomic significance and was the first step in the gradual erosion of Royena as a valid genus. The second point is that hermaphrodite flowers are associated with male flowers! Wright did not make this point. He distinguished between hermaphroditism "due to replacement of a staminode by a stamen, as in D. embryopteris, and that due to the pistil of a male flower exerting its potentiality, as in D. affinis, D. sylvatica and D. gardneri". However, the example of D. embryopteris was quoted from Hiern. What Hiern actually wrote of female flowers of D. embryopteris was "staminodes 1 - 12, hairy (sometimes perhaps perfect stamens)". It is clear that Hiern was unsure about the perfect stamens and nobody has been able to substantiate it since. I think Wright was convinced that hermaphroditism can develop both ways, from males and from females. Yet all his own observations indicate that it develops from the males only. On p. 81, he wrote "polygamous trees have flowers arranged as in a male cyme and among them three type of flowers can be distinguished",

These were (i) hermaphrodite flowers with stamens and pistils, the latter developing into fruits bearing seeds (ii) flowers in which there are stamens and pistils but the pistils never yield good fruits (iii) flowers which are indistinguishable from the male. "It is therefore clear that in the polygamous trees we can obtain every stage from purely staminate to hermaphrodite flowers".

There is no comparable evidence to link hermaphrodite flowers to purely female flowers.

On the other hand, there is supporting evidence from elsewhere that hermaphrodite flowers are associated with males. In 1911, Hague made a study of Diospyros virginiana and wrote that the trees are normally dioecious but "near Auburn (Indiana) there is a cluster of staminate trees.....that are reported to have borne fruit occasionally."

The best evidence is from work done on D. kaki in Japan, where the species is an important fruit tree. Because of the obvious commercial implications, sexual differences in D. kaki have been carefully studied. Yasui (1915) found that where hermaphrodite flowers occur, they occupy the terminal position of an otherwise male cluster. Such flowers produce fruits smaller than those of the female flower and are usually (but not invariably) seedless.

Namikawa et al. (1932), followed up with a very thorough study paying particular attention to pistillodes and staminodes. Describing the male flowers first, they showed that pistillode size ranged smoothly from entirely stunted to very well-developed. The well-developed ones would under certain favourable conditions develop into a fruit smaller in size than a normal fruit.

sometimes bearing seeds which would be smaller in size than normal seeds. Of the female flowers, they found that though pollen may be produced in the staminodes, such pollen was not released at anthesis because the anther sacs failed to dehisce. They took out the pollen artificially and attempted to germinate them on agar with sucrose, but the grains all failed to germinate. Namikawa et al. concluded that hermaphrodite flowers are derived from those staminate flowers that have large pistillodes. Such flowers are usually those that occupy the terminal positions on the male inflorescences.

All the evidence so far available supports the hypothesis that the terminal male flower in Diospyros sporadically, under conditions at present not understood, develops an enhanced pistillode which may grow into a fruit with or without formation of seeds. The evolutionary significance is that hermaphroditism in Diospyros, as exhibited by the present-day species, is secondarily acquired rather than primitive, at least where the Indo-Pacific species are concerned.

In Africa, some further work has been done on Royena which show, ironically, that the flowers are not hermaphrodite as Hiern had thought. Salter (1953), when collecting seeds of Royena glabra, noticed that only a small proportion of the bushes bore fertile fruit. Further study showed the plant to be dioecious : the female flowers having stamens reduced to staminodes devoid of pollen; but the male flowers having ovaries indistinguishable from those of the female flowers except that they are incapable of producing fruit. Hence the structurally hermaphrodite flowers are functionally male.

White & Barnes (1958) followed up with a study of five species of Royena and found three kinds of flowers : male,

female and structurally hermaphrodite. The structurally hermaphrodite flowers have pollen in their anthers and ovules in their ovaries but the ovaries are smaller than those of typically female flowers. This suggests that such hermaphrodites may in fact function only as males. White & Barnes pointed out that this matter can only be settled by study of the living plant, and with this I concur. In the rest of this account, hermaphroditism is taken in the morphological sense, without any functional implications.

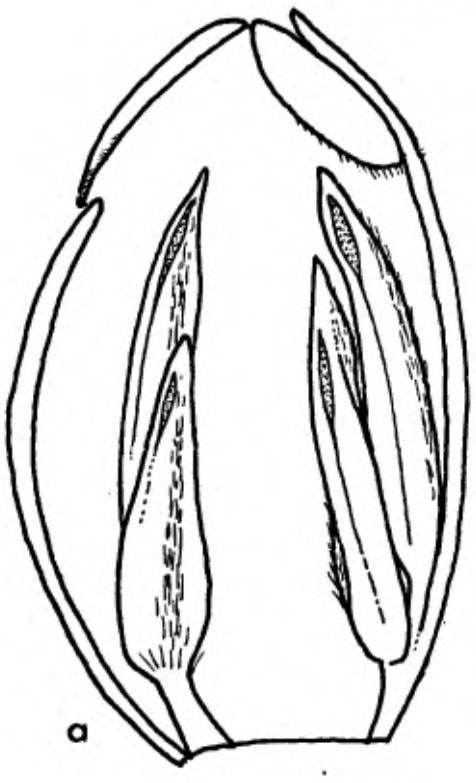
Sex expression in the individual (whole plant) and the species.

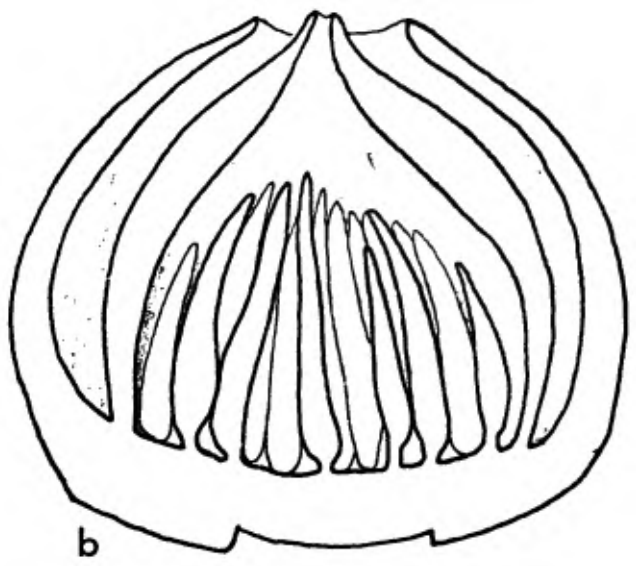
The majority of species in Ebenaceae are believed to be dioecious i.e. the individual plants are wholly male or wholly female. But in the light of Wright's observations on Ceylonese species and those of Yasui and Namikawa et al. on D. kaki, we must accept that male trees may sporadically produce hermaphrodite flowers, hence dioecious species may be sporadically polygamous.

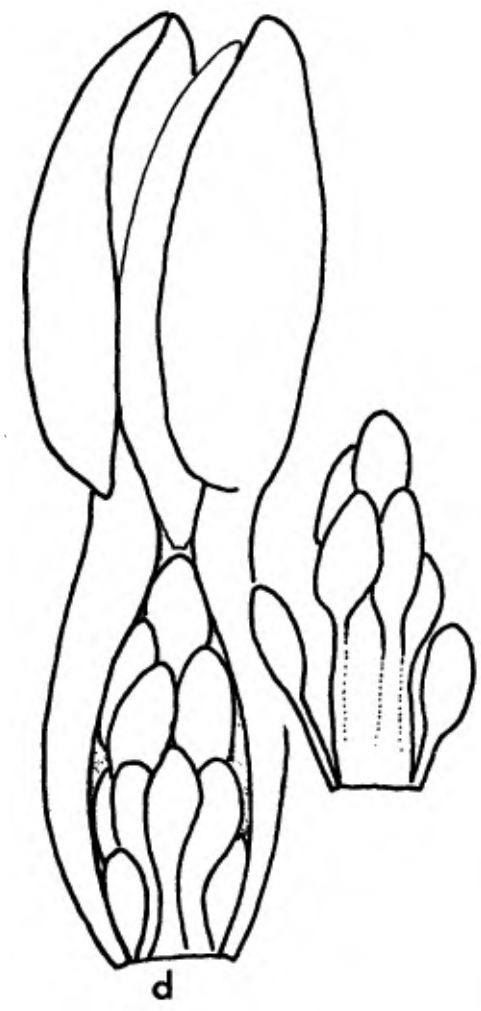
Monoecism is thought to be rare in Ebenaceae, but its frequency is probably underestimated in herbarium studies. If male and female flowers appear on different parts of a tree, it is unlikely that they will appear together on the same herbarium sheet. The same applies if male and female flowers appear at different times, or alternate years, as can happen in D. kaki (fide Yasui l.c.). Wright (l.c.) has observed that flowers of both sexes can occur on the same tree in D. oppositifolia, D. acuta, D. hirsuta, D. thwaitesii and D. ebenum. I have seen them together on herbarium sheets of D. kajangensis, D. evena, D. maingayi and D. rostrata. These species are therefore monoecious, at least sometimes.

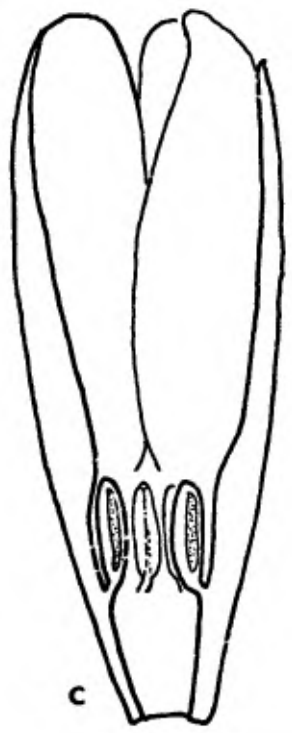
But the real extent of monoecism and dioecism is so

difficult to assess at this stage that in my opinion, sex expression at the level of the individual and the species is best avoided in the classification of the Ebenaceae.









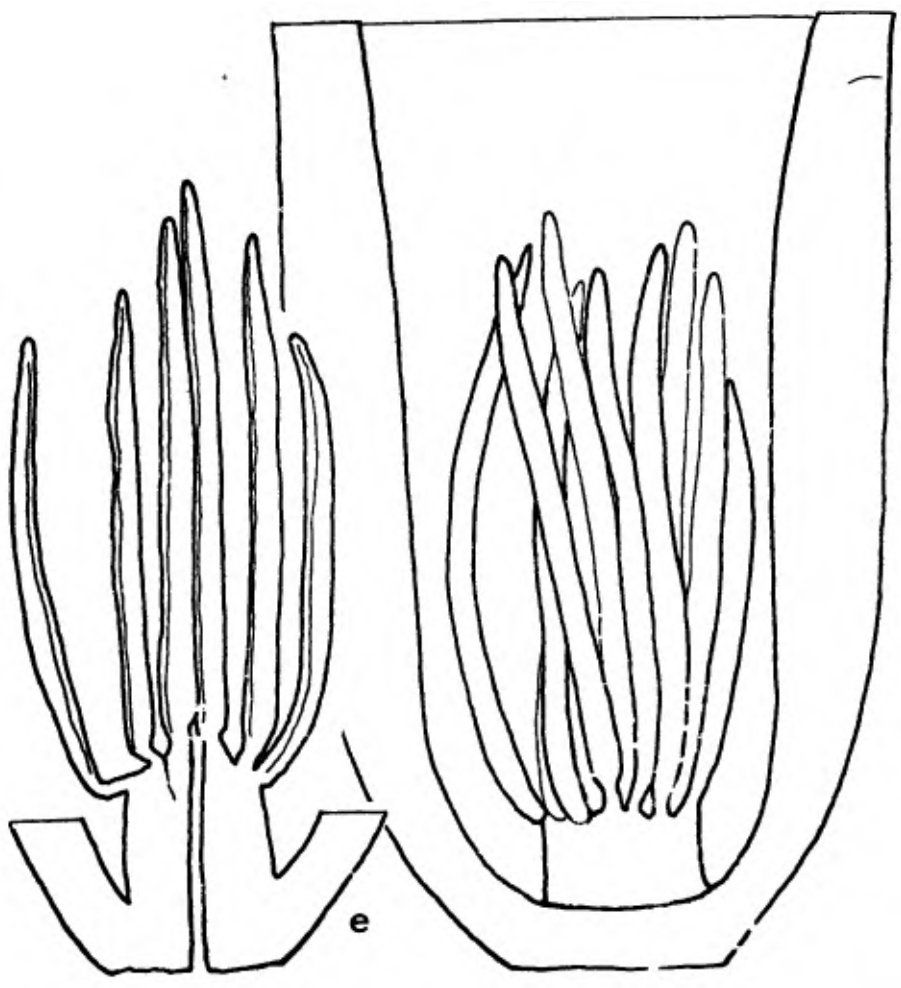


Fig.1.1. Stamens 10x. (a) D. lotus paired (b) D. toposioides massed on receptacle (c) D. latisepala in one epipetalous whorl (d) D. clavigera with filaments of inner whorl fused into a cylinder (e) D. maingayi with all filaments fused into a cylinder.

The gynoecium, fruit and seed

Of the major organs of the Ebenaceae, the gynoecium has probably been the most unsatisfactorily described in the taxonomic literature. Hiern (1873) gathered most of the facts together, but was unable to present them in any simple coherent scheme.

His account of the structure of the ovary is as follows "ovary.....syncarpous.....2 - 16-celled, usually 3- or 6-celled in the genus Maba, 4-celled in Euclea, 4-, 6-, 8-, or 10-celled in Royena, and 4-, 8-, or 10-celled in Diospyros, never with 5 or an odd number of cells except 3; cells 1-ovuled, or 2-ovuled in the section Ferreola of Maba and in the section Cargillia of Diospyros; the septa however are sometimes incomplete, especially in the lower part, and the alternate ones, namely, those opposite the styles or lobes of the style, are often thinner. Styles 1 - 5, distinct or connate at the base....." From this account, it appears that there is no correlation between the number of styles and number of locules in the ovary, and a confused relationship between the number of locules and the various genera and sections mentioned. Other intriguing questions are why do Diospyros and Royena have cells in an even-number series and why 3 is the only odd-number of cells encountered in the family. Also, what is the nature of the septa which are sometimes incomplete and sometimes alternately thick and thin? Finally, what is the relationship between the uni-ovulate and the bi-ovulate locule?

To answer these questions, transverse sections of ovaries were made of about 80 Indo-Pacific species representing most of the sub-genera and sections in Bakhuizen's classification. Such sections were made at various levels of the ovary. In addition, material of six species was embedded in paraffin wax and serial-

sectioned at 5 - 20μ. In all cases, they confirm observations made from rough sections on herbarium material. The results show that the Ebenaceous gynoecium can be explained according to a simple and constant plan. I have checked this against the literature for species outside the Indo-Pacific region , and against dissections of African species kindly made available by White and Caveney.

The ovary is always multilocular and bears, at the apex, two or more free or basally connate styles. Rarely, the styles are completely connate so as to appear as a single simple structure but then the number of stigmatic lobes at the apex indicates the number of styles that have been united. Internally, the ovary is divided into locules each of which may contain one or two ovules. The ovules are suspended from the top of the locules (Fig. 1.2).

Interpretation of the bi-ovulate locule. The bi-ovulate locule is a rare condition but it provides the key to an understanding of the Ebenaceous gynoecium. Only 11 species exhibit this condition out of 190 treated in Bakhuizen's revision. They are accommodated in 3 out of the 5 sub-genera thus :-

Subgenus Maba, Section Ferreola : D. ferrea
D. ellipticifolia
Section Cupulifera : D. cupulosa
D. parviflora
D. foliosa
Subgenus Cargillia : D. australis
D. pentamera
Subgenus Hierniodendron : D. puncticulosa
D. evena
D. maingayi
(Position uncertain) : D. mabacea

In the subgenera Cargillia and Hierniodendron, the bi-ovulate locule is a constant character for all species. The contrasting uni-ovulate condition occurs in part of Maba and all species of

the sub-genera Eudiospyros and Mabacea.

Considered together, the 11 bi-ovulate species have 2-, 3- and 4-locular ovaries. The number of locules is equal to the number of free styles, or style branches, or stigmatic lobes. The septa (fig. 1.3) are axially fused in the basal part of the ovary but higher up, they are free. At or just above the level of fusion, each septum bears a bilobed placenta, each lobe of which gives rise to an ovule. It follows that the total number of ovules in the ovary must always be an even number.

The bi-ovulate condition therefore is quite conventional and easy to interpret in terms of the carpel theory. The number of locules, septa, stylar units and placentas are equal to each other, hence each stylar unit, with its corresponding locule may be taken to be a carpel, and the septa to represent carpellary walls fused in pairs (fig. 1.6).

Interpretation of the uni-ovulate locule. The uni-ovulate condition presents a number of meristic peculiarities. The total number of uni-ovulate locules (and septa) in such an ovary is always an even number, 4, 6, 8, 10, 12, 14, 16. It follows that the total number of ovules must also be an even number. The number of styles, or style branches, or stigmatic surfaces is half the number of locules.

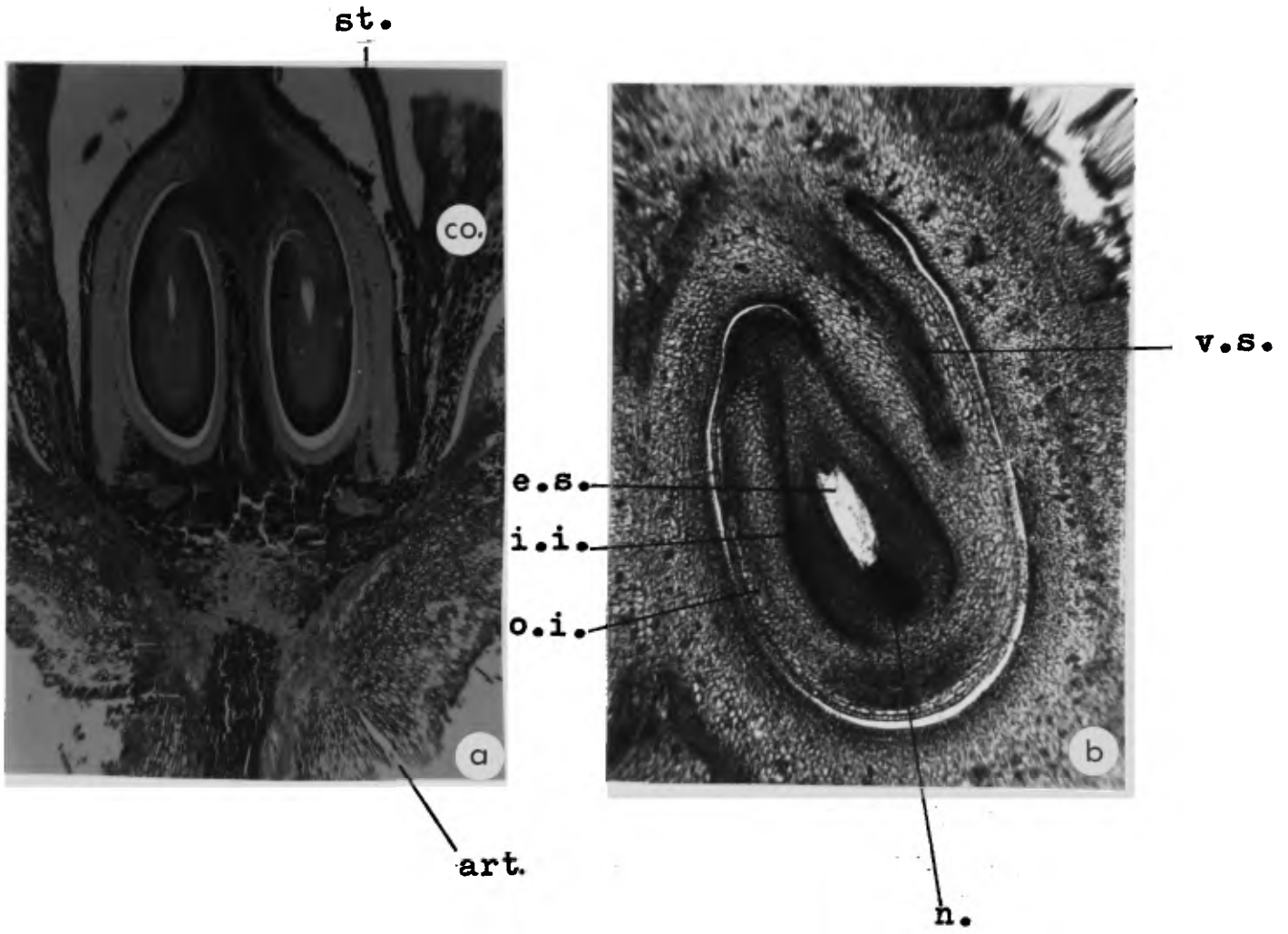
Transverse serial sections (fig. 1.4) reveal that all septa meet and fuse axially in the basal part of the ovary but are free in the upper part. The placentas are visible at or just above the level of fusion of the septa, but are borne on alternate septa only. Comparing the placenta-bearing septa with the septa in the bi-ovulate condition, it is evident from their structure as well as positional relationship to the styles, that they are completely homologous. I refer to them as "primary" or

"true" septa representing in theory the fused walls of the carpels. The septa which do not bear placentas may be thought of as "secondary" or "false" septa that have developed as mid-carpellary partitions between the ovules. Each uni-ovulate locule therefore represents a "half-carpel". The hypothetical relationship between the uni-ovulate and bi-ovulate conditions is illustrated in fig.1.6.

If serial sections of the uni-ovulate ovaries are viewed from apex to base, one sees the free true septa first. At a lower level, the true septa are swollen as placentas, and the false septa become evident as small protrusions from the wall between the placentas. Somewhat lower, the true septa fuse in the middle. The false septa also fuse in the middle, either at the same level as the true septa or slightly below. This sequence, as viewed from apex to base of the mature ovary, is the same sequence in which the septa have been observed to develop ontogenetically. I did not make any ontogenetic observations myself, owing to lack of a good series of buds, but such a study has been published by Yasui (1915) on Diospyros kaki with 8 locules and 4 styles. She wrote : "In the development of the pistil there appear at first four large protrusions, and then four smaller ones between them. The larger ones give rise to two small papillae, which are the initials of ovules..... the small protrusions develop toward the centre of the ovary, resulting, along with the development of larger protrusions, in 8 loculi for the 8 ovules." The large and small protrusions are true and false septa respectively and the papillae are placentas. Since Yasui's study was on a single species, non-comparative and non-taxonomic in scope, the wider significance of this observation was lost.

In Bakhuizen's revision, species descriptions such as "ovary 8 - 12-locular, locules uni-ovulate" should be amended

to read "ovary 8-, 10- or 12-locular, locules uni-ovulate" because an odd number of uni-ovulate locules cannot occur except in rare mis-formed ovaries. Statements such as "ovary 4 - 5-locular, locules uni-ovulate" (e.g. D. gauliflora) are incorrect and must be amended to read "ovary 4- or 6-locular, locules uni-ovulate". Similar amendments must be made in Bakhuizen's conspectus to sub-genera where, for example, Nabg is described as having ovaries with 3 - 6 locules, locules 1 - 2 ovulate. A more correct description would be "ovary 3-locular bi-ovulate or 6-locular uni-ovulate" or, in more concise though abstract terms "ovary 3-carpellate".



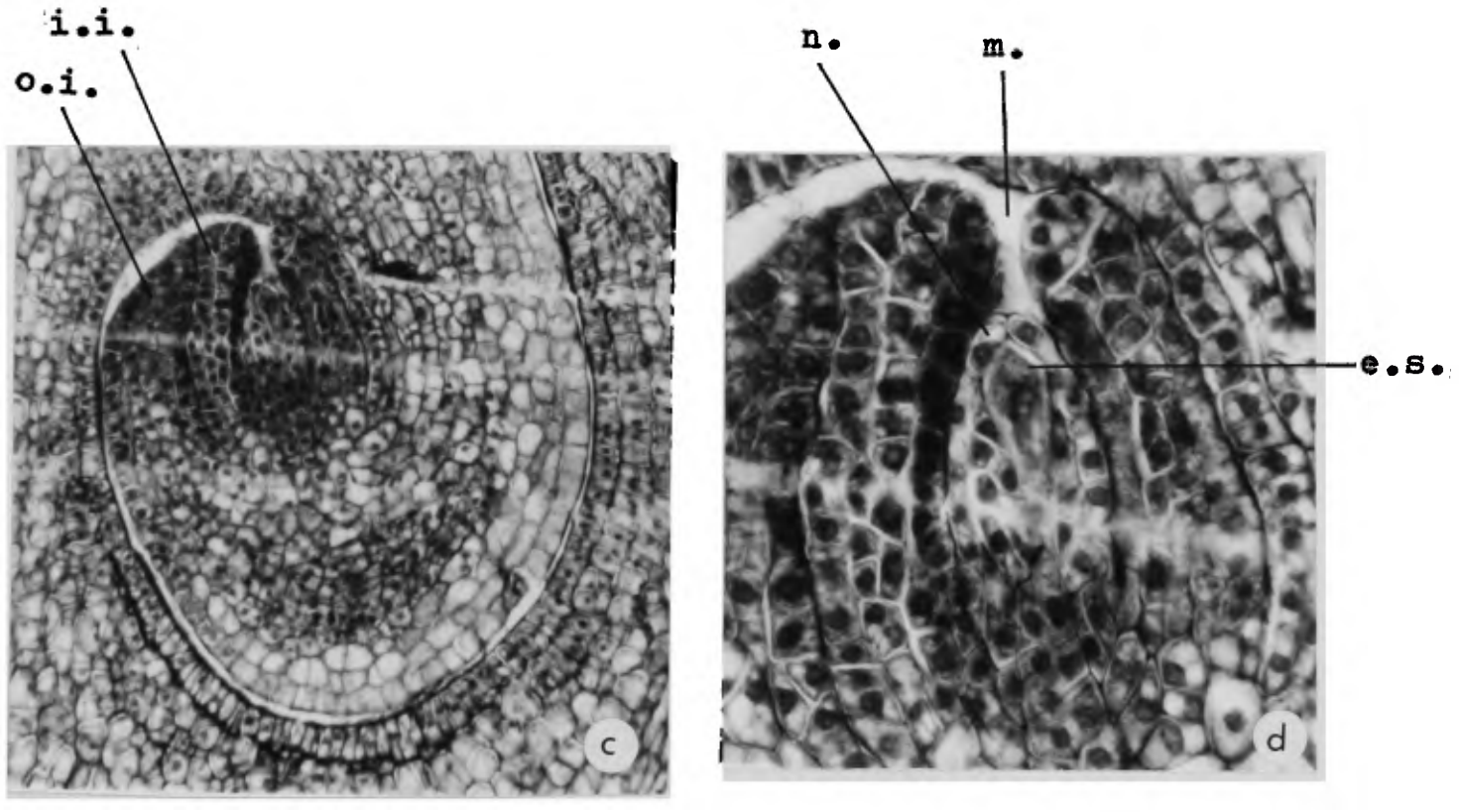


Fig. 1.2. Ovules in longitudinal section: (a) D. sumatrana 20x, showing two penduleous ovules within the ovary; (b) D. cauliflora 50x, showing one ovule; (c) & (d) D. confertiflora 150x and 375x respectively showing a very young ovule with nucellus.

art: articulation; co: corella; e.s: embrye sac; i.i: inner integument; m: micropyle; n: nucellus; o.i: outer integument; st: staminode; v.s: vascular strand.

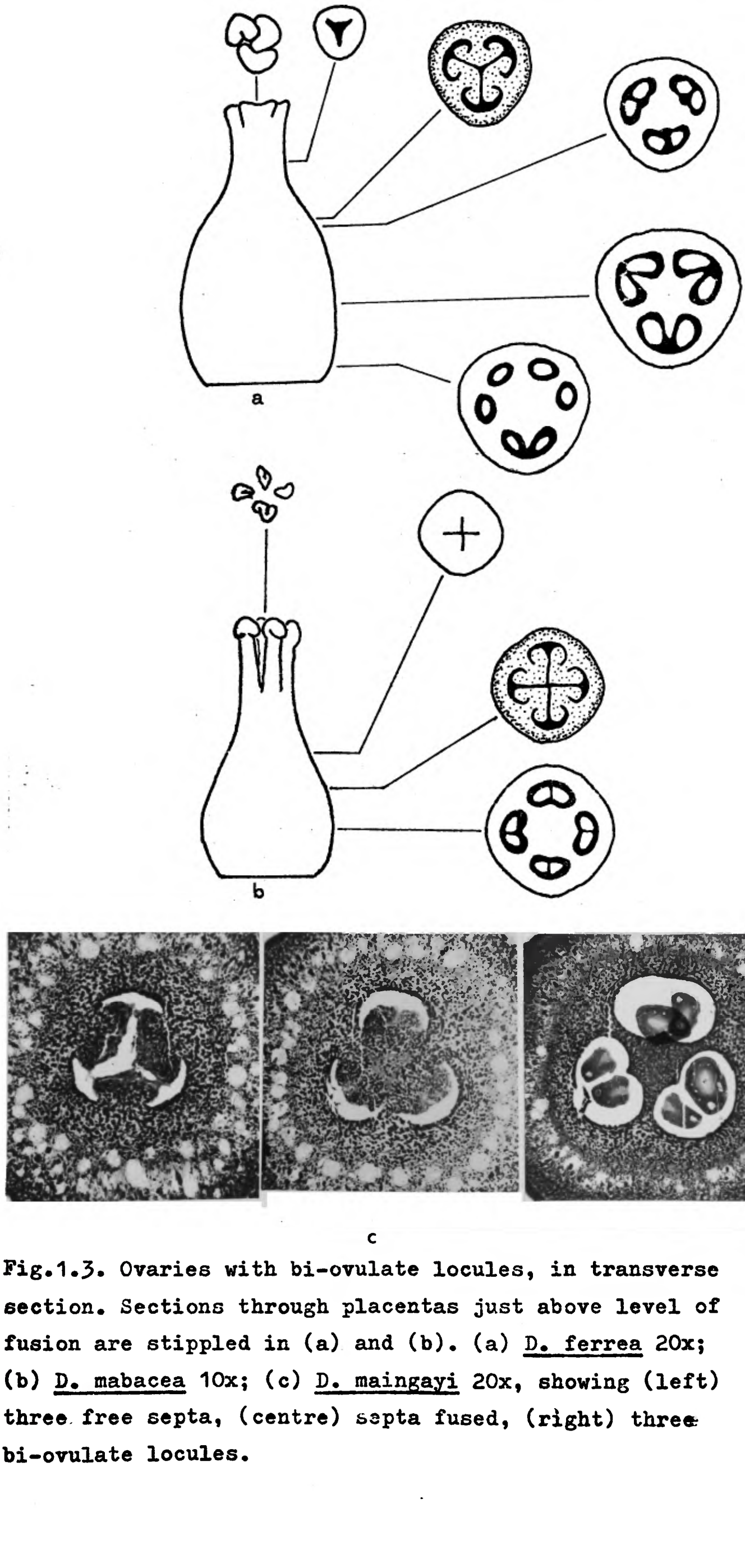


Fig.1.3. Ovaries with bi-ovulate locules, in transverse section. Sections through placentas just above level of fusion are stippled in (a) and (b). (a) D. ferrea 20x; (b) D. mabacea 10x; (c) D. maingayi 20x, showing (left) three free septa, (centre) septa fused, (right) three bi-ovulate locules.

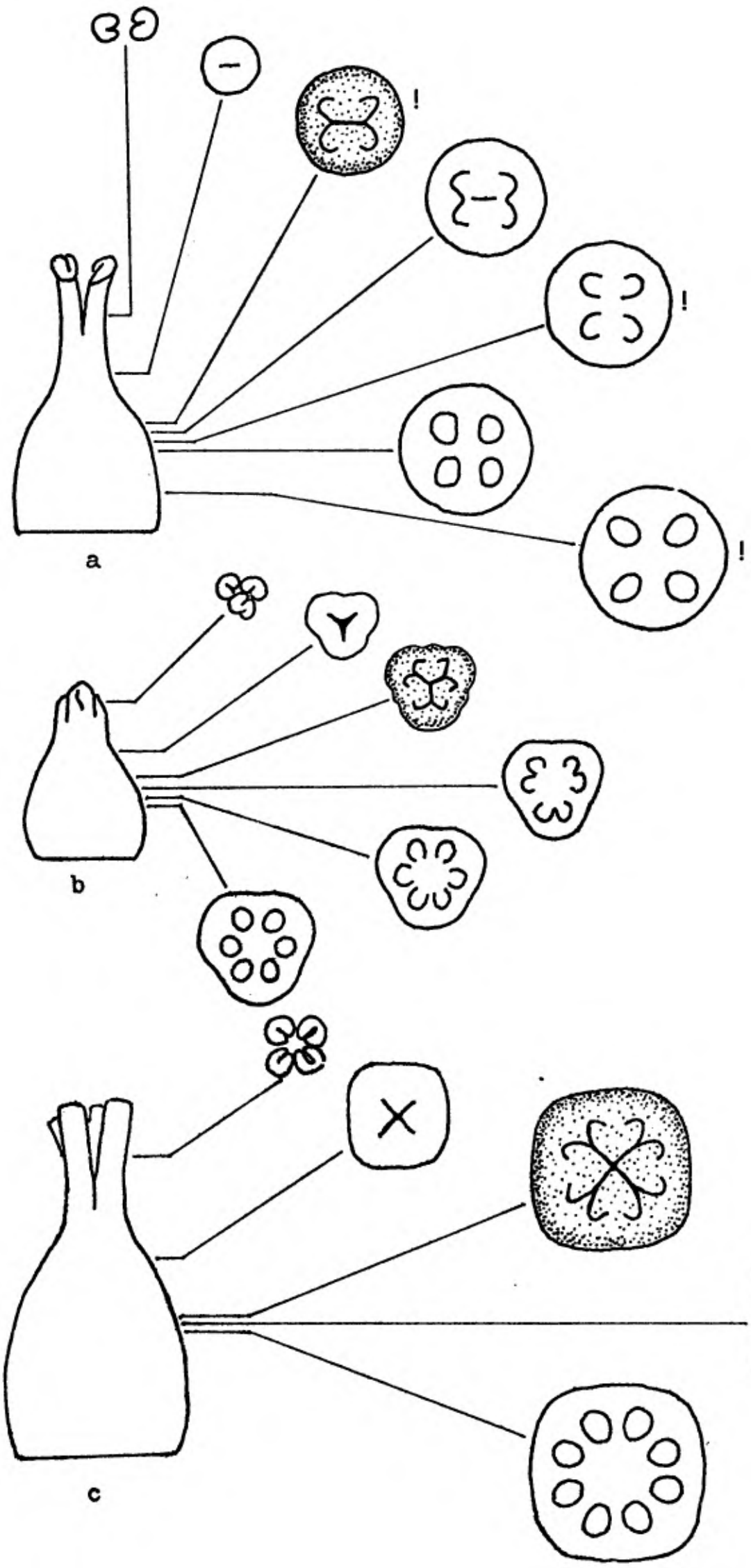
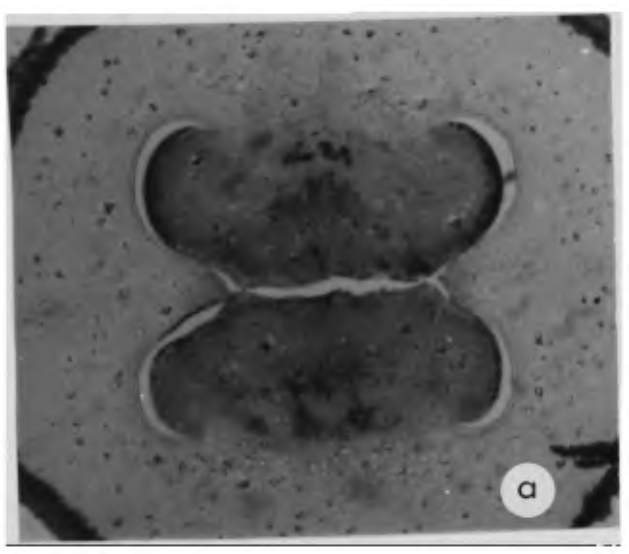
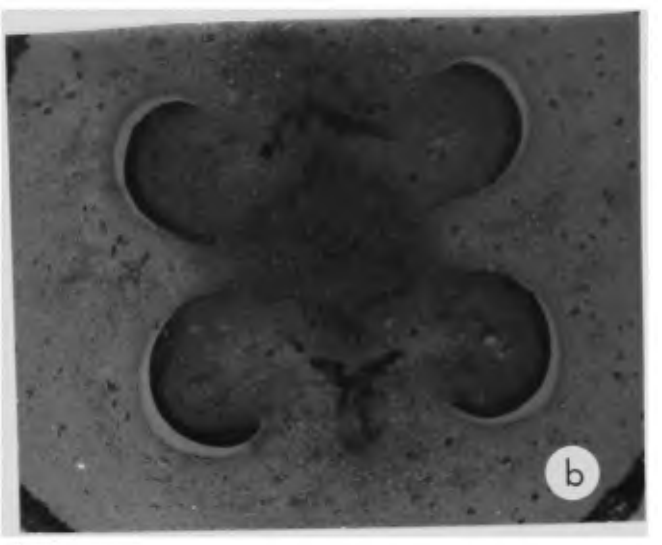
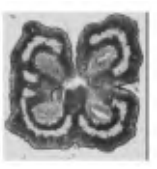


Fig. 1.4. Ovaries with uni-ovulate locules: (a) D. sumatrana; (b) D. confertiflora; (c) D. wallichii. All at 10x. Sections through placentas just above level of fusion, are stippled.







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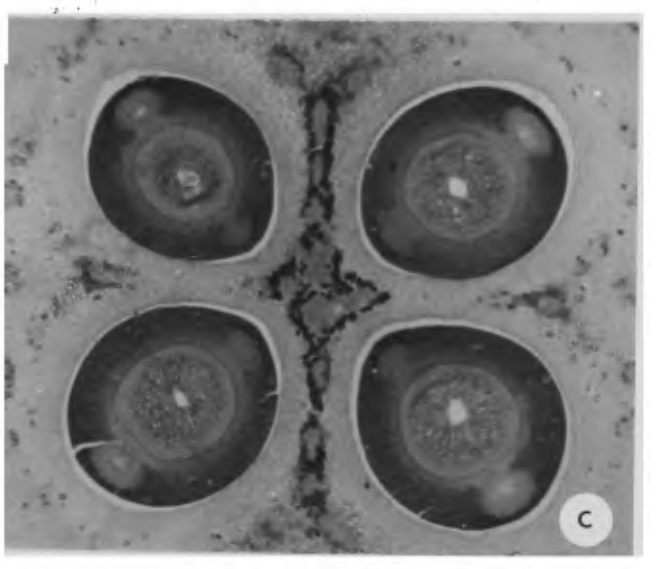


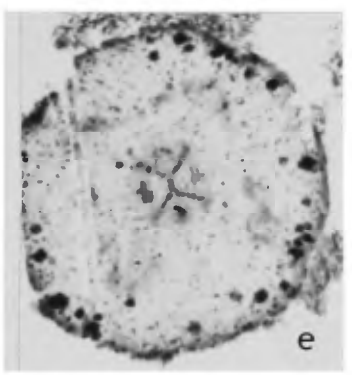


Fig. 1.5. Ovaries with uni-ovulate locules, in transverse section at various levels: (a) - (c) D. sumatrana, 50x, corresponding to the sections marked '1' in fig. 1.4a; (d) - (h) D. wallichii, 20x, corresponding to the sections in fig. 1.4c.

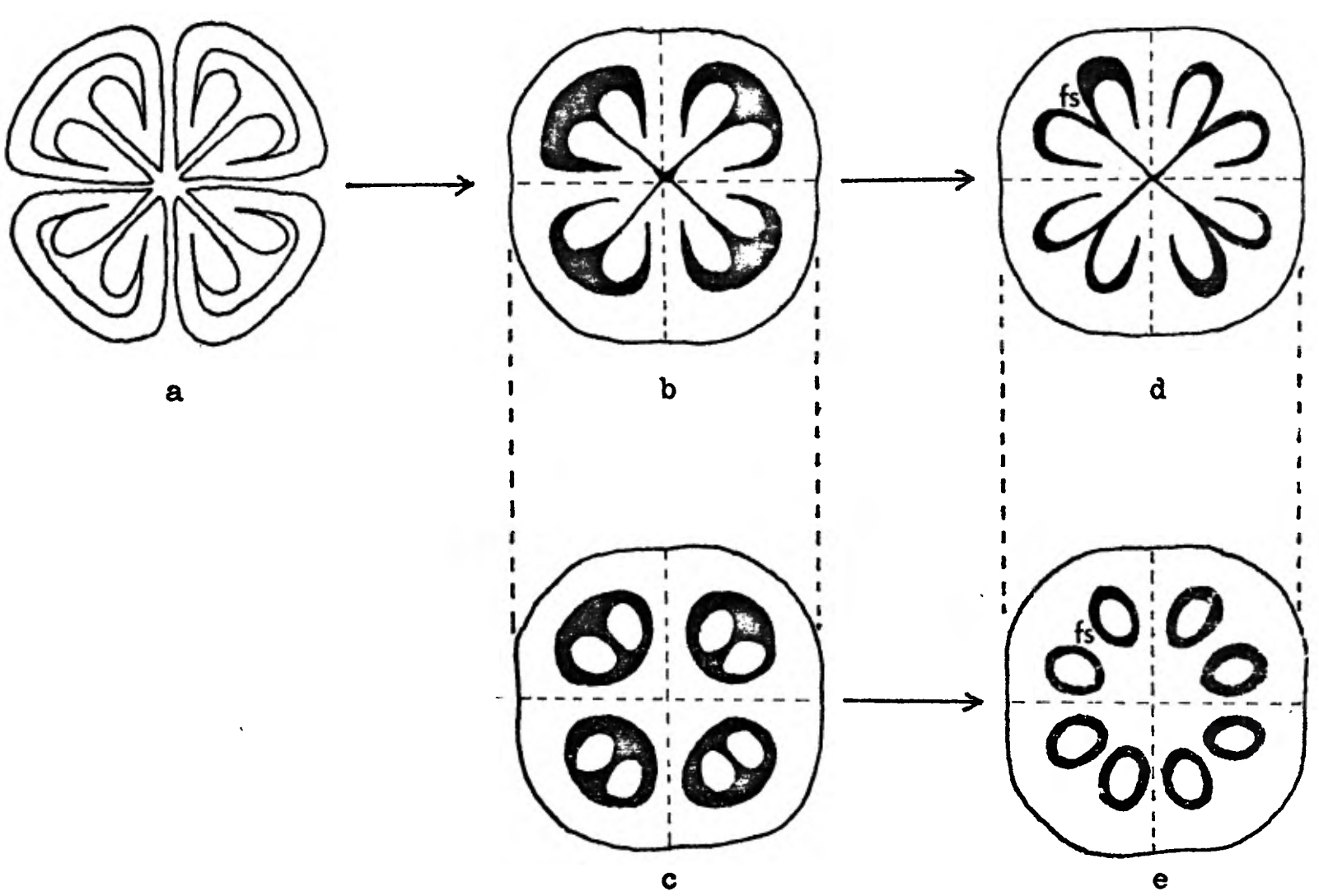


Fig.1.6. Hypothetical relationship between bi-ovulate and uni-ovulate conditions. (a)hypothetical carpels. (b) & (c) bi-ovulate condition as seen in some Ebenaceae. (d) & (e) uni-ovulate condition as seen in most Ebenaceae. (b) & (d):sections through placentas; (c) & (e):sections below level of placentas. fs: false septum.

Variations in carpel merism

In any given flower of Diospyros, the number of parts of the calyx is generally equal to the number of parts of the corolla. Exceptions are not difficult to find, e.g. K3C4, K5C4, K4C5, in which there is a slight difference between the two whorls. Nevertheless, after making hundreds of dissections, I am convinced that equal correspondence of parts between calyx and corolla is the general rule. My conclusion is the same as that reached by Hiern (1873) in his world monograph of the family and Wright (1904) in his study of Ceylonese species.

An attempt was made to see if there is a numerical relationship between the number of locules (of the ovary) and the number of calyx (or corolla) parts. This attempt was based on the assumption that if a floral meristem has produced two successive whorls (calyx and corolla) of symmetrical and equal parts, it may be expected to continue behaving in a predictable manner in the production of subsequent whorls. This assumption is seldom borne out among Dicotyledonous families as an examination of any flora quickly reveals, but as a hypothesis postulating stability of behaviour, it is a convenient starting point for attempting to understand the relationship between floral whorls. In fact it quickly became apparent that there is no simple relationship between the number of locules and number of calyx parts. It was only after solving the problem of the carpel that a simple relationship became apparent (tables 1.1 & 1.2) not between locules and calyx parts but between carpels and calyx parts, locules and carpels not necessarily being equal in Ebenaceae, as has been demonstrated in the first part of this section.

48 of the 76 species (table 1.3) examined had the floral

formula KxCxGx. Stamens, being reduced to vestigial epipetalous staminodes in pistillate flowers, were not considered. This formula summarises the series 1 in table 1.2.

Series 2, represented by 20 species, is seen as a reduction by half in the carpellary whorl. The two series parallel each other; for example, corresponding to K4G4 and K6G6 of series 1, we have K4G2 and K6G3 respectively of series 2. Corresponding to K5G5, we have K5G2 and K5G3 because there cannot be G2½ (half-carpels do not exist). Similarly, corresponding to K3G3, we should expect K3G1 and K3G2, but I have not seen the former condition which involves extreme reduction to a single carpel.

Of the remaining 8 species, two, D. pendula and D. retrofracta, show both reduced and unreduced states, possibly even on the same plant. The other 6 species viz. D. maingayi, D. evena, D. puncticulosa, D. ebreticides, D. nutans and D. diepenhorstii are irregular.

Although based, inevitably, on small samples, due to scarcity of material this analysis suggests that the majority of species fall into two main series only, one with carpels equal in number to calyx and corolla, and the other with carpels reduced to half. These two series represent two evolutionary grades, the first being the primary grade, and the second being derived from the first, probably independently many times. The two species D. pendula and D. retrotracta may be considered to be in a state of transition.

The character gynoecium reduced or not was in fact found experimentally to correlate very poorly with other characters (Table 3.1, character 9).

Table 1.1 : Range of combinations of floral parts as observed in most species of Diospyros (exceptions : D. nutans, D. diepenhorstii, D. ebreticides, D. maingayi, D. evena and D. puncticulosa).

No. of K or C lobes	No. of locules	bi-ovulate	uni-ovulate	No. of carpels
3	3	+		3
3	4		+	2
3	6		+	3
4	4	+		4
4	4		+	2
4	8		+	4
5	10		+	5
5	6		+	3
5	4		+	2
6	12		+	6
6	6		+	3

Table 1.2 : Rearrangement of combinations of table 1 in two series.

Series 1 G=K (or C)	Series 2 G=½K (or ½C)
K3G3	K3G2 (and K3G1 ?)
K4G4	K4G2
K5G5	K5G2 and K5G3
K6G6	K6G3

Table 1.3. List of species of Diospyros and their observed range in merism.(Numbers following the names refer to number of specimens examined.)

Series 1	K3G3	K4G4	K5G5	K6G6
1. adenophora 1		+		
2. areolata 2		+	+	
3. argentea 2		+		
4. aurea 2		+		
5. australis 1		+		
6. bibracteata 1		+		
7. borneensis 1			+	
8. carpinifolia 5	+			
9. castanea 10	+			
10. confertiflora 4	+			
11. discocalyx 1			+	
12. discolor 1		+		
13. ebenum 1		+		
14. elliptifolia 1		+		
15. ferrea 5	+			
16. foxworthyi 2		+		
17. hasseltii 3		+		
18. kaki 8		+		
19. lanceifolia 8	+	+	+	
20. levigata 1		+		
21. lolin 1		+		
22. lotus 10		+		
23. mabacea 1		+		
24. malabarica 2		+		
25. mollis 2		+		
26. montana 11		+		
27. novoguineensis 2		+	+	
28. papuana 4			+	
29. pauciflora 4		+	+	
30. perfida 2		+		
31. pilosanthera 12		+	+	+
32. piscicarpa 1		+		
33. pyrrhocarpa 3		+	+	
34. ridleyi 1		+		
35. rigida 2		+		
36. roxburghii 3		+		
37. siamang 1		+		
38. siamensis 2		+		
39. styraciformis 2		+		
40. subtruncata 1		+		
41. sylvatica 20	+	+		
42. tahanensis 2	+			
43. toposia 2	+	+		
44. transitoria 2		+		
45. truncata 2			+	
46. ulo 1		+		
47. variegata 1		+		
48. wallichii 7		+	+	

Series 2	K3G2	K4G2	K5G3	K5G2	K6G3
49. apiculata 3	+	+			
50. buxifolia 4		+		+	
51. cauliflora 8	+	+			
52. confusa 3		+			
53. dictyoneura 3				+	
				+	
54. elegantissima 1		+			
55. eriantha 1		+			
56. ferrugines-cens 2			+		
57. frutescens 3		+			
58. kajangensis 3		+			
59. kurzii 6		+			
60. latisepala 5		+	+		
61. packmanii 2			+		
62. penangiana 4		+		+	
63. pentamera 3			+		+
64. poncei 1		+			
65. rhodocalyx 2		+			
66. saxosa 1				+	
67. suluensis 4			+	+	
68. sumatrana 12		+		+	

69. pendula 4								+	
70. retrofracta 4								+	
71. maingayi 5					K4G3	K4G4			
72. evena 4				K4G2	K4G3	K4G4			
73. puncticulosa 1					K4G3				
74. ehretioides 3	K3G3	K4G2	K4G3						
75. nutans 7							K5G2	K5G3	K5G4	K6G4
76. diepenhorstii 8					K5G6	K5G7	K5G8	K6G6	K6G7	K7G7

The ovule

The following description of the ovule is based mainly on my study of pickled material of *D. cauliflora*, *D. sumatrana*, *D. nutans*, *D. wallichii* and *D. confertiflora*. It agrees in all essential details with the earlier observations on the ovules of *D. virginiana* by Hague (1911) and on *D. kaki* by Yasui (1915).

As earlier mentioned, the ovule (fig. 1.2a) is pendulous, suspended from the apical region of the ovary. It is ellipsoid, anatropous, bitegmic, tenui-nucellate. The vascular trace passes into and down the outer side of the outer integument and may (a) end in the chalaza, (b) continue past the chalaza up the inner (axial) side to terminate near the micropyle, or (c) branch several times over the sides of the ovule. In all cases the vascular tissue remains in the outer integument. The inner integument is totally devoid of vascular tissue, and through its apex runs the micropylar channel. The nucellus is represented by a single layer of cells surrounding the embryo-sac except at the chalazal end where it forms a small multicellular "stalk" of tissue (fig. 1.2d). At the time of fertilisation, the peripheral layer of nucellus has usually disintegrated leaving the embryo-sac sitting on the nucellar "stalk" but otherwise naked within the inner integument (fig. 1.2b).

After fertilisation, or sometimes even before, the inner integument disintegrates (fig. 1.7) except for its inner epidermis and a plug of tissue around the micropyle. The former persists as an endothelium and behaves hereafter as if it were the surface layer of the embryo-sac. The nucellar stalk also disintegrates. Within the embryo-sac, endosperm

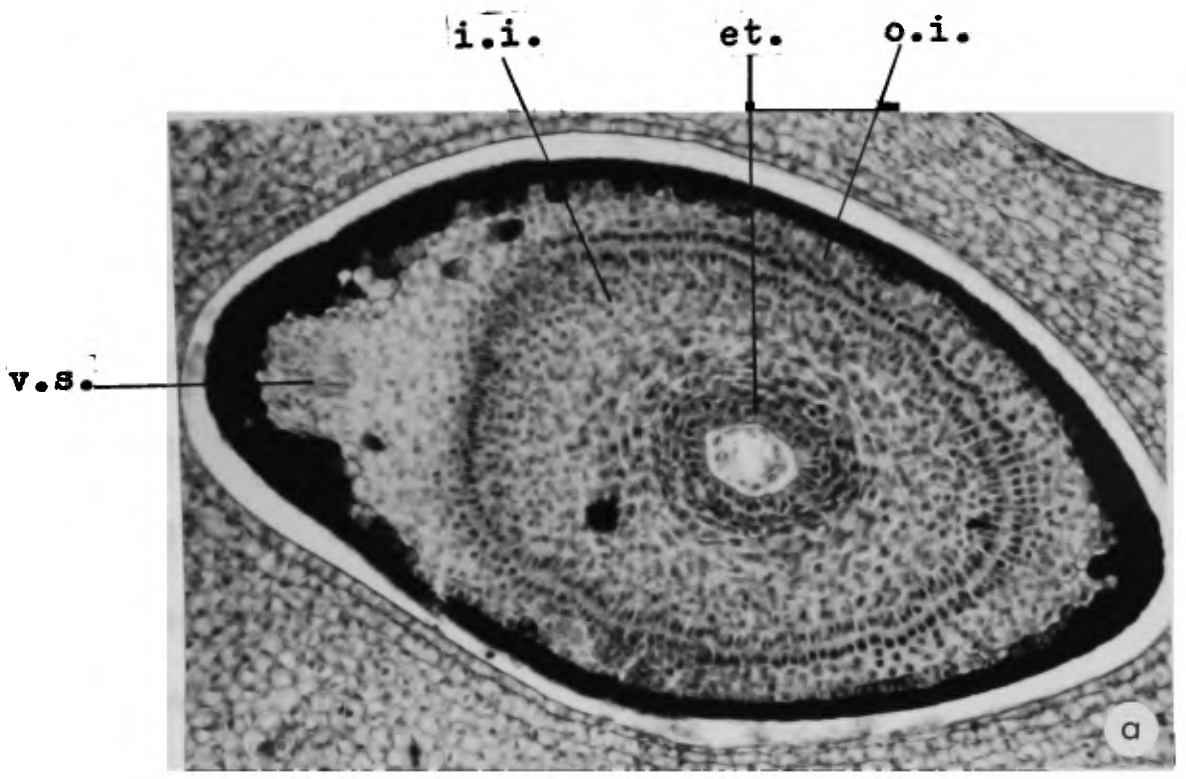


Fig. 1.7. Ovule to young seed. D. wallichii (a) ovule in transverse section, at anthesis, 150x; (b) young seed in transverse section, 50x; (c) young seed in longitudinal section through apical half, 20x. The inner integument disintegrates, leaving only the endothelium and a plug of tissue around the micropyle.

es: endosperm; et: endothelium; i.i: inner integument; m: micropyle; o.i: outer integument; v.s: vascular strand.

formation proceeds rapidly and, long before any embryo becomes visible, the sac is filled with large, very thin-walled endosperm cells, of gelatinous consistency. To get material at this stage properly fixed and embedded for sectioning it was found necessary to make a cut through the developing seed-coat to allow the chemicals to penetrate. The seed-coat consists of outer integument only. In those species where the vascular trace initially ends in the chalaza, further differentiation of vascular elements takes place to prolong the trace up the axial side to end near the micropyle.

The seed

The Ebenaceous seed consists of testa, endosperm and embryo. At the apical end, the hilum is represented by a small scar. Next to the hilum is the micropyle, which is inconspicuous except in section.

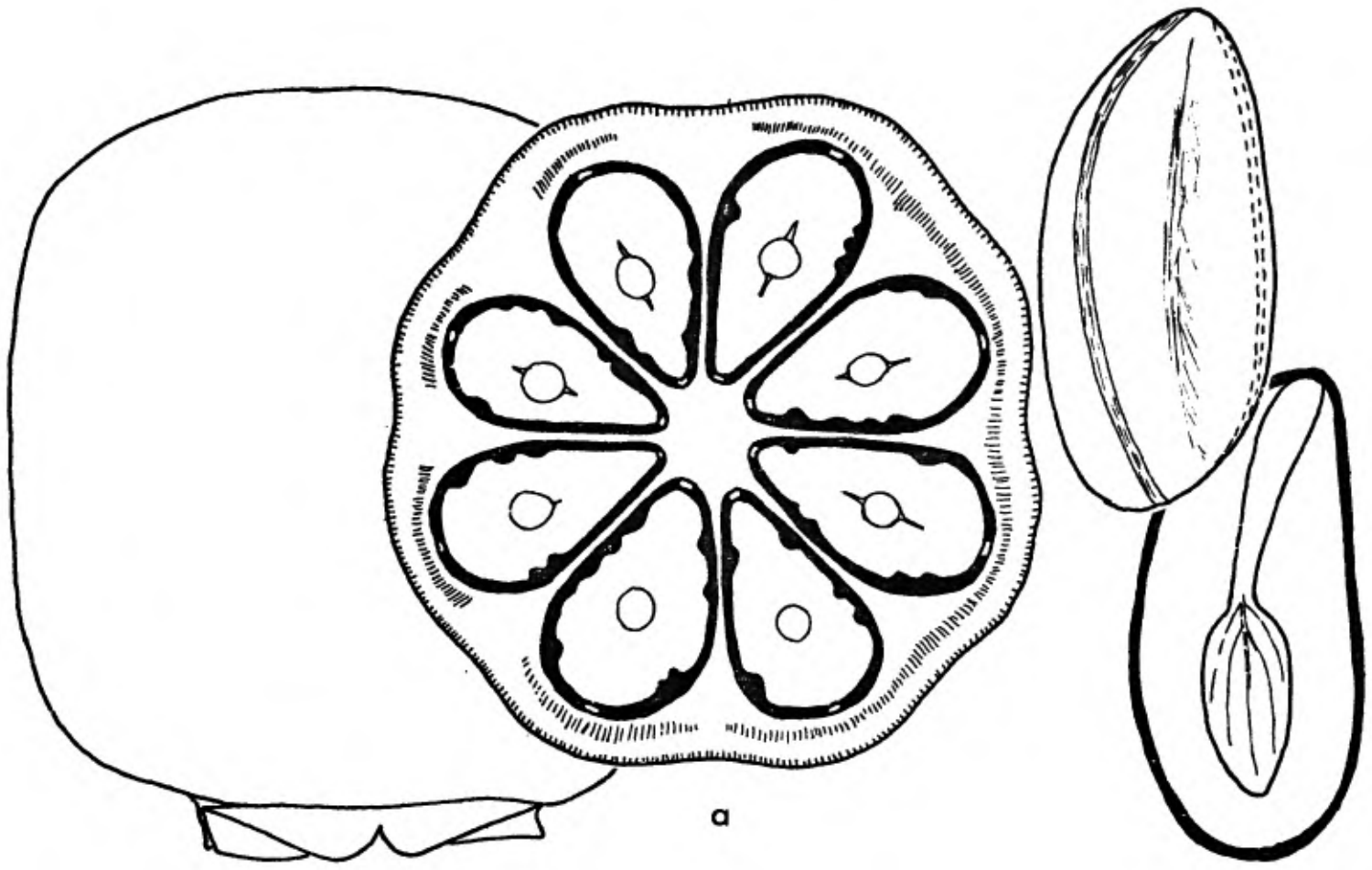
The testa is pigmented, thin, parenchymatous, relatively unhardened (membraneous to coriaceous), and vascularised. Its most notable feature is its structural simplicity. There is no internal mechanical tissue except vascular tissue, and no internal differentiation into histologically distinct layers. However, its epidermis is variable from species to species in shape, size and degree of cell-wall thickening. Fig.1.10 illustrates some of the variations, selected from the material (Appendix II) examined.

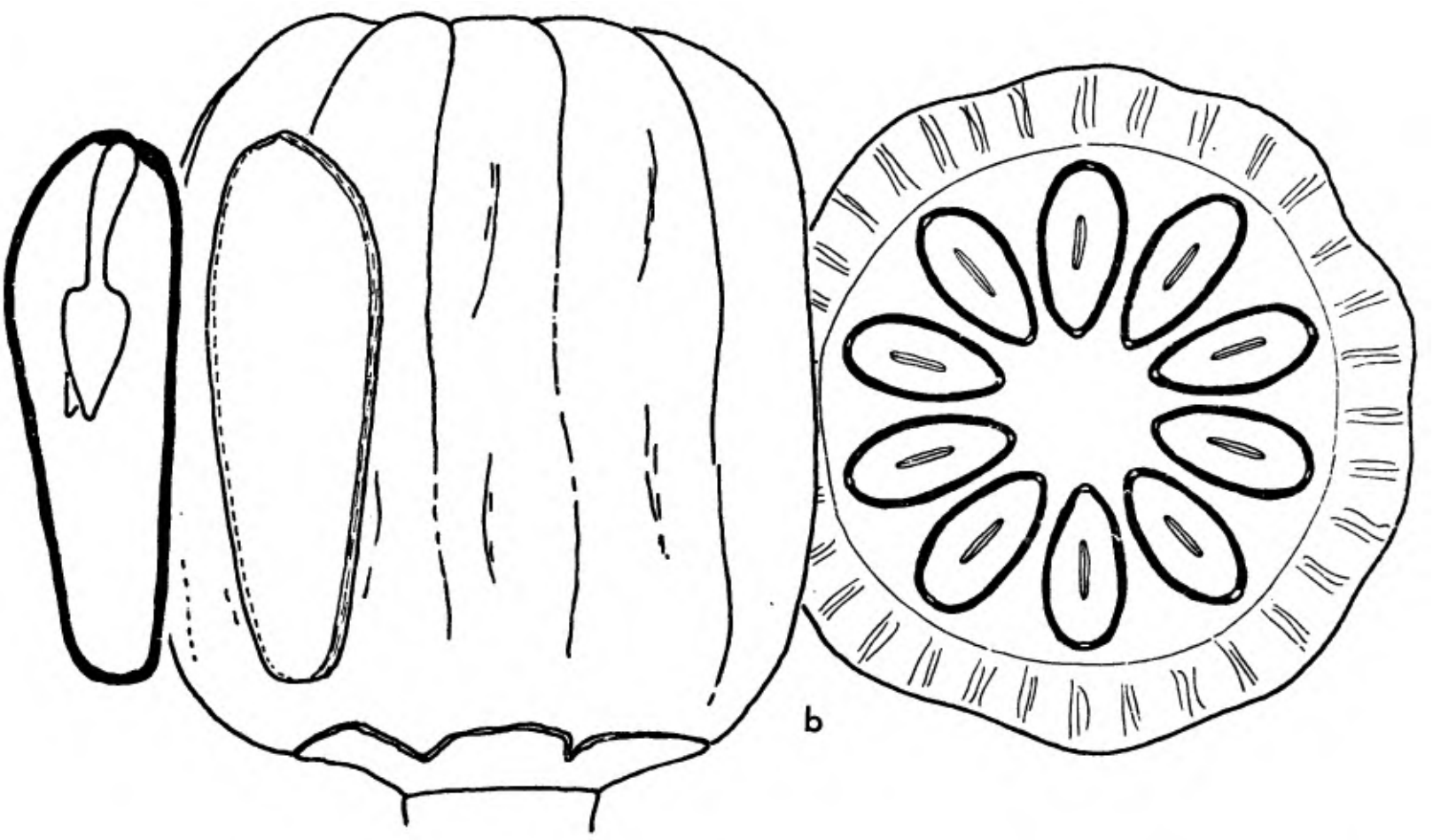
In the great majority of species, a single vascular strand runs round the seed, its passage marked externally by a groove, a ridge, or a line of lighter pigmentation, reminiscent of the ways a vein may be indicated on a leaf. But in some species the vascular strand is branched (fig. 1.8e, g). Rarely the vascular tissue is so deeply embedded that its course is not visible on the surface (fig. 8c, g).

Beneath the testa is the endosperm (fig. 1.10b, c; 1.11; 1.12), consisting of closely-packed, usually thick-walled, oil-containing cells. Intercellular spaces seem to be absent. The mature tissue is hard and usually described as 'horny' or 'cartilaginous'. It is certainly a characteristic feature, always present and always hard, and it provides the embryo with additional mechanical protection as if to compensate for the softness of the testa.

In some species, the endosperm takes on a ruminate appearance. This is due to the development of ingrowths from the testa or rarely, by actual invagination of the testa (D. sylvatica, D. ehretioides) while the endosperm is still semi-fluid. The endosperm merely fills in the spaces between the ingrowths or invaginations (see Periasamy 1962). Whether the endosperm is ruminate or not is not always a constant specific character in the Ebenaceae. I find an increasing number of species to have both ruminate and non-ruminate endosperms, e.g. D. carpinifolia, D. forworthyi, D. sumatrana, D. confertiflora, D. montana and D. buxifolia. The same plasticity occurs in Africa, in D. boyleana (White, personal communication). Variation occurs especially where the rumination is not very deep and the ingrowths not vascularised. However, rumination in the sub-genus Hierniodendron (fig. 1.8c, D. ovena) falls into a different category. Here the ingrowths are deep and each ingrowth is supplied with a deep-seated vascular trace. The rumination therefore appears to be of a highly organised and permanent nature.

Embedded in and completely surrounded by the endosperm is the embryo (fig. 1.8). It consists of a strongly developed radicle pointing upwards towards the micropyle, hence towards the fruit apex. At the other end are a pair of flat, oval,





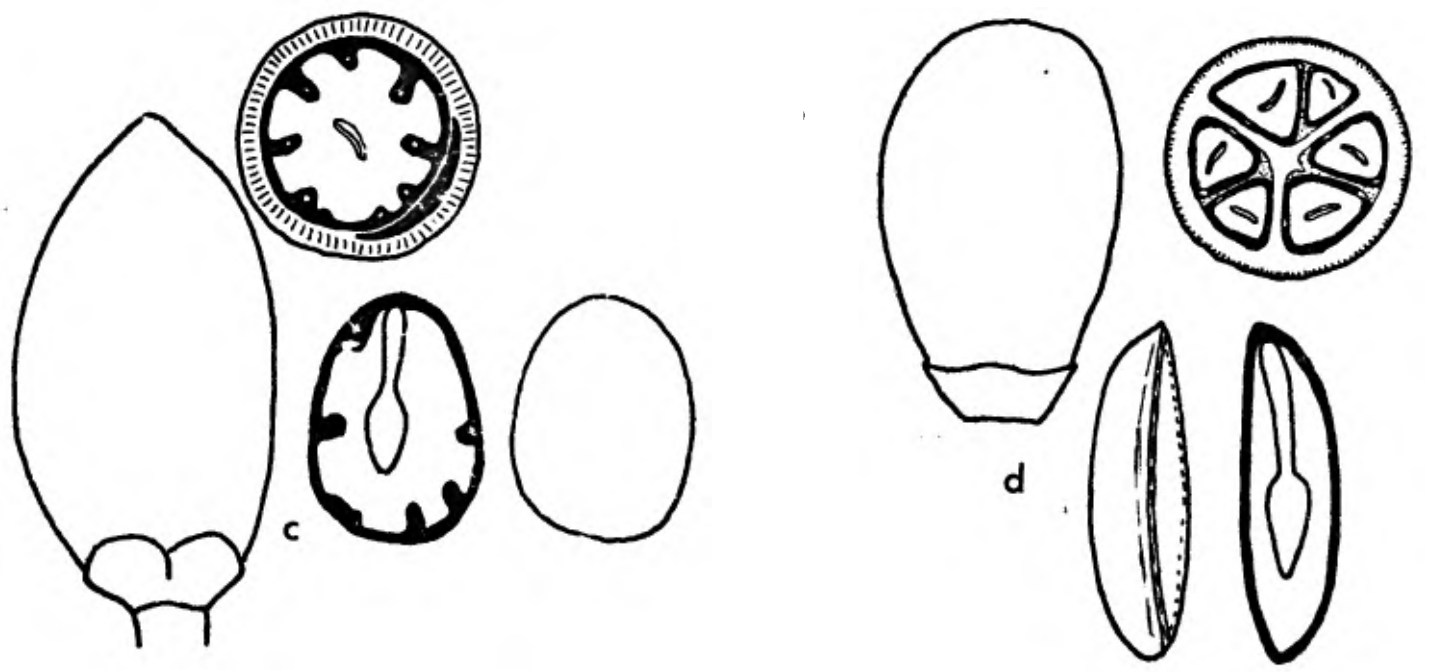


Fig. 1.8. Fruits and seeds 2x. (a) D. foxworthyi (b) D. borneensis (c) D. evena (d) D. ferrea. Conventions on next page.

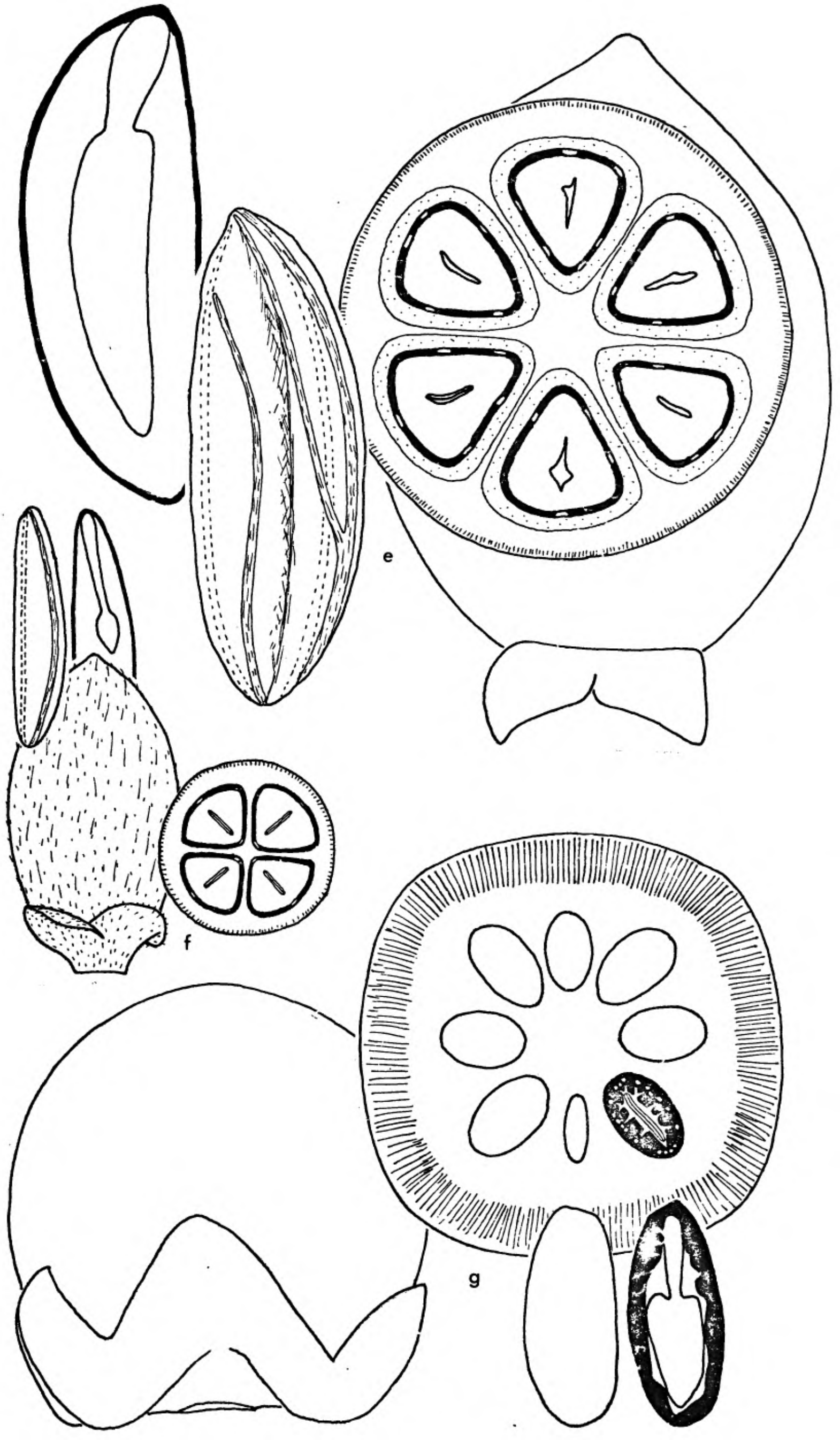


Fig. 1.8 continued. (e) D. toposioides (f) D. nutans (g) D. rigida. testa and vascular strand in section; pseudo-sarcotesta; stone cells; fibres; vascular trace surface.
Each group shows a fruit in surface side view, fruit in t.s., seed in surface side view, seed in median l.s.

leafy cotyledons. The cotyledons are orientated in the plane of the vascular loop, i.e. in the raphe/anti-raphe plane. (The raphe is the line along which the vascular trace descends from the funicle to the chalaza; the anti-raphe is the line on the opposite side, along which the vascular trace ascends from the chalaza to the micropyle). In most fruits, the seeds are so orientated that the raphe/anti-raphe plane is also the median radial plane of the seed, hence the cotyledons occupy a median radial position. But sometimes the seeds are displaced in growth (fig. 1.8d) and it then becomes apparent that what determines the orientation of the embryo is the vascular plane of the seed. The size of the embryo is always small with respect to the seed, and even at its largest extent, it seldom approaches the testa except at the micropyle.

This general description of the seed is applicable to both the genera Diospyros and Euclea although based originally on material of Diospyros. I examined seeds of Euclea linearis (fig. 1.9) and E. lanceа and found that the Euclea seed has several peculiarities. All of them may be interpreted as specialisations upon the basic plan. It has already been mentioned that sometimes, the seed is displaced in growth so that the plane of the vascular loop fails to coincide with the median radial plane. Such a situation is illustrated in fig. 1.8d where the plane of the vascular loop is at right angles to the median radial plane. This situation, rare and sporadic in Diospyros, has become fixed in Euclea. Furthermore only one seed regularly develops in the fruit of Euclea. During the development of this seed, the other (abortive) ovules and the axis are pushed to one side of the fruit, but the axis leaves an impression on the seed in the form of a lateral groove down one side. Viewed from the top, the Euclea seed shows three radiating lines, consisting of the lateral groove (impression of the displaced axis) and the two ends of the

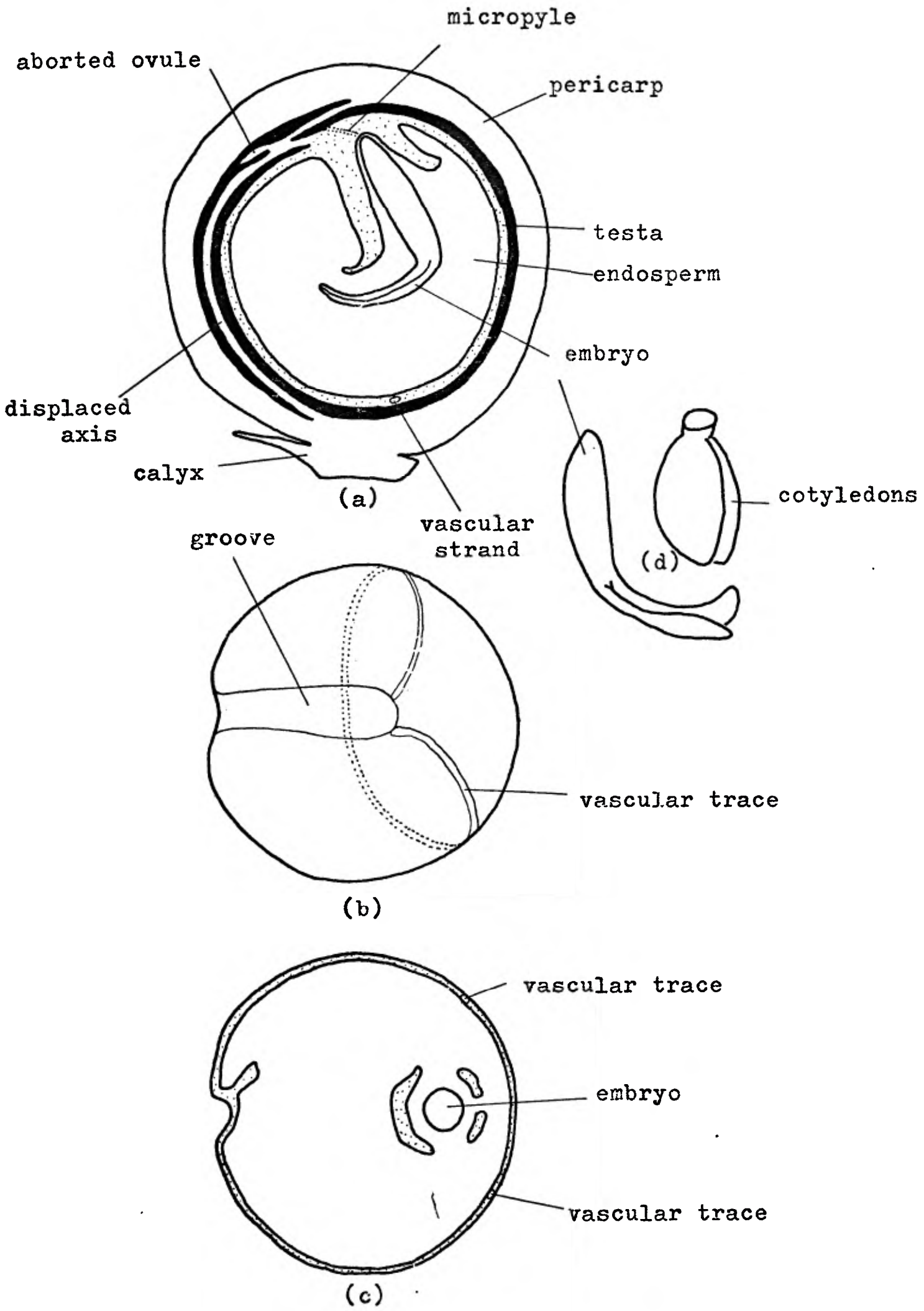


Fig.1.9. Seed of Euclea linearis 10x: (a) l.s. through seed and fruit through the lateral (axial) groove; (b) apical view; (c) t.s. through radicle; (d) isolated embryo.

vascular loop meeting at the apex. Internally, the embryo is orientated, as expected, in the plane of the vascular loop, but the cotyledons are strongly curved towards the axis. This is a peculiarity not found in Diospyros where the embryo is straight or curved in its own plane (fig. 1.8). Finally, ruminations in Euclea takes the peculiar form of ingrowths from the testa forming a partial cylinder round the radicle.

In summary, the Ebenaceous seed has a histologically simple, parenchymatous, pigmented, relatively soft testa of outer integumentary origin, in which runs a simple or branched vascular trace. Beneath the testa is a ruminate or non-ruminate endosperm of horny consistency, composed of closely packed, thick-walled cells. The embryo, straight or curved, is embedded upside-down in the raphe/anti-raphe plane, surrounded by endosperm and consisting of a precociously-developed radicle and a pair of oval foliaceous cotyledons.

The pericarp

The ovary wall may be visualised as consisting of an epidermis, under which is parenchymatous ground tissue with scattered vascular bundles. The development of strictly mechanical tissue, i.e. stone-cells and fibres, does not usually take place until after fertilisation.

The vascular bundles run generally in a vertical (base-apex) direction, and are found in the centre of the fruit, in the septa, as well as in the inner part of the pericarp. The outer part of the pericarp, between the outermost vascular bundles and the epidermis, may be called a hypodermis. This is a layer of varying thickness, consisting initially of parenchyma, but during the development of the fruit, it becomes

significant as the site of differentiation of mechanical tissue. Of 89 species examined, the mechanical tissue consisted of stone-cells in 87. Of the remaining two, D. borneensis has radial fibres while the closely-related D. sp. nov. (FRI 4618) has a mixture of radial fibres and stone-cells. Hence the hypodermal stone-cell layer is a fairly constant feature of Ebenaceous fruits.

The course of stone-cell differentiation has been described for D. kaki by Namikawa et. al. (1932). According to their description such cells begin to differentiate at anthesis in the upper part of the ovary. Differentiation proceeds basipetally until a complete layer is formed. To the naked eye, the hypodermis is seen at this stage to contain crystalline hard grains; under a microscope, each grain is revealed to be an aggregate of several to many closely adhering stone-cells. I followed the course of stone-cell differentiation in D. wallichii and found the details to be the same as described for D. kaki.

Dispersal and edibility

The Ebenaceous fruit is a berry, indehiscent except in a few African species where it may be tardily dehiscent (de Winter 1963), ranging in diameter when mature from 5 mm. (e.g. D. ferrea) to 100 mm. (D. discocalyx). The seeds range in size from that of an orange pip to that of a durian seed i.e. about 8 x 4 x 2 mm. (D. ferrea) to 40 x 25 x 7 mm. (D. discocalyx), or 40 x 20 x 20 mm. (D. macrophylla). Practically all the species with fruits larger than 50 mm. diameter and seeds longer than 25 mm. are to be found in tropical rain forest only.

Dispersal is by fruit-eating animals, although coastal and riverine species may perhaps also be water dispersed. Ridley

(1930) records that the fruits of *D. discolor* are eaten by civet cats, *D. embryopteris* by monkeys, bats and bears, *D. melanoxylon* by bats and hornbills, *D. virginiana* by the American blue-bird and the American mallard, *D. sp.* in the U.S. by skunk, *Royena pubescens* and *Euclea lanceolata* by pigeon. In all these cases, the seeds tend to be swallowed intact and passed out unharmed.

The most palatable species have been taken into cultivation in different parts of the world. The best known of these are *D. kaki* (E. Asia), *D. lotus* (Eurasia), *D. virginiana* (N. America), *D. malaberica* (Indo-Malesia) and *D. discolor* (Philippines); each of these is now grown to some extent outside their countries of origin. *D. kaki*, the oriental persimmon, is, however, the only one of economic importance, especially in Japan and China where it is grown on a commercial scale.

A number of other species are cultivated and eaten locally e.g. *D. dictyoneura* and *D. oblonga* in the villages of N. Malaya (Corner 1952). Aboriginal tribesmen in the forests of Malaya eat the fruit of *D. pyrrhocarpa* and probably a good number of other species which are never cultivated.

Edibility is governed by the degree of astringency of the fruit. In all species, the fruit is very astringent until it has become quite ripe and even then the astringency does not always disappear. In *D. kaki*, the fruit may lose its astringency and become sweet only when it has gone very soft. The fruits of some species e.g. *D. wallichii* are poisonous, especially to fish (Burkill 1935, Corner l.c.), presumably when raw.

Of interest to the morphologist is the nature of the edible tissue. In *D. kaki*, *D. virginiana* and probably the majority of

species, the edible tissue is the pericarp, which is differentiated into a pulp of varying degrees of fibrousness and astringency depending on the species, and a ____ skin. In D. kaki, the skin consists of the epidermis and the hypodermal stone-cell layer, and is easily peeled off before eating the pulp.

In several species, the pericarp has differentiated further so that there is a pulpy endocarp distinct from a somewhat fibrous mesocarp. The endocarp forms a distinct layer around each seed individually and adheres closely to it. When such a fruit is cut open, the seeds appear to be enveloped in sarcotesta (fig. 1.11a) and indeed if the seeds are prised out, the pulp comes away still surrounding the seed. The pulp is endocarp and not sarcotesta because if very thin sections are examined (fig. 1.11b) it is seen that on the inner side of the pulp, there is a contact zone of epidermal layers between pulp and testa. On the outer side there is merely a transition zone in which the large cells of the pulp give way to the smaller cells of the mesocarp. The pulp in such a situation might be called a pseudo-sarcotesta.

So far, I have seen a pseudo-sarcotesta in D. pyrrhocarpa, D. toposioides, D. pendula, D. latisepala and D. dictyoneura, of which spirit-preserved fruits have been available for study. It is also present in D. malabarica (fig. 54 in Corner l.c.). It is impossible to deduce, with certainty, the presence of such tissue from a study of dried fruits, hence we must expect many additions to this list in the future as more pickled or fresh material becomes available.

In D. confertiflora, edibility seems to be transferred from the periarp to the epidermis of the testa. In development, the epidermis of the young seed becomes securely cemented to the

pericarp. As the fruit ripens, the epidermal cells of the testa swell greatly, become filled with a jelly-like translucent white substance, and eventually the cross walls rupture. When the fruit is cut open at this stage, the seed is seen to be surrounded by a translucent white pulp. Under a microscope (fig. 1.[12]) the pulp is seen to be non-cellular except for the remains of the epidermis part of which is attached to the pericarp and the rest to the seed.

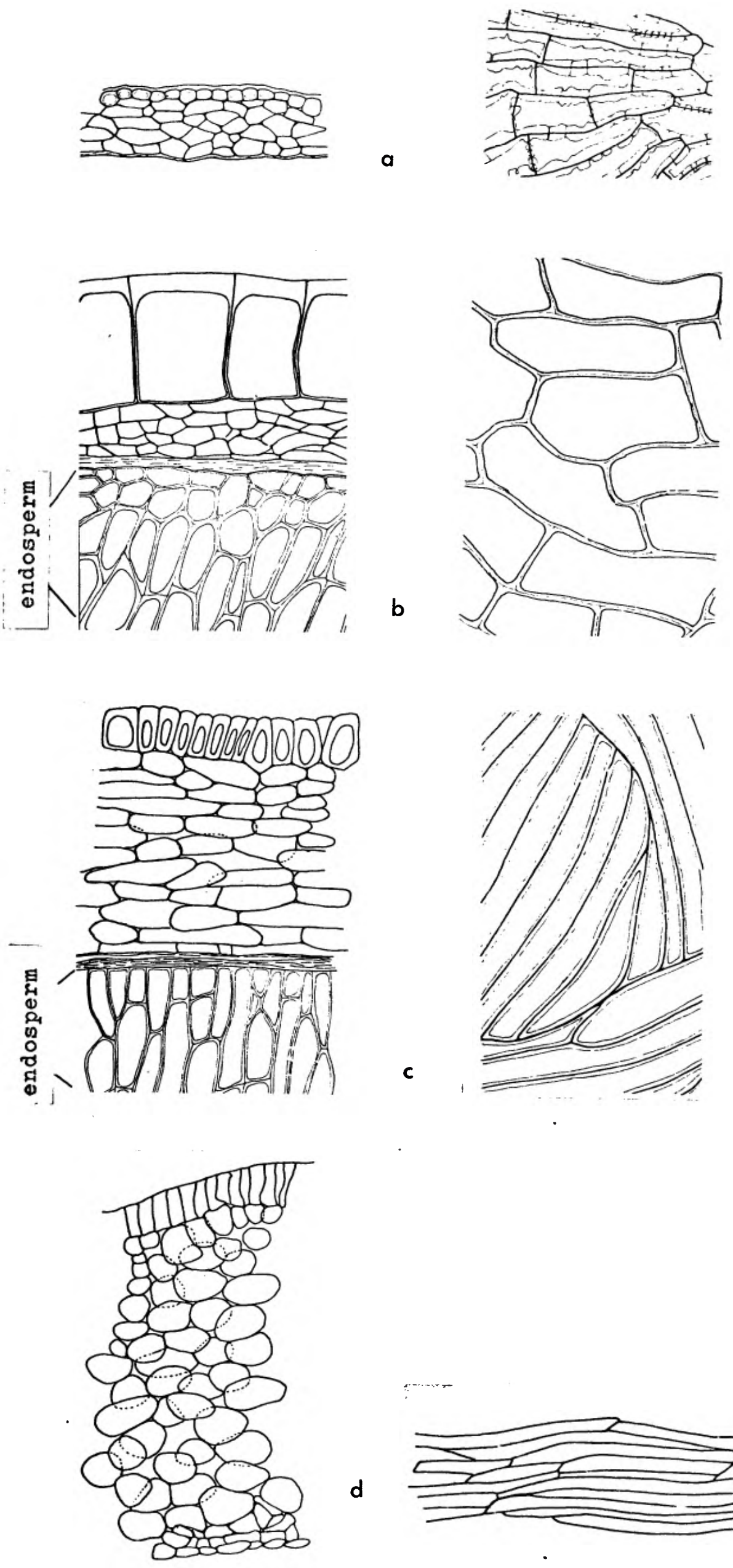
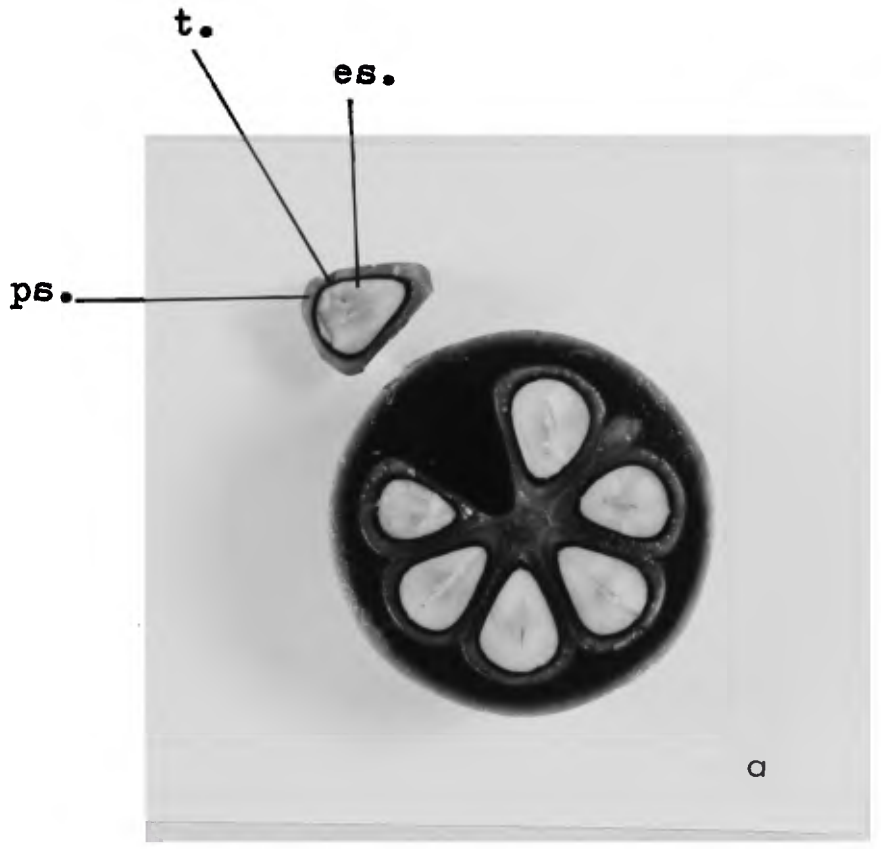


Fig.1.10. Testas in transverse section (left) and surface view (right): (a) D. wallichii (b) D. ferrea (c) D. sp. ncv. (FRI 4618) (d) D. borneensis. All at 400x.



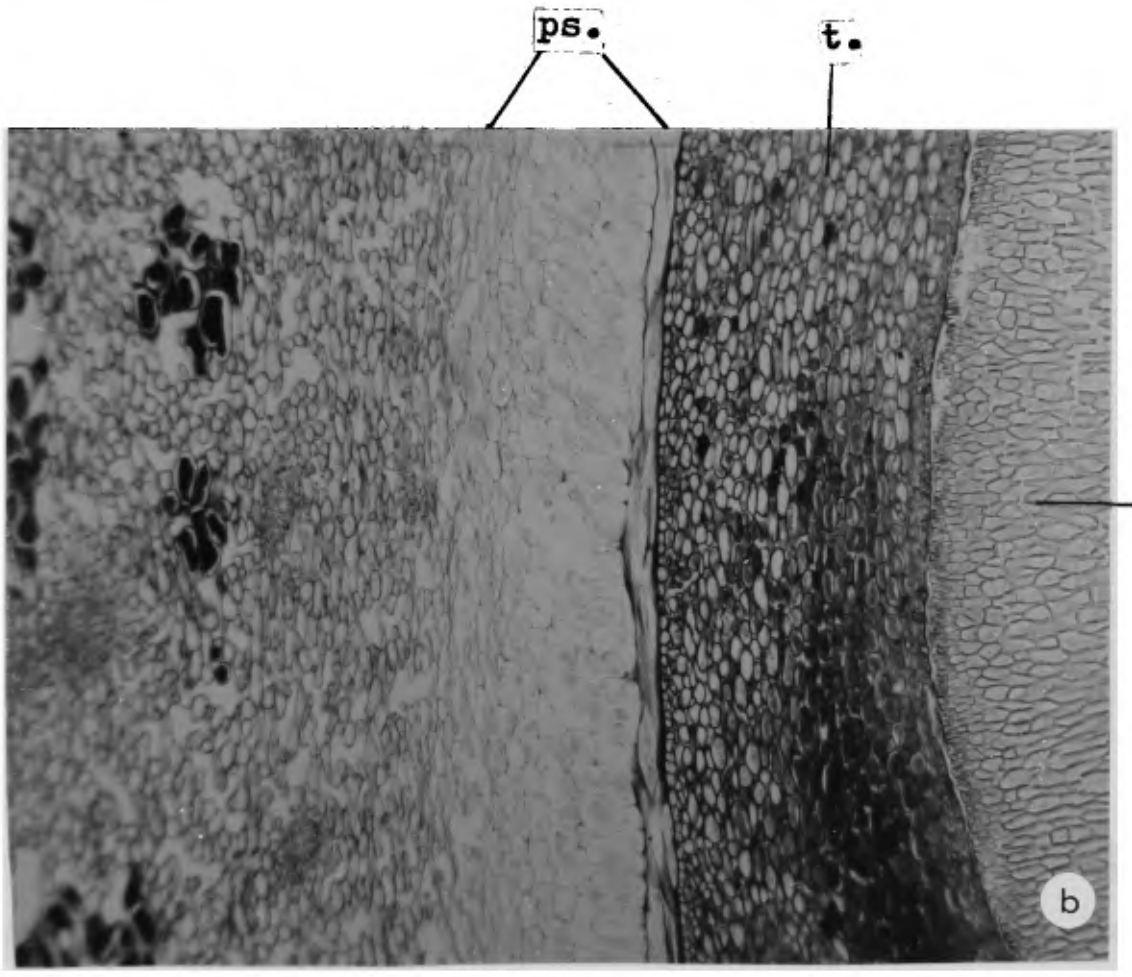


Fig. 1.11. Diospyros pyrrhocarpa: pericarp and seed: (a) transverse section of mature fruit with seven seeds fully developed and one aborted, all surrounded by pulpy endocarp which adheres to the seed forming a pseudo-sarcotesta, 1x; (b) transverse section of part of young fruit showing immature pseudo-sarcotesta, 50x. Note contact zone of epidermal layers between testa and pseudo-sarcotesta and absence of such a zone between the latter and the rest of the pericarp.

es: endosperm; ps: pseudo-sarcotesta (pulpy endocarp); t: testa.

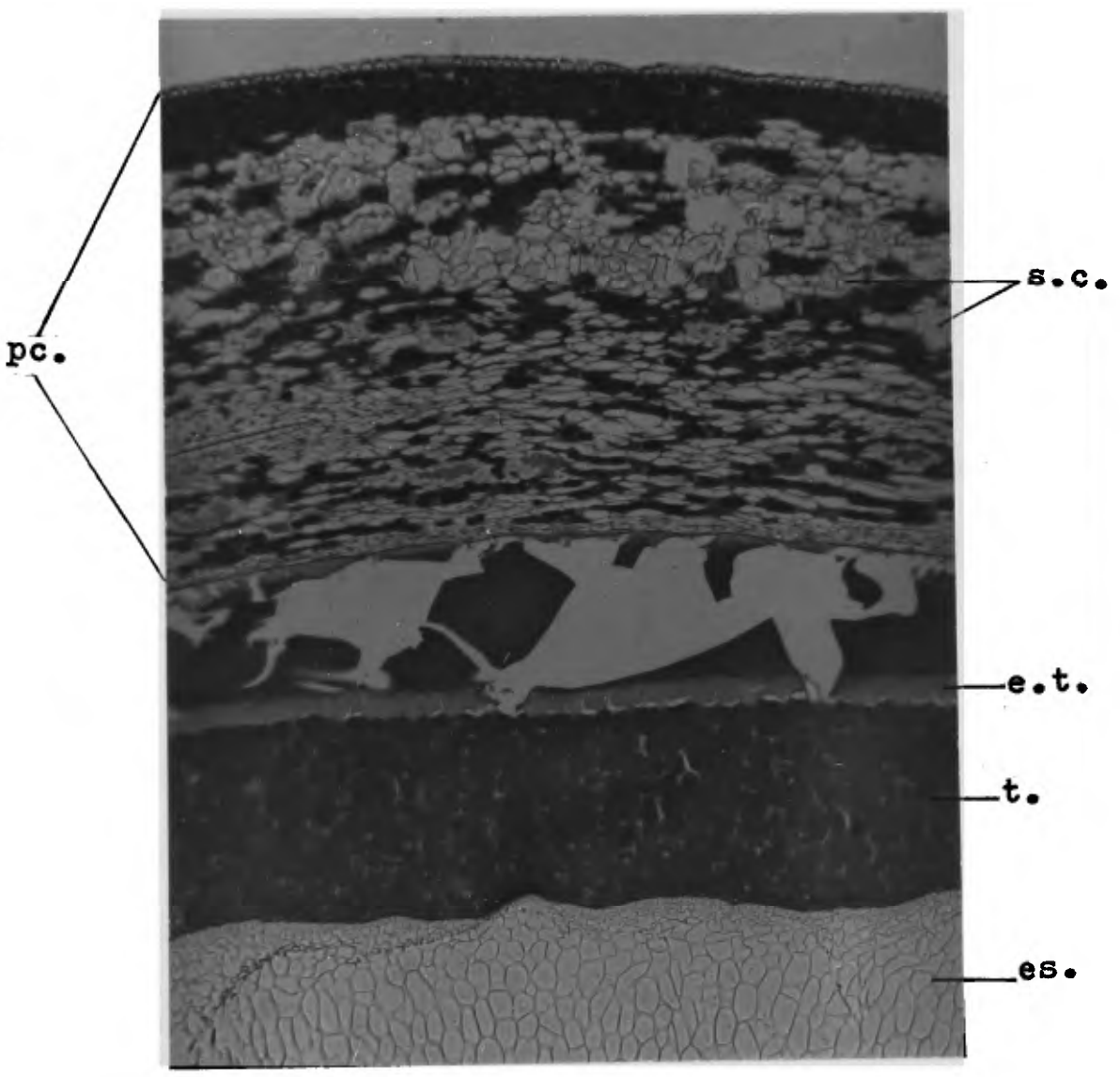


Fig. 1.12. Diospyros confertiflora: transverse section through pericarp and part of seed, showing the ruptured epidermis of the testa and the jelly-like substance released. 50x.

es: endosperm; e.t: epidermis of testa; pc: pericarp; s.c: stone cells; t: testa.

Seedlings and germination.

Studies on the seedlings of Diospyros have been published by Lubbock (1892) on D. embryopteris, Wright (1904) on D. acuta, D. affinis, D. attenuata, D. crumenata, D. ebenum, D. embryopteris, D. gardneri, D. hirsuta, D. insignis, D. montana, D. moonii, D. oocarpa, D. ovalifolia, D. pruriens, D. quaesita, D. sylvatica, D. thwaitesii and D. toposia and Troup (1921) on D. embryopteris and D. melanoxylon. To this list, I now add D. confertiflora, D. maingayi, D. siamang, D. toposioides and D. wallichii, making a total of 24 species, all from the Indo-Pacific region.

In all these species, germination first becomes evident by the emergence of the radicle out of the micropyle. The radicle develops into a strong, usually black, taproot. An arched hypocotyl slowly develops, and as it straightens out, it lifts up the seed body. After this stage, there is a divergence of behaviour between the species.

Wright divided his species into two groups according to behaviour of the cotyledons. In D. ebenum, D. gardneri, D. sylvatica and D. montana, the cotyledons emerge and become photosynthetic. In his other species, the cotyledons have no photosynthetic function, and are dehisced very early. Often, the plumule in such cases would be trapped in the seed-shell (composed of testa and endosperm). The decay of the dehisced cotyledons and endosperm leads to infection of the trapped plumule and death of the seedling ensues. To this "suicidal" mode of development, Wright attributed the rarity of some of the species involved.

Troup did not comment on Wright's observation although one of the two species he examined, D. embryopteris, comes under Wright's "suicidal" class. In his account, the cotyledons of both D. melanoxylon and D. embryopteris are either cast off with the seed-shell, or they emerge and are then cast off, almost immediately. It is clear that in either case, the cotyledons do not function as photosynthetic organs.

My own observations suggest that cotyledon-behaviour in Indo-Pacific species of Diospyros falls into three classes as set out in the scheme below, into which the observations of Wright and Troup and can be easily fitted.

In the first class, the cotyledons function in germination initially as organs of digestion. As the endosperm is absorbed, the cotyledons enlarge and pressure builds up which eventually splits the testa. The cotyledons, now free, function for several months as photosynthetic organs. In this class, belongs D. wallichii, D. confertiflora, D. siamang and Wright's first group comprising D. ebenum, D. gardneri, D. sylvatica and D. montana. Although Wright does not mention the fact, the endosperm is almost fully absorbed when the testa is cast off (fig. 1.13e). Another important point is that the testa splits along the plane of the vascular loop. I have observed when examining seeds of herbarium material that the vascular loop of the seed in Diospyros is a line of weakness. Boiled seeds will usually crack along this line, and old seeds often show fraying of the vascular strands. The arrangement of the cotyledons, in the plane of the vascular loop, places them in the best position for applying pressure to the line of weakness, but a high degree of pressure is built up in the cotyledonary stalks as well, as may be deduced from the appearance of the

cotyledons in fig. 1.13a. The cotyledons, at first held vertically within the testa, are reflexed a full 180 degrees on emergence, as if suddenly flicked backwards. It takes several days for the cotyledons to expand, harden and assume the horizontal position which they then maintain until finally shed, several months afterwards.

In the second class, may be placed Troup's D. melanoxylon and D. embryopteris, all of Wright's "suicidal" species viz. D. aguta, D. affinis, D. attenuata, D. crumenata, D. embryopteris, D. hirsuta, D. insignis, D. meonii, D. occarpa, D. ovalifolia, D. pruriens, D. quaesita, D. thwaitesii, D. toposia, and one of the species I examined, D. toposioides. These species share in common the fact that the cotyledons do not have any photosynthetic function. In D. toposioides, of which I had one seedling under observation, the cotyledons absorbed the endosperm and in expanding slightly, brought about a small split in the testa. Insufficient final pressure was developed to split the testa off. Instead the cotyledons gradually weakened and died inside the seed-shell. The plumule, trapped between the cotyledons inside the shell, became weakened and infected, and the seedling soon died. I cannot believe that this course of events is inevitable since D. toposioides is not a rare plant. Together with D. toposia, with which it is very closely related (perhaps conspecific), it ranges from India to Borneo. I expect that a good proportion of seedlings, perhaps the more

to accident. The successful splitting off of the seed-shell is the crucial part of the operation. This is, as we have seen in the first class of seedlings, achieved by strong pressure developing in the cotyledonary stalks. In the second class of seedlings, the cotyledons, at the end of their digestive role, are due to be shed; their stalks develop lines of weakness i.e. dehiscence zones. But weak cotyledonary stalks are incompatible with the final role of the stalks which is to split off the seed-shell. The problem has to be resolved by exact timing - strong pressure developing in the stalks, followed by dehiscence. If the latter process begins too soon, failure results.

In the third class of seedlings, we see now a better solution to the problem has evolved. In this class may be placed D. malngayi and probably all species of the subgenus Hiemiodendron. Here, the seed is deeply ruminate and the vascular system branched. The ruminations run longitudinally and deeply embedded in each is a branch of the vascular system. (see fig. 1.8c). Hence the vascular system here does not provide a simple line of weakness along which the seed-shell may be split. In D. malngayi, the seed body is lifted up partially and remains at an inclined angle until the endosperm has been absorbed (fig. 1.13d). The cotyledons are then dehisced, and the seed-body slides off exposing the tightly rolled plumule. The hypocotyl now straightens up and the foliage leaves unfurl (fig. 1.13e). The efficient manner in which the cotyledons are cast off, marks this as a specialised mode of germination within the Ebenaceae, corresponding to a well-defined taxonomic group.

Terminology

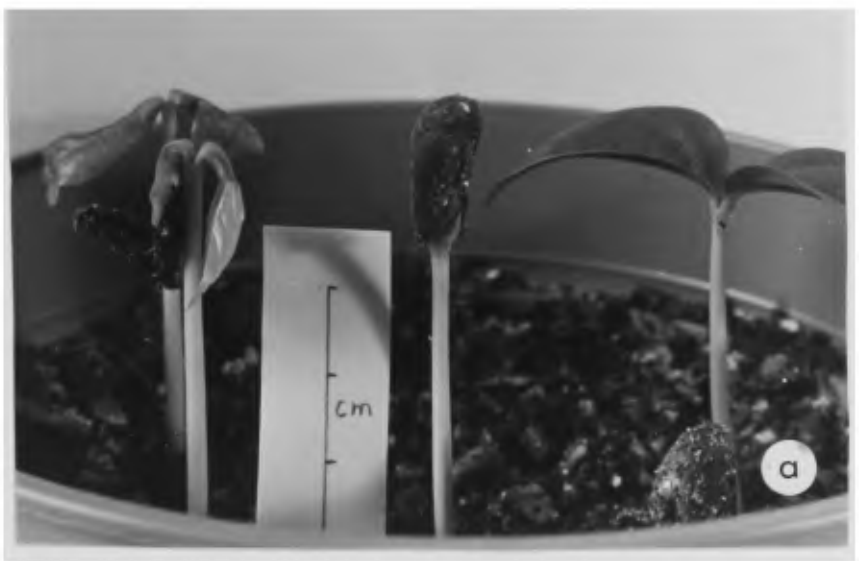
The cotyledons in the third class are definitely non-emergent. Those of the first class are definitely emergent. Those of the second class may therefore be termed sub-emergent.

The classic terms "epigeal" and "hypogeal," referring to whether the cotyledons are "spread above" ground or remain "below ground" (Jackson, 1928) have been criticised by Duke (1965) as being etymologically incorrect because in nature, seeds germinate on the surface of the ground rather than below. He proposed the adjectives "phanerocotylar" and "cryptocotylar", indicating whether the cotyledons are emergent or non-emergent from the testa during germination, to replace the terms "epigeal" and "hypogeal" respectively. I think the distinction between cotyledons emergent and non-emergent is an important one but it is a mistake to equate these two conditions with epigeal and hypogeal. The etymological problem is unimportant compared to the more fundamental problem that there are more variations in germination behaviour than can be covered by two terms.

It seems to me that the concept of epigeal versus hypogeal involves two independent variables, (a) whether the cotyledons emerge from the seed or not, and (b) whether the cotyledons are lifted above the ground or not, i.e. whether a prominent hypocotyl develops. In theory, four possible situations can

covered by either of these terms. Neither is the second condition, of which an example is illustrated by Lubbock (1892, Lucuma sp. p. 202). Mr. F. White has recently found that the African Diospyros lycioides behaves in the same way i.e. the cotyledons emerge and become photosynthetic at ground level. In a general scheme for describing germination, it would allow for greater flexibility if the behaviour of the cotyledons and the behaviour of the hypocotyl are described separately, as was done by Lubbock, rather than rigidly combined in two contrasting terms which do not cover the full range of expressions that may be encountered in nature.

To complete this account of seedlings in Ebenaceae, it may be mentioned that the epicotyledonary leaves are alternate (spiral) but the first two may be sub-opposite. D. pruriens is exceptional in that the earliest leaves are reduced almost to scales (Wright l.c.). In general however, the seedling leaves do not differ greater from adult leaves of the same species except in being smaller.



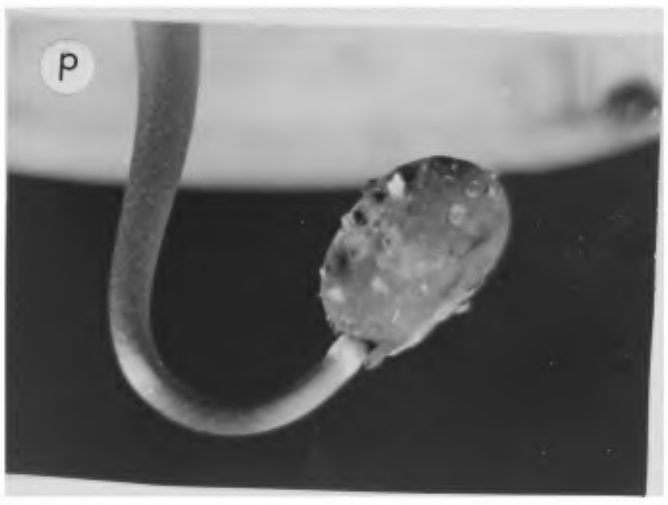


Fig. 1.13. Seedlings and germination: (a) D. wallichii, showing cotyledons about to emerge (centre), newly-emerged (left), and fully expanded (right); (b) D. confertiflora, with expanded cotyledons; (c) D. confertiflora, seed-shell consisting of testa and scanty remains of endosperm; (d) D. maingayi, before shedding of seed-shell; (e) D. maingayi, after shedding of seed-shell; (f) D.maingayi, seed-shell cut transversely to show cotyledons. Note disappearance of endosperm from spaces between ingrowths of testa.

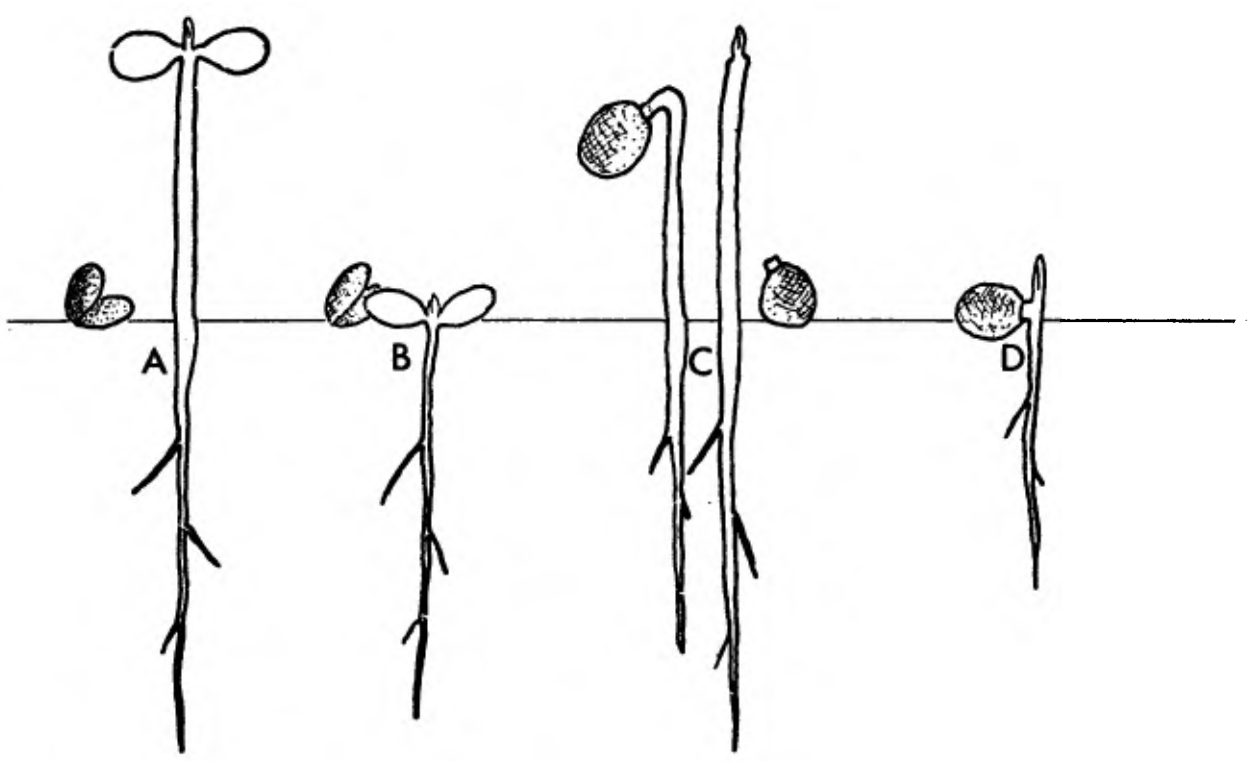


Fig.1.14. Types of germination.

A. Hypocotyl prominent, cotyledons emergent; most species in Ebenaceae, although in many, the cotyledons sub-emergent only (see text).

B. Hypocotyl undeveloped, cotyledons emergent; D. lycioides.

C. Hypocotyl prominent, cotyledons non-emergent; D. maingayi.

D. Hypocotyl undeveloped, cotyledons non-emergent; not observed in Ebenaceae.

Pollen

A description of Ebenaceous pollen has been published by Erdtman (1966), based on material of Diospyros bipindensis, D. ferrea, D. virginiana, Euclea tomentosa, Maba warneckei, Royena glabra. I have studied material of 45 species (Appendix 1) all of which except one, D. ferrea, have not been examined before. My list includes three species of Euclea, representatives of Royena and Maba (now both reduced to Diospyros) and representatives of nearly all sub-genera and sections in Bakhuizen's classification of Diospyros. The material was prepared by acetolysis following the schedule in Appendix 1. A few species were also examined by scanning electron microscope (Appendix 1b).

The pollen is remarkably uniform : 3 - colporate, oblate spheroidal to prolate $\bar{P}/e(0.9)1.2-1.57$, smooth to very finely varty with ora usually lalongate.

The main variations are in size, shape, and ora appearance. In fig. 1.15, pollen grains of 9 species are illustrated to represent the full range of variation observed in the family. In fig. 1.16 are matched photographs of 5 species taken by light microscope and S.E.M.

Ora are generally lalongate, sometimes very prominently so (e.g. D. mainganii, fig. 1.15e), sometimes with lateral edges indistinct (e.g. D. topogioides fig. 1.15f), rarely indistinguishable (D. latisepala, fig. 1.15b).

Size and shape as observed on mounted material are dependent to some extent on the ability of the grains to resist shrinkage during preparation. When suspended in water or alcohol, grains swell up to maximum roundness, but when mounted in glycerine

jelly, some shrinkage often takes place along the furrows. Shrinkage is most severe when the grains are being air-dried for scanning electron microscopy. But some grains hardly suffer any shrinkage, perhaps because they have thicker walls relative to grain size. The following comments on size and shape are based on the most distended undamaged grains in each preparation.

The size range observed was 24 x 20μ (D. ferrea, fig. 1.15a) to 75 x 60μ (D. argentea, fig. 1.15h) i.e. the largest grains being 3x the linear dimensions of the smallest. Within each anther the largest grains may be up to 50% larger than the smallest, but most grains in each anther are about the same size. When the species are arranged in order of pollen size, it becomes obvious that variation is overlapping and smoothly continuous.

Shape varies from prolate to oblate spheroidal (p/e 1.5 - 0.9). All grains have polar axis longer than equatorial axis i.e. prolate to subprolate (p/e 1.5 - 1.2) except D. cauliflora (p/e 1.0 - 0.9). In polar view, the grains are three-sided, with sides convex to concave, and with all possible degrees of intermediates. The concave sides are probably artifacts caused by shrinkage in preparation.

S.E.M. photographs confirm that the pollen walls are smooth to very finely warty. The colpi (furrows) are distinct but ora are not visible externally except where ora and colpi cross each other, and the thin membrane where the crossing occurs, has ruptured.

All in all the pollen of Ebenaceae is quite homogeneous and provides no characters for sub-division of the family.

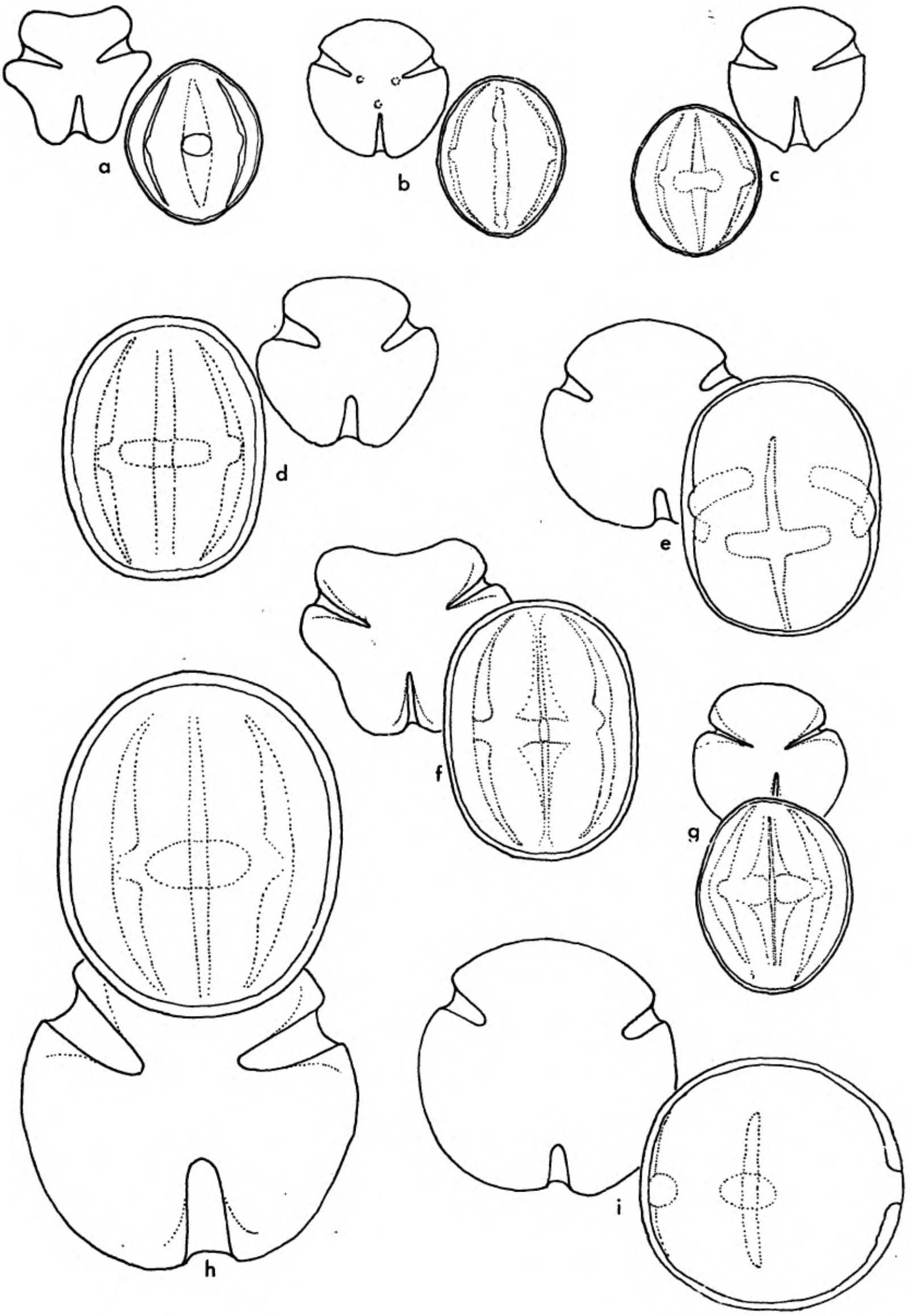
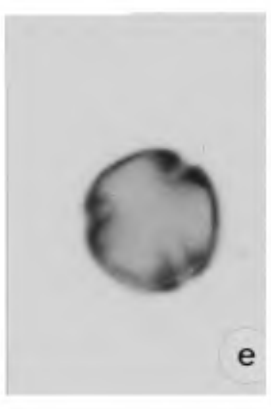
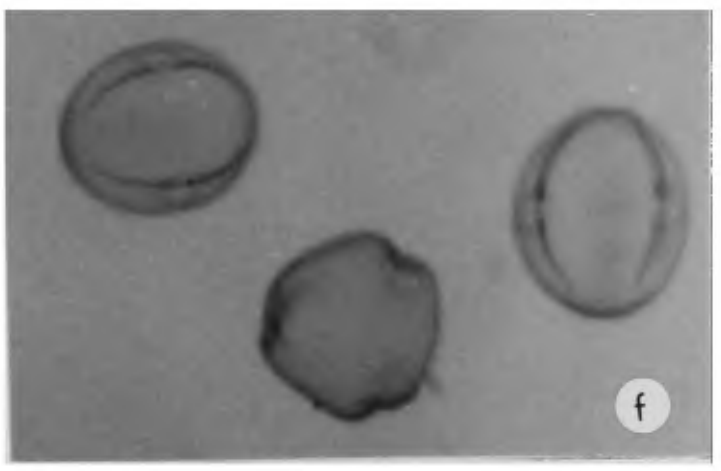
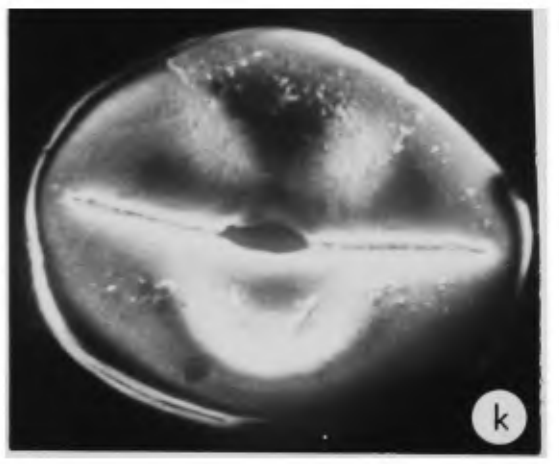


Fig. 1.15. Pollen at 1000x. (a) D. ferrea (b) D. latisepala (c) Euclea schimperi (d) D. sumatrana (e) D. maingayi (f) D. toposioides (g) D. hermaphroditica (h) D. argentea (i) D. cauliflora.







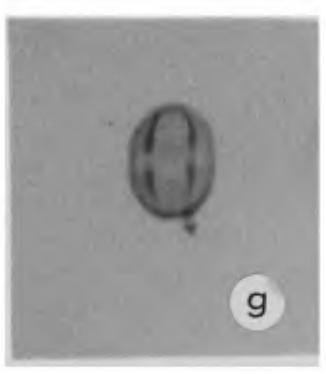


Fig. 1.16. Pollen: (a) - (g) light-microscope photographs at 300x; (h) - (l) scanning electron microscope photographs at 700x. (a) & (h) D. lotus; (b), (c) & (i) D. maingayi; (d), (e) & (j) D. pentamera; (f) & (k) D. villosa; (g) & (l) Euclea divinorum.

Secondary xylem

The secondary xylem in Ebenaceae has been fully described by Metcalfe & Chalk (1950). I have re-examined 89 slides from the Commonwealth Forestry Institute collection belonging to 56 species (table 1.4).

Features which characterise the family are (fig. 1.17, 1.18) : Vessels solitary and in radial multiples of 2, 3, 4 or (sporadically) more, with simple perforations; pits small (to 8μ diameter) between vessels as well as between vessels and ray cells or parenchyma. Parenchyma predominantly apotracheal, scattered and in numerous uniseriate lines; sometimes also forming vasicentric sheaths round the vessels. Rays 1 - 2 cells rarely to 3 or 4 cells wide; less than 1 mm. high; heterogeneous. Fibres with small pits; walls thinner than lumina, rarely thicker.

Major sources of variation are in (1) number of vessels in each cluster (2) arrangement of parenchyma (3) width of rays (4) thickness of fibre walls.

Number of vessels per cluster. Solitary vessels are common in the family as a whole, and present on every specimen examined, but all specimens also have radial clusters of 2 or more vessels, as seen in transverse section. In table 1.4 column 1, the dominant pattern is given first, followed by rare numbers within brackets e.g. 1 - 2(-7) means that 90% of vessel clusters have 1 or 2 vessels each. The remaining 10% have 3 - 7 vessels each.

Parenchyma is predominently apotracheal, mostly in uniseriate lines but with some cells scattered. A few parenchyma cells are usually found adjacent to each vessel

cluster. In about 35% of the specimens seen, such cells formed a more or less complete vasicentric sheath of one-cell thickness. In the table, column 3, the entry + indicates that on the specimen, over 75% of vessel clusters had a sheath composed of over 75% parenchyma.

The only deviation from uniseriate lines of apotracheal parenchyma was observed in D. variegata with a mixture of uni- and bi-seriate lines (table column 2).

Ray width is nearly always 1 - 2 cells, rarely to 3 or 4. In table column 4, the dominant (90%) pattern is given first, followed by rare values within brackets.

Fibre wall thickness is indicated in table column 5 by the symbols < , = , > which means wall thinner than lumen, equal to lumen, thicker than lumen, respectively. Walls equal to or thicker than lumen were seen on only 11 specimens.

In general the wood is very uniform in Ebenaceae. Such variation as there is does not appear to correspond to any of genera, sub-genera or sections that have been defined in the past. There are no striking internal discontinuities in the variation pattern of any character that may be worth further study for possible use in a new infra-family classification.

Table 1.4. Wood characters.

(1) Number of vessels per cluster: 90%(10%)

(2) Parenchyma: +: scattered and uniseriate

-: Scattered, uniseriate and biseriate or more

(3) Vasicentric sheaths: +: conspicuous (75% of vessel-clusters with sheaths 75%-100% complete)

-: inconspicuous

(4) Width of rays, expressed as number of cells: 90%(10%)

(5) Fiber wall thickness: < narrower than lumen

= equal to lumen

> thicker than lumen

		(1)	(2)	(3)	(4)	(5)
1.D.abyssinica	IFI 83	1-4(-8)	+	-	1(-2)	=
	IFI 2401	1-3(-6)	+	-	1-2	<
	IFI 18270	1-2(-6)	+	-	1(-2)	<
	Q5	1-4(-12)	+	-	1-2	>
2.D. australis	-	1-3(-4)	+	-	1-2	<
3.D. brachiata	FPRL 4559	1-2(-3)	+	-	1	<
	IFI 15887	1-2(-3)	+	+	1(-2)	<
	IFI 4485	1-3(-5)	+	+	1(-2)	<
4.D.brandisiana	IFI 2379	1-3(-7)	+	-	1-2	<
5.D.burmanica	FPRL 4563	1-5(-6)	+	-	1	=
	IFI 416	1-5(-6)	+	-	1	<
	IFI 2699	1-4(6)	+	-	1(-2)	<
6.D.crassiflora	IFI 1601	1-4(6)	+	-	1	=
	IFI 5442	1-4	+	-	1-2	<
7.D. decipiens	IFI 7620	1-5	+	-	1(-2)	<
	IFI 10612	1-3(-6)	+	+	1(-2)	<
8.D.diepenhorstii						
	IFI 7619	1-2(-4)	+	+	1-2	<
9.D. ebenum	IFI 413	1-2(3)	+	-	1-2	=
	IFI 158	1-3(8)	+	-	1-2	<
10.D.ehretioides	IFI 6506	1-2(-4)	+	+	1-2	<
11.D.embryopteris						
	IFI 1975	1-5	+	-	1(-2)	<
	FPRL 159	1-3(-5)	+	-	1(-2)	<
	FPRL 6048	1-3(-4)	+	-	1(-2)	<
12.D.foxworthyi	IFI 15899	1-4(-6)	+	-	1(-2)	<
	IFI 10559	1-3(-5)	+	-	1	<
	IFI 10555	1-2(-7)	+	+	1	<
	IFI 10540	1-2(-5)	+	+	1(2)	<
	IFI 10514	1-3(-5)	+	-	1-2	<
13.D.gabunensis	IFI 4062	1-2(-3)	+	-	1(-2)	<
14.D.glandulosa	IFI 2698	1-3(-5)	+	+	1-4	<
15.D.hoyleana	IFI 18276	1-3(-10)	+	-	1	<
16.D.insculpta	FPRL 6661	1-2(-4)	+	-	1(-2)	=
	FPRL 6660/1	1-2(6)	+	-	1(-2)	<
	FPRL 5720	1-3(-5)	+	-	1	<
17.D. kaki	FPRL 1351	1-4(-7)	+	-	1(-2)	<
	FPRL 16984	1-2	+	+	1-3	<
	IFI 2086	1(-4)	+	+	1-2	<
18.D.kamerunensis						
	IFI 5887	1-3(-4)	+	-	1-2(3)	>
	FPRL 5472	1-2(-4)	+	-	1-2	=
	IFI 4097	1-2(-4)	+	-	1	<
	IFI 3772	1-3(-6)	+	-	1	<
	FPRL 5472	1-2(-3)	+	-	1-2	=
19.D. kirkii	IFI 18277	1-3(5)	+	-	1-2	<
20.D.latisepala	IFI 15007	1-3(-5)	+	+	1-2	<

			(1)	(2)	(3)	(4)	(5)
21.D.lotus	-		1-3(-5)	+	+	1-2	∧
22.D.lucida	IFI	8680	1-3(-11)	+	-	1(-2)	∧
23.D.maingayi	IFI	7621	1-2(-4)	+	+	1-2	∧
24.D.malaccensis	IFI	8751	1-3	+	-	1-2	∧
	FMS	1084	1-3	+	-	1(-2)	∧
25.D.melanida	FPRL	2641	1-3(-6)	+	-	1-2	∧
26.D.mespiliformis	FPRL	6428	1-3(-4)	+	-	1(-2)	∧
	IFI	5146	1-4(-7)	+	-	1(-2)	∧
	IFI	6884	1-4(-5)	+	-	1-2	∧
27.D.montana	-		1-4(-11)	+	-	1-2	∧
	FPRL	1218	1-3(-4)	+	-	1-2	∧
28.D.moonii	IFI	714	1-2(-3)	+	+	1	∧
29.D.multiflora	IFI	18273	1-4(-13)	+	+	1-4	∧
30.D.oblonga	IFI	15857	1-2(-5)	+	+	1-2	∧
31.D.oocarpa	IFI	1306	1-2(-5)	+	+	1(-2)	∧
32.D.pendula	IFI	7446	1-3(-5)	+	-	1(-2)	∧
33.D.pentamera	IFI	11115	1-3(-5)	+	-	1-2	∧
34.D.piscatoria	IFI	8495	1-2(-3)	+	+	1-2	∧
	FPRL	6494	1-2(-4)	+	+	1(-2)	∧
35.D.polyalthioides	IFI	7573	1-2(-4)	+	+	1-2	∧
36.D.pseudo-malabarica							
	IFI	15798	1-3(-6)	+	-	1-2	∧
37.D.quaesita	IFI	1308	1-3(-6)	+	-	1-2	∧
38.D.rufa	IFI	7615	1-3(-4)	+	-	1	∧
39.D.sanza-minika	IFI	4046	1-2(-5)	+	-	1	∧
	FPRL	5491	1-3(-7)	+	-	1-2	∧
	IFI	4719	1-2(-5)	+	-	1	∧
40.D.sumatrana	IFI	2491	1-3(-8)	+	+	1(-2)	∧
41.D.tomentosa	FPRL	6050	1-3(-16)	+	-	1-2	∧
42.D.toposicides	IFI	10541	1-3(-5)	+	+	1-2	∧
43.D.tristis	FMS	1083	1-2(-3)	+	-	1	∧
44.D.undulata	IFI	4495	1-3(-7)	+	+	1	∧
45.D.variegata	C	5420	1-4(-6)	-	-	1-2	∧
46.D.vestita	IFI	8203	1-3(-8)	+	+	1-2	∧
47.D.virginiana	IFI	3219	1-4(-8)	+	+	1-2	∧
	FPRL	9708	1-3	+	+	1-2	∧
48.D.wallichii	IFI	1975	1-2(-5)	+	+	1-2	∧
49.Euclea divinorum	IFI	18274	1-3(-5)	+	+	1-2(-3)	∧
50.E.lanceolata	IFI	11195	1-4(-5)	+	-	1-3	∧
51.E.multiflora	IFI	18272	1-4(-7)	+	+	1-3(-4)	≡
52.E.schimperi	IFI	18275	1-4(-8)	+	-	1-2	∧
53.Maba buxifolia*	IFI	716	1-2(-4)	+	+	1	∧
54.M.geminata*	-		1-4(-10)	+	-	1-2	∧
55.Royena lucida**	IFI	6805	1-3(-9)	+	-	1-4	∧
56.R.sericea**	IFI	18271	1-3(6)	+	+	1(-2)	∧

* These two species of Maba have been reduced to Diospyros ferrea.

**Royena has been reduced to Diospyros.

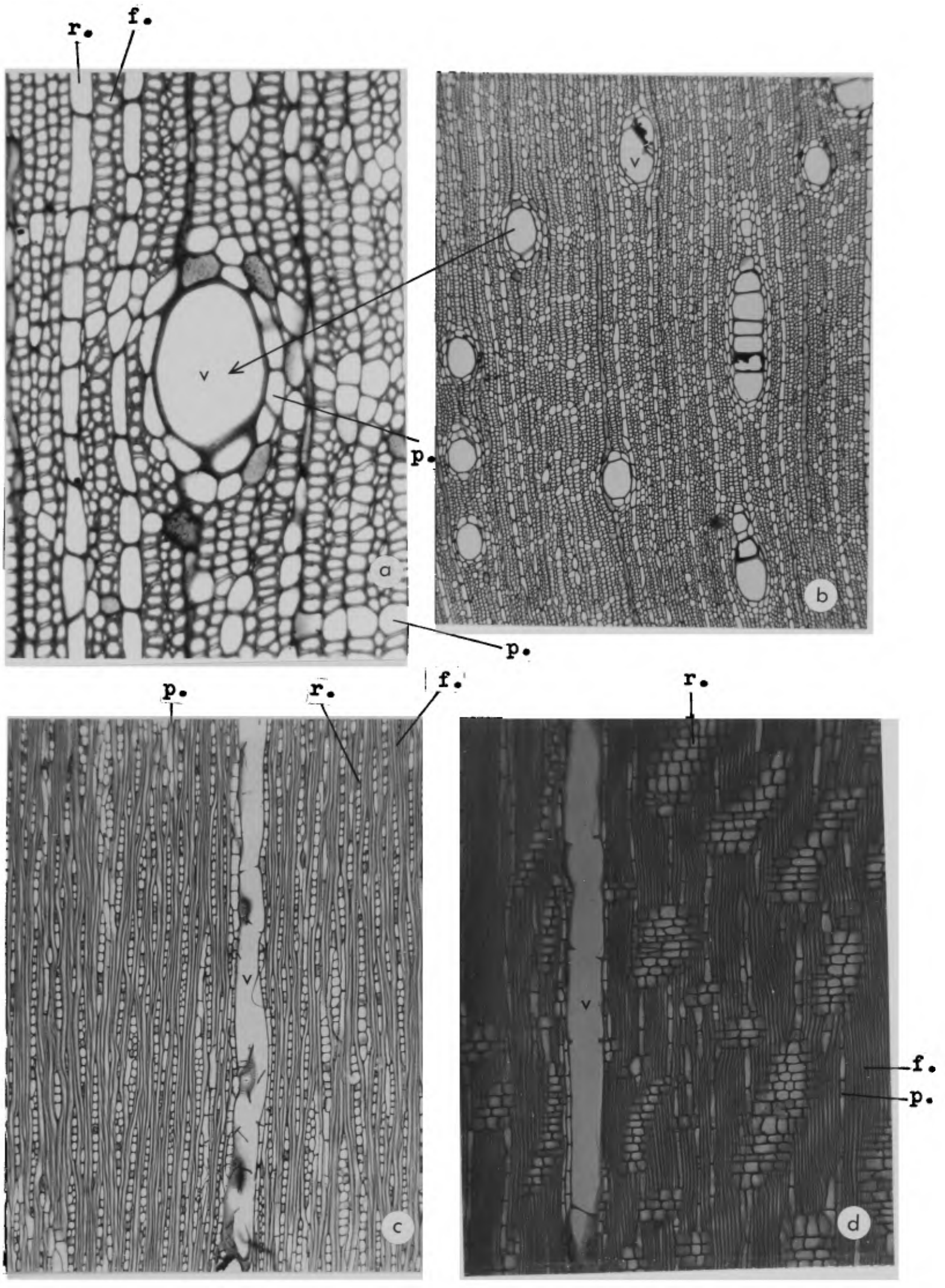
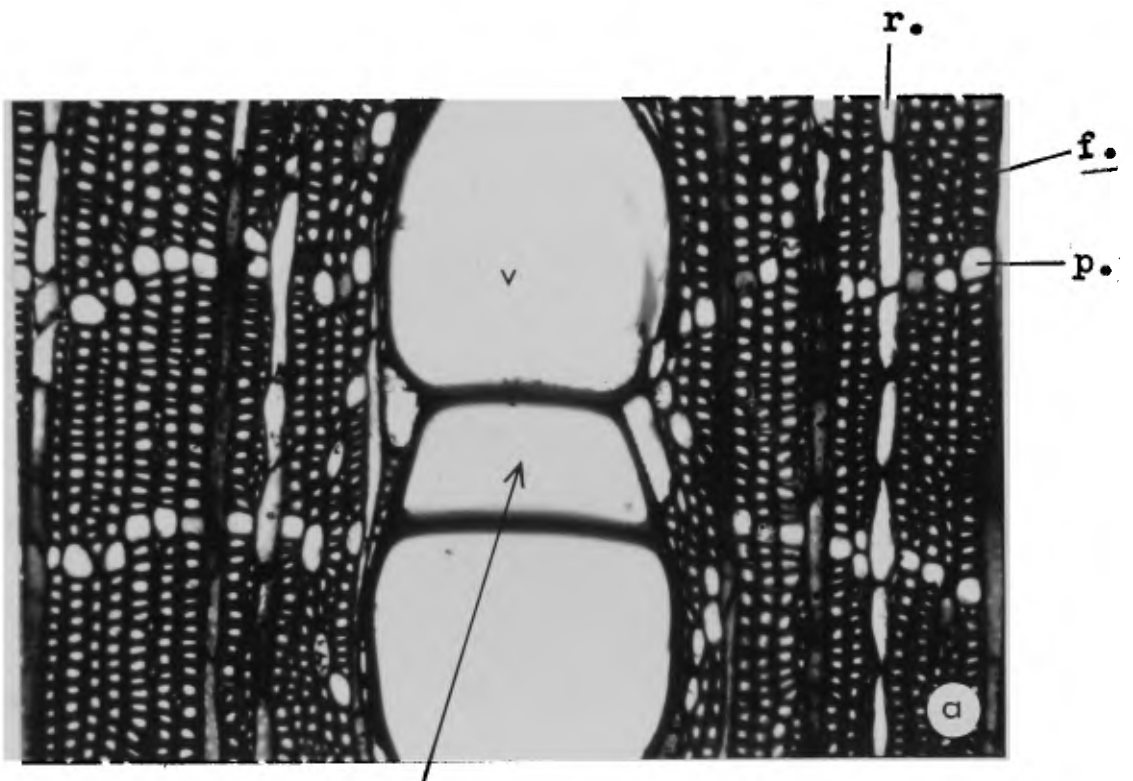


Fig. 1.17. Secondary xylem of Diospyros latisepala:
(a) transverse section 150x; (b) transverse section 50x;
(c) tangential section 50x; (d) radial section 50x.
In (a) note that the parenchyma is scattered, in vasicentric sheaths, and in uniseriate lines.

f: fibre; p: parenchyma; r: rays; v: vessel.



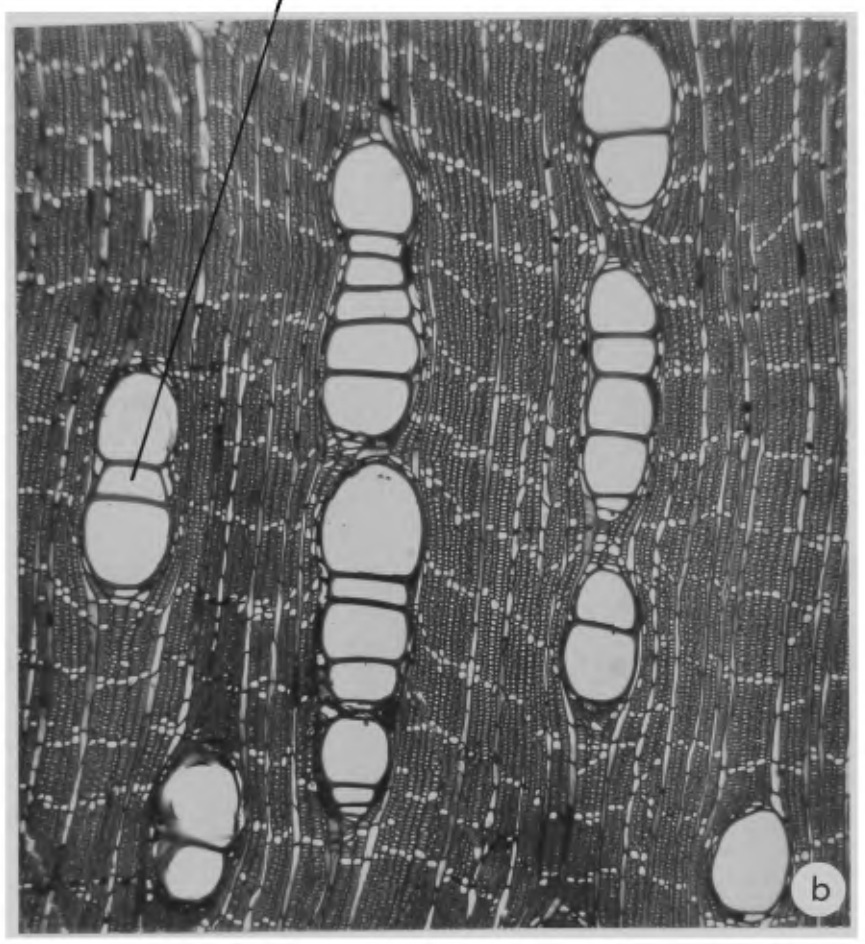


Fig. 1.18. Secondary xylem of Diospyros pseudo-malabarica in transverse section: (a) 150x (b) 50x. Note that parenchyma is in uniseriate lines, with a few scattered, but not forming vasicentric sheaths.

f: fibre; p: parenchyma; r: ray; v: vessel.

Epidermis

After examining the epidermis of the seeds of 22 species (Appendix II), described under the section "gynoecium, fruit and seed", I became interested in the taxonomic possibilities of epidermal hairs. Initially, the hairs on the ovaries of the 76 species in table 1.3 were examined. Supplementary observations were made on calyces, corollas and finally on leaves. With regard to leaves, epidermal preparations of 41 species were made according to the method described in Appendix III. Transverse sections were also made whenever necessary. It became apparent as the study progressed that, unlike wood and pollen which are relatively uniform throughout the family, the epidermis offers a range of potentially useful characters for infra-family classification. Table 1.6 summarises the main features observed.

Hairs

Four kinds of hairs were detected (fig. 1.19): (i) multicellular glandular (ii) unicellular simple (iii) unicellular two-armed, (iv) peltate. This fully confirms the range of types established by Solereder (1908, 1914).

Multicellular glandular hairs are club-shaped, consisting of a narrow uniseriate stalk and a swollen usually multicellular head. Apparently unicellular heads occur in *D. ehreticoides* and *D. sylvatica*. The heads eventually disintegrate so that on old organs, only the stalks may be seen. Such hairs are sometimes concentrated on particular organs (e.g. calyx or ovary), sometimes dispersed over several organs, but in many species they are scarce, sporadic, and detectable only after a hard search among unicellular hairs. It will not be surprising if such hairs are eventually detected in most species of the

family. As they have never been recorded for other families in the Ebenales, such glandular hairs may prove to be diagnostic for Ebenaceae within the Order.

Table 1.5 ; Occurence of glandular hairs.

1.	Diospyros argentea	scarce, on leaves
2.	D. carpinifolia	scarce, on leaves
3.	D. cauliflora	scarce, on leaves
4.	D. dictyoneura	ovaries and corollas
5.	D. discolor	scarce, on leaves
6.	D. ebenum	calyx
7.	D. ehreticides	scarce, on leaves
8.	D. kaki	leaves and calyces
9.	D. latisepala	calyces and corollas
10.	D. lotus	scarce, on calyces
11.	D. malabarica	very dense on ovaries and fruits
12.	D. mutans	scarce, on leaves
13.	D. oldhamii	leaves and calyces
14.	D. rigida	dense, on ovaries and fruits
15.	D. roxburghii	calyces and leaves
16.	D. sumatrana	scarce, on leaves
17.	D. sylvatica	scarce, on leaves
18.	D. toposioides	leaves
19.	D. wallichii	leaves; scarce on ovaries

[In Africa, glandular hairs occur in several species of Royena. Solereder (1914) has also observed them on Tetraclis elusiaefolia.]

Unicellular hairs are simple or two-armed. If simple, they may occur in clusters (tufts) of two or more, but such clusters are rare. In Indo-Pacific species, I have seen only sporadic clusters of two, never more, hairs. But Mrs Caveney has drawn may attention to D. austro-africana in which dense tufts occur. In two-armed hairs, the arms are usually quite unequal. On nearly all the leaves examined, the unicellular hairs were either simple only or two-armed only, but in D. cauliflora, D. elmeri, and D. rigida, both types were found

on the same leaf. In D. foxworthyi both types were also seen but they can be arranged in a smooth sequence from simple hairs which are all small and deeply stained to large unstained hairs all of which are two-armed. The arms are always unequal. My interpretation is that in D. foxworthyi, the small deeply staining hairs are young and that as they mature, they develop a second arm and finally lose their cell contents in old age. Consequently in table 1.6, D. foxworthyi is entered as having two-armed hairs only. This example strongly indicates that the simple and two-armed conditions in Ebenaceae are developmentally very simple modifications of each other.

It is unusual to see a sequence of developing hairs on a mature leaf preparation, because hairs usually develop precocieusly, and, in many species, are shed as the organs bearing them become old. The degree of persistence of unicellular hairs varies greatly from species to species. Each unicellular hair has a basal portion or foot embedded in the epidermis, taking the place of an epidermal cell. As the hair grows old, loses its cell contents, dies, and drops off, it leaves behind a minute pit looking like a small domatium or gland. Such pits often form a regular pattern on the mature glabrous leaf.

Peltate hairs were first observed in D. hildebrandtii, D. nodosa and D. melanida (Solereder 1914). In D. hildebrandtii, they occur densely on young leaves but are mostly lost on mature ones except where sheltered in the upper groove of the midrib. Similar hairs occur in Euclea undulata where they were described by de Winter (1963) as "rust-coloured glands". In other species of Euclea, de Winter also mentions specks of "rust-brown granules" or "rust-brown granular exudate" on leaves, inflorescences or calyces. These are probably all peltate hairs. In D. hildebrandtii and E. undulata, such hairs

consist of plates of 6 - 10 or more radiating cells attached centrally by a uniseriate stalk of 1 - 4 cells.

Stomata

Stomata are located on the lower epidermis of leaves. The guard cells, which in surface view vary little from species to species, are level with other epidermal cells or slightly protruding or slightly sunken, but in five species, D. argentea, D. discolor, D. amboinensis, D. lolin and D. poncei, they are deeply sunken and surrounded by papillae. Papillae are described in more detail below. In D. austro-africana, stomata occur in the bottom of crypts.

Epidermal cells

Ordinary epidermal cells, i.e. those that are not guard cells nor hair-bearing cells, vary in shape and size, as seen in surface view. In outline, the walls (anticlinal walls) may be straight, curved or undulate (sinuate) but all degrees of gradation are seen from species to species, and it is consequently impossible to divide up this character into sharply defined states. In table 1.6 only two states are given, non-undulate (straight or curved) and undulate. The outlines of cells in the upper epidermis may differ from those in the lower of the same leaf. In general, Stace's (1965) observation that in leaves with undulate epidermal cells, the amount of undulation is greater on the lower than upper epidermis, is confirmed in Ebenaceae, but one exception is D. diepenhorstii which shows the reverse.

Epidermal cell size is difficult to measure because of the irregular shapes that may be involved. My impression is

that variation is smoothly continuous from the smallest to the largest, regardless of shape.

Subsidiary cells. The cells around each stoma vary in number from 3 to 9, but 4 - 6 is the commonest range encountered. In general, such cells do not differ from other epidermal cells and the condition is described as anomocytic (Metcalfe & Chalk 1950) but in some species, they differ somewhat in shape, size, or orientation (fig. 1.20). In all such cases, Stace's (1965) term "cyclocytic" might be applied in a broad sense for lack of a better term although strictly, "cyclocytic" should only be applied when such subsidiary cells form a narrow ring i.e. when they are elongated tangentially round the stoma (fig. 1.20b), as in D. sylvatica, D. buxifolia and D. argentea. In D. lanceifolia, subsidiary cells are recognisable by being distinctly smaller. In the some of the species described below, subsidiary cells are distinguished by the arrangement of papillae.

Papillae (fig. 1.21) are projections from the surfaces of epidermal cells. They occur on the lower epidermis of D. argentea, D. discolor, D. amboinensis, D. lolin, D. poncei, D. lotus, D. australis and (fide Solereder 1908) D. pentamera. In D. argentea, D. discolor and D. poncei, each cell bears a papilla, more or less centrally placed. In D. amboinensis and D. lolin, papillae tend to be restricted to the cells around the sunken stomata. The correlation between papillae and sunken stomata is taxonomically significant because the five species in which these two characters appear together seem, on other evidence to belong together. All of them except D. poncei were in fact placed together in section Ebenaster by Bakhuizen. The position of D. poncei therefore needs to be re-assessed. In D. lotus, D. australis and presumably D. pentamera, the papillae occur one to each cell but the stomata are not sunken. In D. lotus papillae are indistinct or absent on some specimens.

Table 1.6. Epidermal characters.

(1) Glandular hairs: + observed
- not observed

(2) Unicellular hairs: 1 simple, 1* tufted
2 two-armed
- not observed

(3) Upper epidermal cells: und undulate
non non-undulate

(4) Lower epidermal cells: und undulate
non non-undulate

(5) Guard cells: sk sunken
ns not sunken

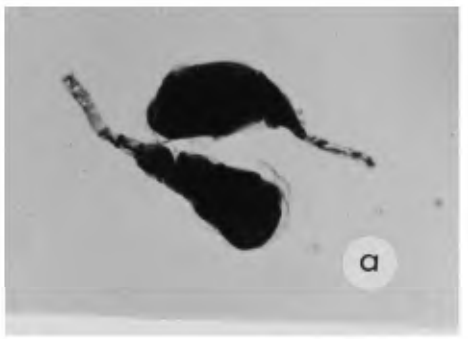
(6) Number of cells around stomata

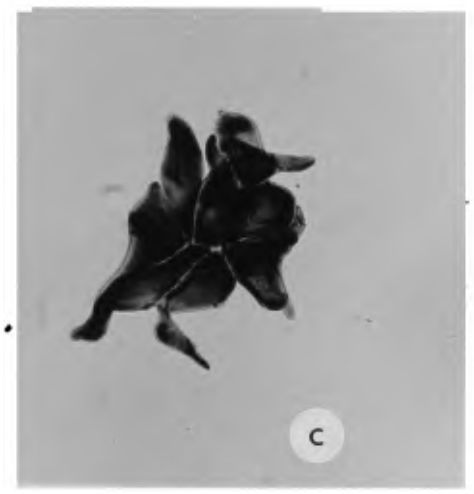
(7) Stomata: ano anomocytic
cyc cyclocytic

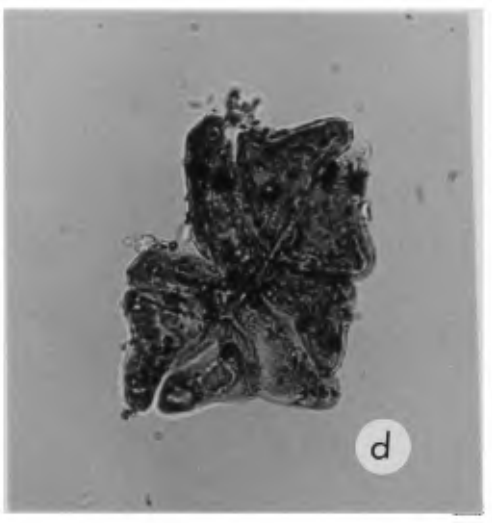
(8) Papillae: + present
- absent

Specimen	1	2	3	4	5	6	7	8
1. D. ambcinensis Teysmann 1917	-	2	non	non	sk	5-7	cyc	+
2. D. argentea FRI 11175	+	2	non	non	sk	4-6	cyc	+
3. D. australis Cunningham s.n.	-	1	non	non	ns	6-8	ano	+
4. D. austro-africana Wurts 1485	-	1*	non		ns			-
5. D. brideliifolia Elmer 9722	-	1	non	non	ns	5-6	ano	+
6. D. buxifolia FMS 13242	-	1	non	und	ns	4-6	cyc	-
7. D. carpinifolia Achmad 1081	+	1	non	und	ns		ano	-
8. D. cauliflora FRI 8562	+	1&2	und	und	ns	4-6	ano	-
9. D. clavigera RD 658	-	-	non	non	ns	3-4	ano	-
10. D. confertiflora FRI 2809	-	1	non	non	ns	4-7	ano	-
11. D. diepenhorstii SAN 16696	-	1	und	non	ns	4-6	ano	-
12. D. discocalyx SAN 26208	-	2	non	non	ns	4-6	ano	-
13. D. discolor Abu Bakar s.n.	+	2	non	non	sk	6-8	cyc	+
14. D. ebenum CF 105	-	-	und	und	ns	5-7	ano	-
15. D. ehretioides Kostermans 728	+	1	non	und	ns	4-6	ano	-
Kerr 1147	+	1	non	non	ns	6-7	ano	-
16. D. elmeri SAN 213629	-	1&2	und	und	ns	4	ano	-
17. D. ferrea FRI 5153	-	1	non	und	ns	4-6	ano	-
CF 874	-	1	non	und	ns	4-6	ano	-
Hoogland 6198	-	2	non	non	ns	4-6	ano	-
18. D. foxworthyi FRI 12546	-	2	non	non	ns	4-5	ano	-

Specimen	1	2	3	4	5	6	7	8
19. D. frutcscens								
FMS 28438	-	-	und	und	ns	5-6	ano	-
20. D. kaki								
Henry 3485	+	1	non	non	ns		ano	-
Savatier 809	+	1	nor	non	ns		ano	-
Parker s.n.	+	1	non	non	ns	4-5	ano	-
21. D. hildebrandtii								
Hildebrant 3319	-	1	non	non	ns	4-7	ano	-
22. D. kurzii								
KEP 76341	-	1	und	und	ns	5-6	ano	-
23. D. lanceifolia								
FRI 8194	-	1	und	und	ns	8-9	cyc	-
24. D. latisepala								
FMS 31211	-	-	non	non	ns	5-6	ano	-
25. D. lolin								
Beguin 2212	-	2	non	non	sk	6-8	cyc	+
26. D. lotus								
Faurie 13303	-	1	non		ns	4-5	ano	±
Wright 189	-	-	non		ns	4-6	ano	+
27. D. maingayi								
FRI 2807	-	-	non	non	ns	3-5	ano	-
FMS 41735	-	2	non	non	ns	4-5	ano	-
28. D. malabarica								
SFN 3447	-	-	non	non	ns	7-9	ano	-
29. D. montana								
Parkinson 1133	-	1	non	non	ns	5-6	ano	-
30. D. nutans								
SFN 32304	+	1	non	non	ns	4-5	ano	-
31. D. oblonga								
FRI 16106	-	-	non	non	ns	3-6	ano	-
32. D. oldhamii								
Wilson 10262	+	1	non	non	ns		ano	-
33. D. packmanii								
Nai Noe 89	-	2	non		ns			-
34. D. poncei								
Simeon 28720	-	2	non	non	sk	5-6	cyc	+
35. D. pyrrhocarpa								
KL 2087	-	1	und	und	ns	6-8	ano	-
36. D. ramulosa								
Thompson 457	-	1	non	non	ns	4-5	ano	-
37. D. ridleyi								
Ridley 1889	-	2	non	und	ns	4-6	ano	-
38. D. rigida								
FMS 28622	-	1&2	non	non	ns	5-9	ano	-
39. D. roxburghii								
Kerr 8851	+	1	non	non	ns	5	ano	-
Henry 11618	+	1	non	non	ns	5	ano	-
40. D. sumatrana								
FRI 104586	+	2	non	und	ns	4-6	ano	-
41. D. sylvatica								
Haines 2368	+	1	non	non	ns	3-6	cyc	-
42. D. toposioides								
FRI 6853	+	2	non	non	ns	4-7	ano	-
43. D. truncata								
FRI 5963	-	1	und	und	ns	5-6	ano	-
44. D. wallichii								
FRI 13049	+	1	und	und	ns	5-6	ano	-
45. Euclea ovata								
Fauresmith s.n.	-	1	non	non	ns	5-6	ano	-
46. E. undulata								
Collino 55	-	-	non	non	ns	5-8	ano	-







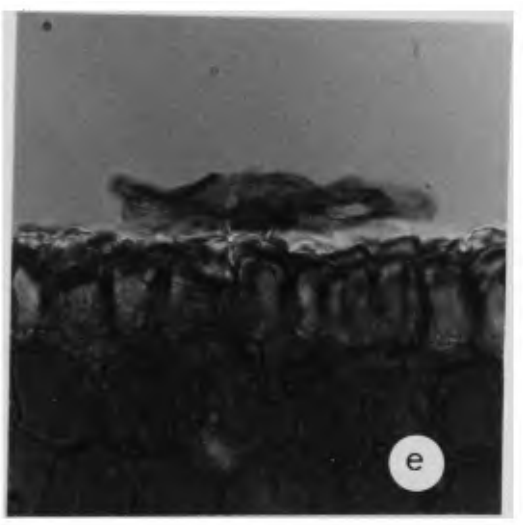
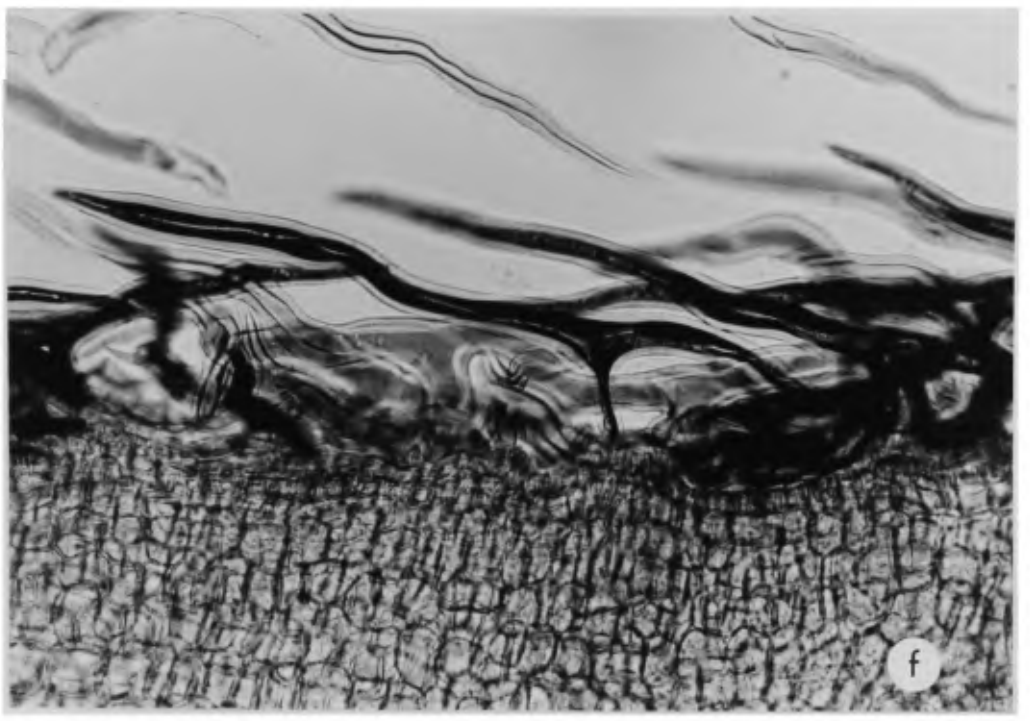
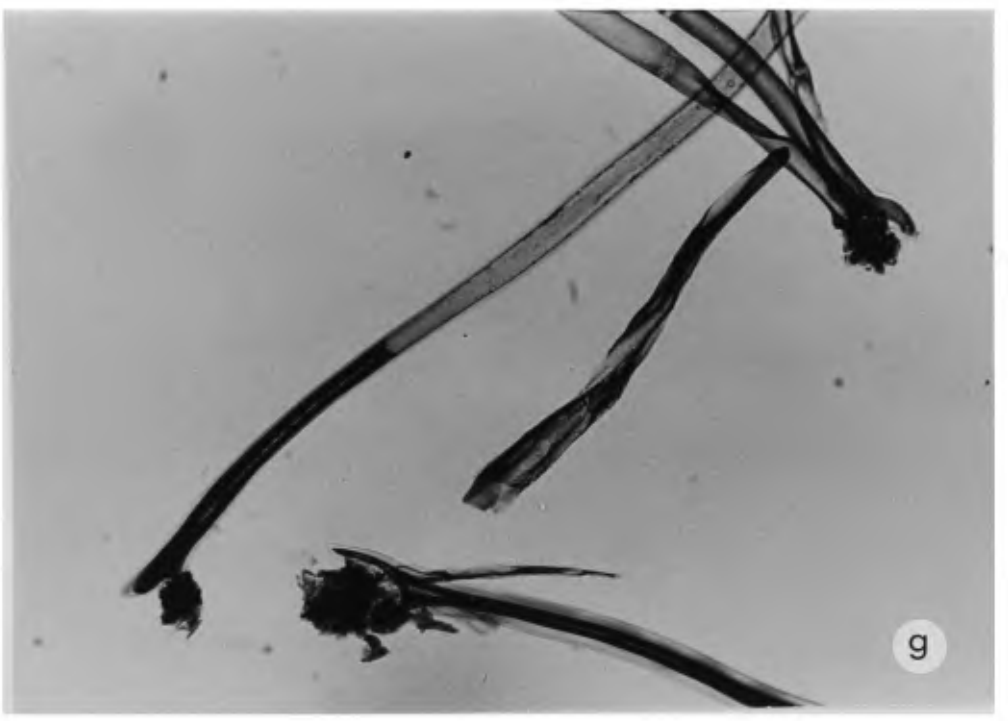


Fig. 1.19. Hairs: (a) multicellular glandular, from ovary of D. malabarica 150x; (b) mixture of multicellular glandular and unicellular simple, from ovary of D. dictyoneura 150x; (c) peltate, from leaf of D. hildebrandtii 150x; (d) & (e) peltate, in surface and side view respectively, from leaf of Euclea undulata 375x.





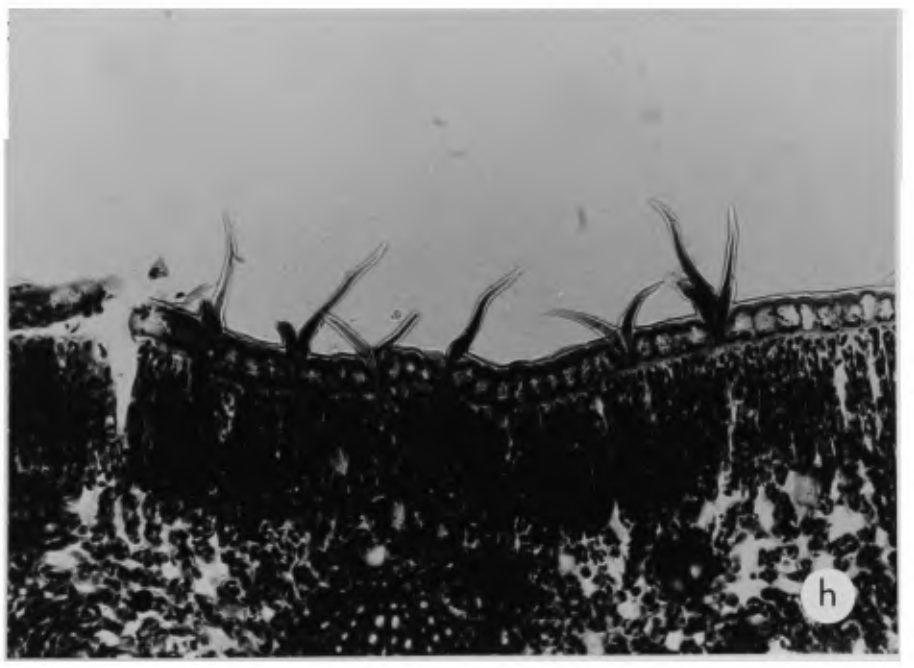


Fig. 1.19 continued. (f) unicellular two-armed, from male corolla of D. rufa 150x; (g) unicellular two-armed, but one arm very short, from ovary of D. oblonga 150x. (h)tufted, on leaf of D. austro-africana 150x.

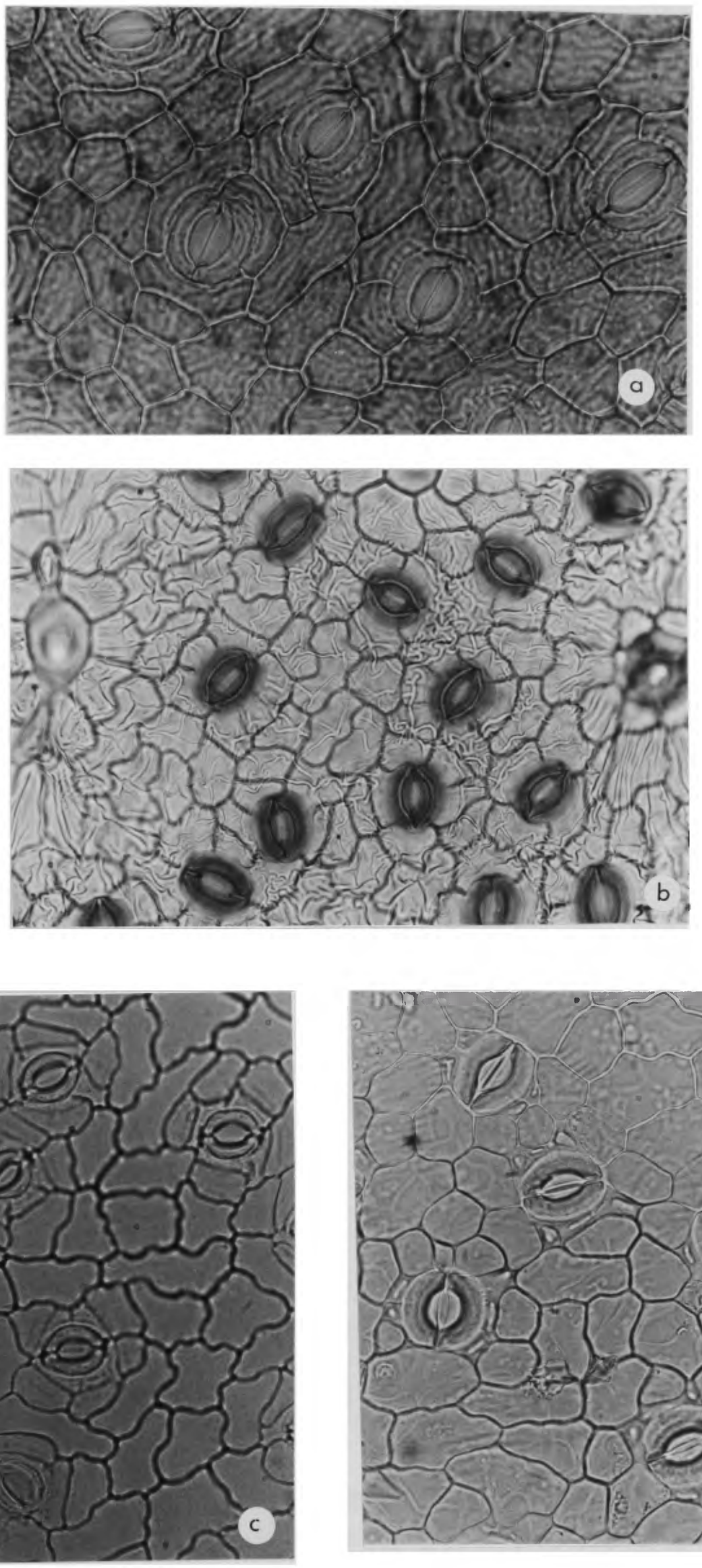


Fig. 1.20. Stomata and subsidiary cells at 375x:
(a) *D. maingayi*, anomocytic; (b) *D. wallichii*, anomocytic;
(c) *D. buxifolia*, cyclocytic; (d) *D. lanceifolia*, "cyclocytic" with 5 - 6 small subsidiary cells.

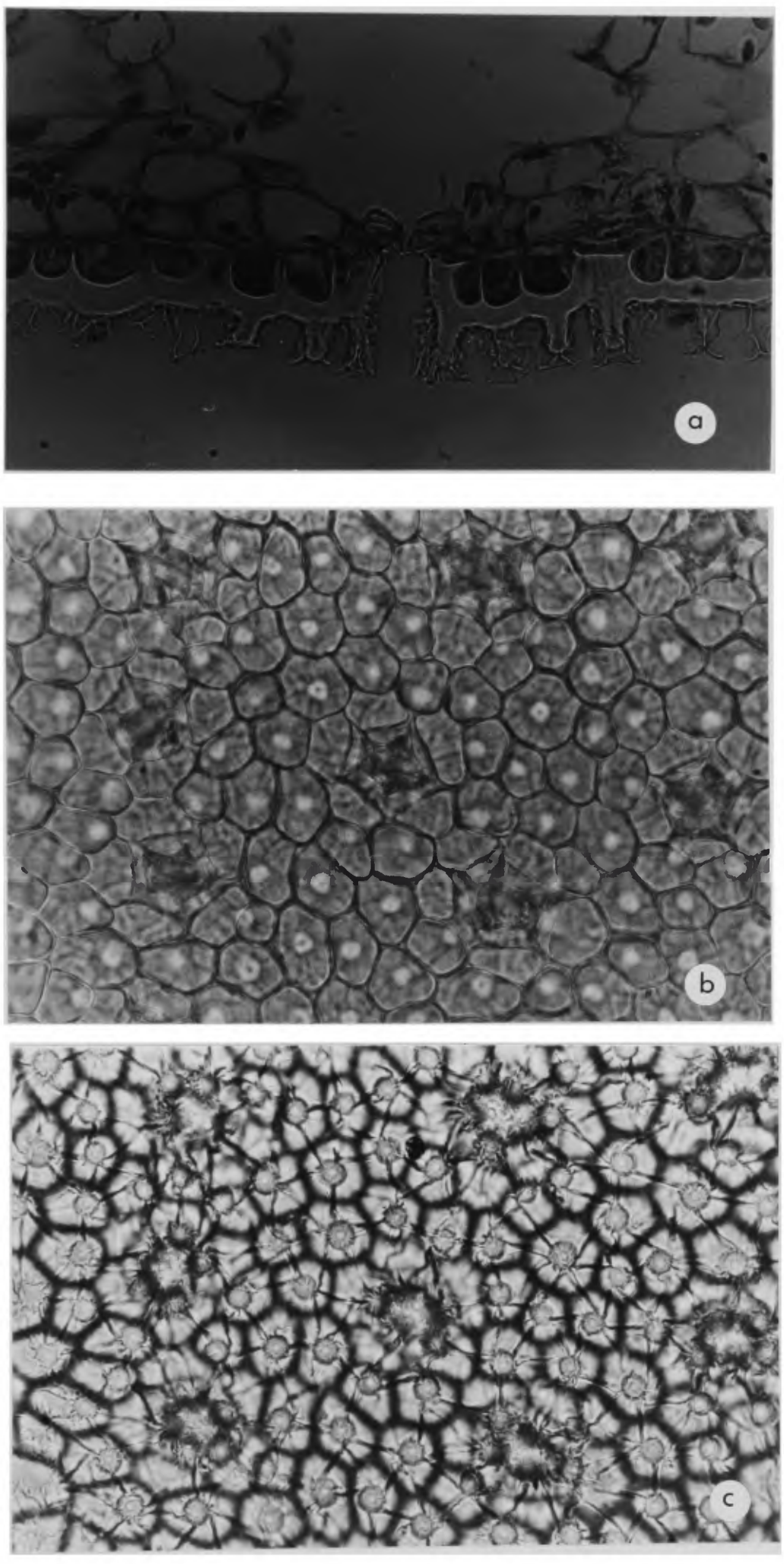
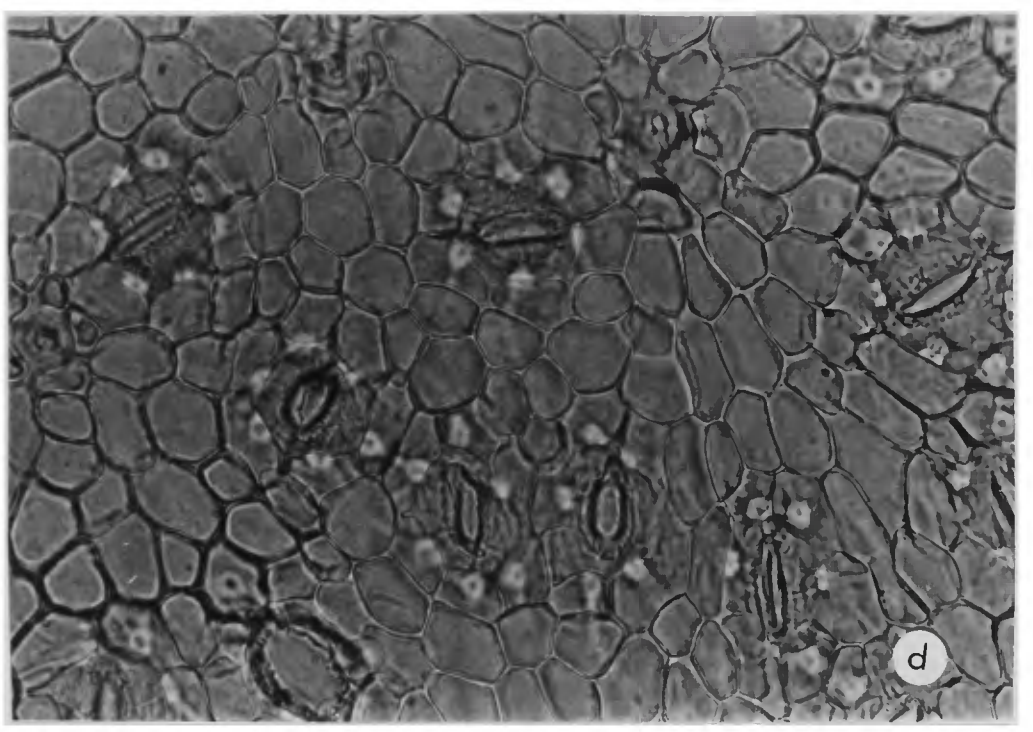


Fig. 1.21. Papillae at 375x: (a) - (c) D. argentea: (a) lower epidermis of leaf in transverse section showing papillae in side view, and a sunken stoma; (b) surface view with epidermal cells in focus; (c) same but papillae in focus. Note that the papillae are distributed one to each cell including subsidiary cells. The latter are arranged in polygons round the sunken stomata.



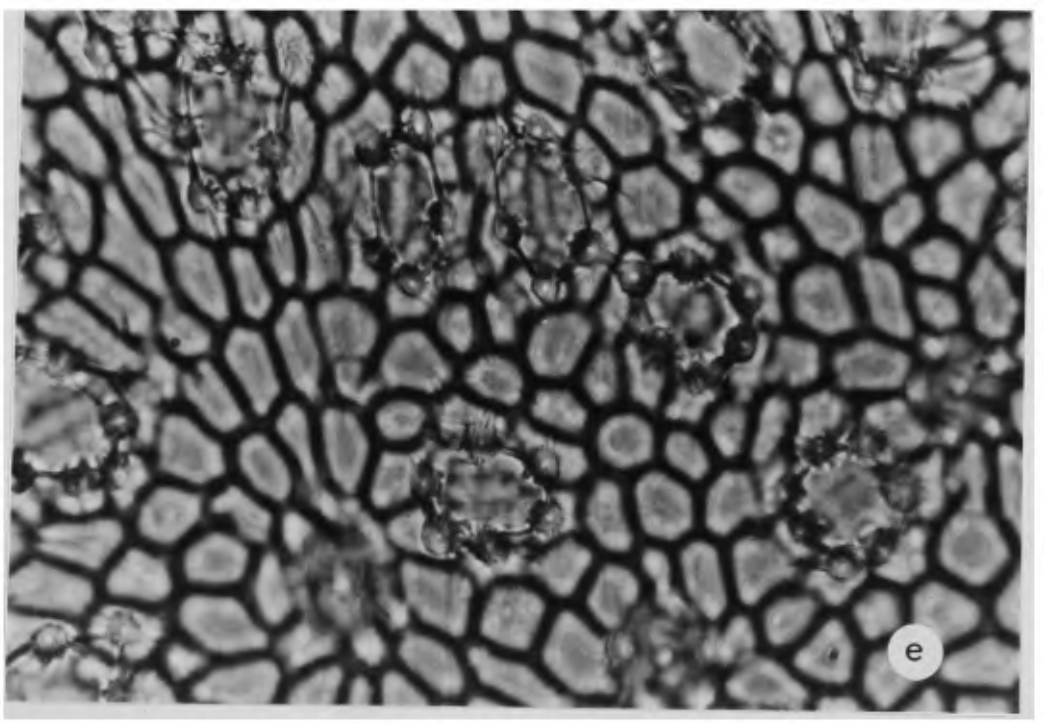


Fig. 1.21 continued. (d) - (e) *D. amboinensis*: (d) lower epidermis of leaf in surface view, with epidermal cells in focus; (e) same, but with papillae in focus. Note that the papillae are restricted to cells around the sunken stomata.

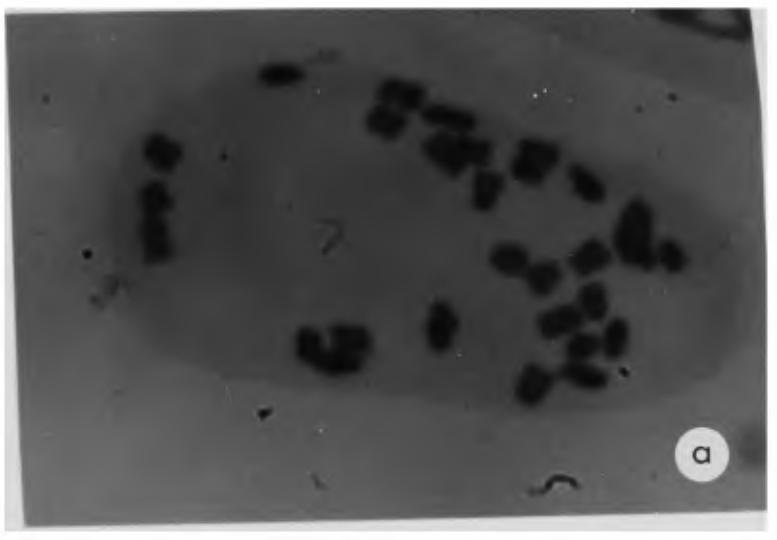
Chromosome numbers

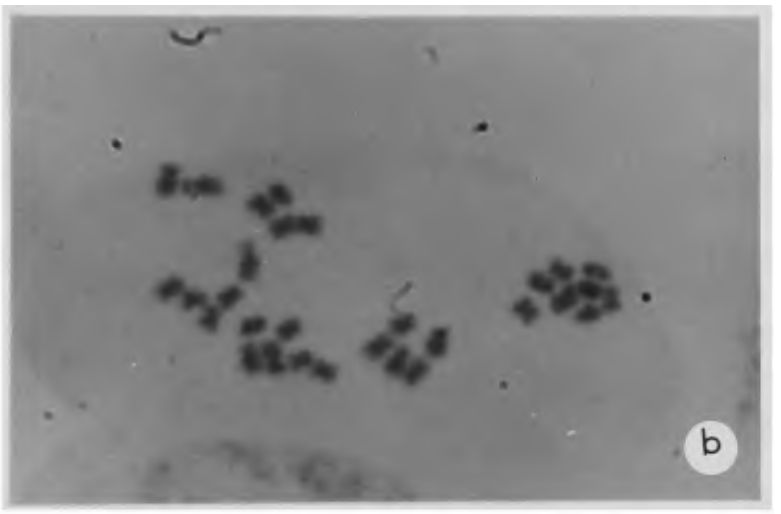
Chromosome counts have now been made for the 22 species of *Diospyros* and two species of *Euclea* listed below. Three of these counts were made by me during the course of this work. In the list, all the genera recognised by Hiern are represented except *Royena* and *Tetraclis*, and all the sub-genera recognised by Bakhuizen except *Cargillia* and *Mabacea*.

	2n	
D. confertiflora	30	Ng & Vosa unpublished.
D. discolor	30	Namikawa et al 1932
		Chatterji 1964
D. ebenum	90	Delay 1947
D. embryopteris	30	Chatterji 1964
D. eriantha	30	Hsu 1967
D. heudelotii	30	Mangenot S. & Mangenot G., 1957
D. ferrea subsp. sandvicensis	c. 48	Skottsberg 1955
D. ivorensis	30	Mangenot S. & Mangenot G., 1958
D. kaki	c. 54-56	Yasui 1915
	90	Namikawa & Higashi, 1928
		Namikawa et al. 1932
D. lotus	30	Namikawa & Higashi 1928
		Namikawa et al. 1932
D. macrophylla	30	Mangenot S. & Mangenot G., 1957
D. maingayi	30	Ng & Vosa, unpublished.
D. mespiliformis	30	Mangenot S. & Mangenot G., 1958
D. monbuttensis	30	Mangenot S. & Mangenot G., 1962
D. montana	30	Chatterji 1964
D. oocarpa	30	Chatterji 1964
D. sanza-minika	30	Mangenot S. & Mangenot G., 1957
D. soubreana	30	Mangenot S. & Mangenot G., 1962

	2n	
D. texana	30	Baldwin & Culp 1941
D. tricolor	30	Mangenot S. & Mangenot G., 1962
D. virginiana	60, 90	Baldwin & Culp 1941
	90	Namikawa et al. 1932
D. wallichii	30	Ng & Vosa, unpublished.
E. divinorum	30	Vosa, White & Styles, unpublished.
E. natalensis	30	Vosa, White & Styles, unpublished.

If we ignore the two approximate counts, by Skottsberg (D. ferrea subsp. sandvicensis) and Yasui (D. kaki) it becomes quite clear that a simple polyploid series 2n = 30, 60, 90 exists in the family with the basic number x = 15. Hence the karyotype emphasises the basic unity of the family Ebenaceae and provides no grounds for subdividing it.





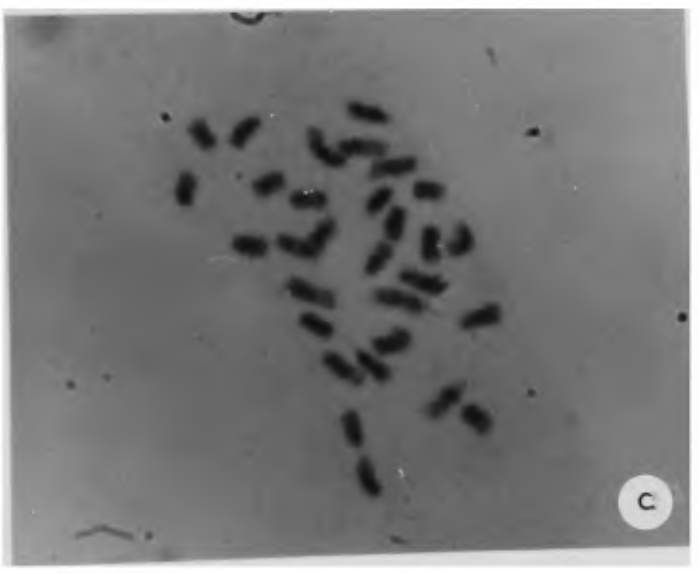


Fig. 1.22. Root-tip chromosomes at 1,500x (a) D. maingayi (b) D. wallichii (c) D. confertiflora.

Summary: a family description and discussion

The preceeding reports, together with other more generally known facts about the Ebenaceae, may be combined and summarised into a concise family description.

Trees or shrubs, without latex. Leaves simple, exstipulate; alternate, rarely opposite or sub-opposite, very rarely in whorls of three (some Euclea); with margins entire (except Euclea ovata crenulate); petiolate.

Inflorescence determinate, axillary, multi-bracteate, multi-florous, sometimes (especially in females) reduced to uniflorous condition by suppression of lateral buds. The resulting solitary flower terminates a bracteate peduncle.

Flowers articulated at base, unisexual, sporadically structurally hermaphrodite; regular; 3 - 5 (-8) merous.

Calyx mostly gamosepalous, sometimes polysepalous; lobes valvate or imbricate but absent in some gamosepalous species (calyx then truncate); persistent in fruit, when often accrescent; spreading, erect, or reflexed.

Corolla sympetalous; isomerous with calyx; the lobes contorted sinistrorsely (rare sporadic exceptions); tube always prominent; neck extremely narrow to quite wide.

In male flowers, stamens (3) - 12 - 20 (-100); commonly inserted at base of corolla tube, rarely towards the neck, sometimes on the receptacle; usually hidden within the corolla tube; often in two whorls; anthers ovate, lanceolate, or linear, erect, basifixed, dehiscing by longitudinal slits

which sometimes gape open near apex initially to resemble pores; filaments free or united in pairs, triads or larger fascicles, or into a central column. Pistillode rarely absent, usually represented by a conic lump of tissue without ovules or styles, sometimes well-formed enough in the terminal flower of a male cyme for the flower to be structurally hermaphrodite, and perhaps sporadically functionally so.

p/e(0.9)1.2-1.5,
Pollen globular to ellipsoid, tri-colporate, smooth.

In female flowers, ovary superior, sessile, multilocular, 2 - 8 carpellate with corresponding number of styles free or basally to fully connate. Internally, each carpel bears a pair of ovules, but in all except 11 species, each carpellary chamber is bisected by a false septum so that each ovule lies in its own locule. The resulting number of locules are double the number of carpels, i.e. 4, 6, 8, 10, 12, 14, 16. Staminodes reduced to a single whorl of sterile epipetalous lobes fewer in number than stamens of corresponding male, rarely altogether absent.

Ovules with apical placentation, oblong, anatropous, bitegmic, tenuinucellate, with raphe descending on outer side. Total number 4, 6, 8, 10, 12, 14 or 16.

Fruit a berry with fibrous to pulpy pericarp, nearly always with a hypodermal stone-cell layer; indehiscent except some African species; always with a persistent calyx at base.

Seeds 1 (by abortion) to 16, pendulous, usually with a distinct vascular loop round the periphery; hilum small, apical, inconspicuous; testa thin, parenchymatous soft to leathery; endosperm horny, abundant, smooth to ruminate; embryo upside-down, with two well-developed foliaceous cotyledons and a

strongly developed radicle.

Seedling with prominent taproot emerging from apex of seed (through micropyle); cotyledons emergent and photosynthetic, sub-emergent (shed as it is about to emerge or soon after) or non-emergent (shed with seed body); a strong hypocotyl develops usually, but rarely it does not (D. lycioides) and the photosynthetic cotyledons lie on the ground.

Wood with vessels solitary and in radial multiples of 2, 3, 4 or sporadically more; with simple perforations; small (to 8μ diameter) vessel-to vessel, vessel-to-ray, and vessel-to-parenchyma pits. Parenchyma predominantly apotracheal, scattered and in numerous uniseriate lines; sometimes forming vasicentric sheaths round the vessels. Rays 1 - 2 cells, rarely 3 - 4 cells wide; less than 1 mm. high; heterogeneous. Fibres with small pits.

Unicellular trichomes occur on all species and may be simple (solitary except densely tufted in D. austro-africana), or two-armed. Club-shaped multicellular glandular hairs occur sporadically, probably throughout the family but conspicuous only in a few species. Peltate hairs occur in some African and Mauritian species.

Chromosome series 2n = 30, 60, 90; basic number x = 15; most species diploid.

Discussion

The description of the Ebenaceae may be considered to consist of (a) constant characters and (b) variable characters. Constant characters e.g. leaves simple, corolla sympetalous, ovules anatropous, are uni-state characters i.e. they have a

single expression throughout the family. Variable characters are those that have a range of expressions e.g. leaves alternate rarely opposite or whorled, pistillode present or absent, pollen globular to ellipsoid.

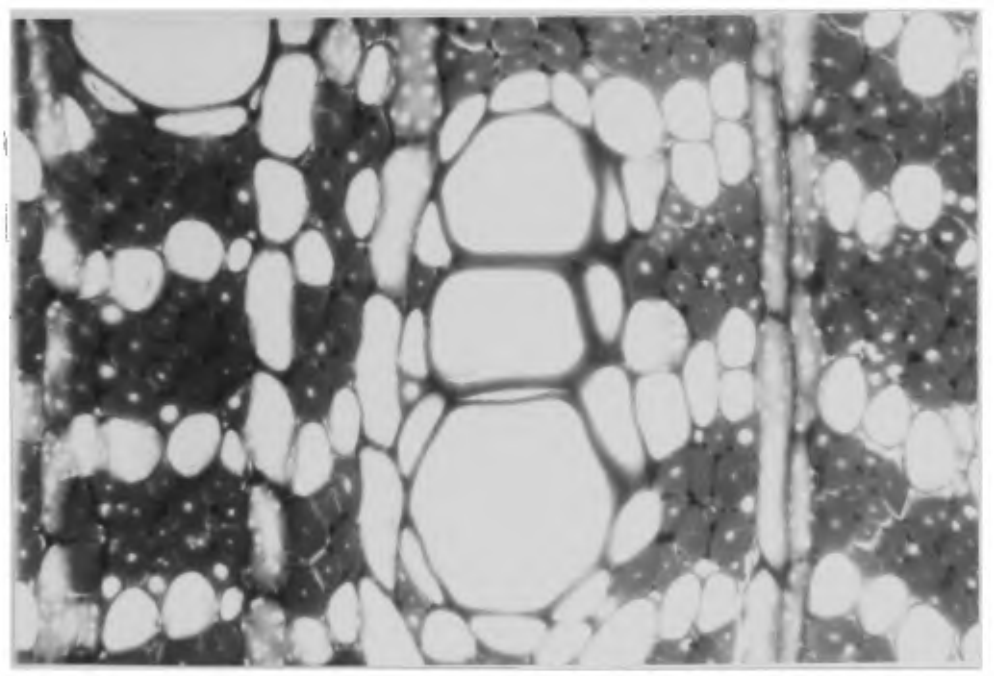
From the point of view of describing a taxon, constant characters are valuable because the larger the number of such characters, the more unified a mental or verbal picture of the taxon that can be built up.

The Ebenaceae is a family with a relatively large number, so far as angiosperm families go, of constant characters :- Woody plants without latex. Leaves exstipulate, petiolate. Inflorescence determinate, axillary, bracteate. Flowers articulated at base, regular. Calyx persistent. Corolla sympetalous. Anthers erect, basifixed, dehiscing by longitudinal slits. Pollen tri-colporate, smooth. Ovary superior, sessile, multi-locular, each carpel bi-ovulate. Ovules pendulous, oblong, anatropous, bitegmic, tenuinucellate, with raphe descending on outer side. Fruit a berry with persistent calyx at base. Seeds pendulous; hilum small, apical, inconspicuous; testa smooth, parenchymatous; endosperm horny, abundant; embryo upside-down, with two well-developed foliaceous cotyledons and a strongly-developed radicle. Seedlings with prominent taproots. Wood vessels with simple perforations and small pits, rays short and heterogeneous. Basic chromosome number x = 15.

In addition, the family has a number of characters with one state extremely common and the others rare. Such characters are very nearly constant : Leaves alternate, rarely opposite or whorled; margins entire very rarely crenulate. Flowers unisexual rarely hermaphrodite. Corolla isomerous with calyx (sporadic exceptions), corolla lobes contorted sinistrorsely (rare sporadic exceptions). Carpel-chambers in

all except 11 species bisected each by a false septum to give uni-ovulate locules. Male flowers nearly always with pistillodes. Female flowers nearly always with staminodes. Fruit indehiscent except a few African species.

The abundance of constant and nearly-constant characters, contributing to a very strongly unified ground-plan or type-image of the family, makes it easy to recognise species of the family and conversely, to exclude specimens erroneously placed in it. In the course of this work five species were so excluded. Four of these exclusions have been published (Ng 1970, see Appendix 9).



secondary xylem of Lissocarpa guianensis in t.s., 150x

PART 2: THE LIMITS of the FAMILY: A CRITICAL COMPARISON of EBENACEAE with RELATED FAMILIES of the ORDER EBENALES

Introduction

Secondary xylem

Pollen

Gynoecium

Trichomes

Inflorescence

Comparison with Sapotaceae

Sarcospermataceae

Comparison with Lissocarpaceae

Comparison with Symplocaceae

Comparison with Styracaceae

The taxonomic structure of the Order

Introduction

The Order Ebenales, as constituted by Bentham and Hooker (1873) consisted of the families Ebenaceae, Sapotaceae (including Sarcosperma), and Styracaceae (including Symplocos and Lissocarpa). In the systems of *Engler (1964), Cronquist (1968) and Takhtajan (1969), the composition of the Order remains unchanged but there have been some internal readjustments due to the recognition of the monotypic families Symplocaceae and Lissocarpaceae by all three authors, and Sarcospermataceae by Engler. Engler groups the families into two sub-orders: Sapotineae, comprising the two families Sapotaceae and Sarcospermataceae, and **Ebenineae comprising Ebenaceae, Styracaceae, Lissocarpaceae, Symplocaceae.

Hutchinson (1959) differs from the others in segregating the families into two widely separated Orders: Ebenales comprising Ebenaceae, Sapotaceae, Sarcospermataceae, and Styracales comprising Styracaceae, Symplocaceae, Lissocarpaceae.

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* In this account, all references to Engler refer to the current (12th) edition of the 'Syllabus', unless otherwise specified, in which the Ebenales is by Wagenitz, but the main outline of classification of the Order remains as it was set by Engler in previous editions.

** The Hoplestigmataceae is doubtfully placed in Ebenineae in the Engler system. It appears in Bixales, Violales and Polemoniales in the systems of Hutchinson, Cronquist and Takhtajan respectively. For this study, I have ignored the family.

In this part of the study, I was concerned with testing the limits of the Ebenaceae against those families that have been reputed to be closest related to it. It has been established in Part I that the Ebenaceae enjoys a high degree of internal coherence as measured by the large number of characters shared in common by all its species. However its validity as a natural group depends not only on its internal coherence but also on its distinctness from all its relatives, i.e. on the presence of a taxonomic "gap" (i.e. sum total of differences between taxa) around the Ebenaceae isolating it from other families of the Order. The nature of this "gap" is closely examined here but as a side-effect of such a study, light is also thrown on the taxonomic structure of the Order as a whole.

For the purposes of this study, the Order Ebenales is considered to consist of Ebenaceae, Sapotaceae, Sarcospermataceae, Lissocarpaceae, Symplocaceae and Styracaceae. In making comparisions, I have used the literature as a guide but in all cases, I have checked the accuracy of previously published descriptions by examining a range of representatives of each family. For Sapotaceae and Sarcospermataceae, I have also been able to draw upon previous experience in revising these two families for the Tree Flora of Malaya (Ng, in press). The weakest link in this account is the Styracaceae which badly needs another world revision because the number of genera has increased since the last (Perkins 1907) from 6, to 12 (Hutchinson 1967), and most of these are poorly understood. My impression of the family is that it is far more variable than all the others and possesses sharp internal discontinuities. The main published sources I have used are as follows:

Sapotaceae	:	Lam (1925, 1927)
Sarcospermataceae	:	Lam (1925, 1926)

Lissocarpaceae	:	Oliver (1895)
		Gleason (1926)
Symplocaceae	:	Brand (1901)
		van Steenis (1948)
Styracaceae	:	Copeland (1938)
		Perkins (1907)
		van Steenis (1932)

and also Bentham & Hooker (1876), Hutchinson (1959, 1967), Engler (1964), Cronquist (1968).

I had originally intended to present the results as a series of comparisons taking, each time, Ebenaceae with one other family and examining their differences. However certain organs and structures require detailed commentaries which are more conveniently made for the Order as a whole. Hence I present these commentaries first, and tabulate the family comparisons later.

Secondary Xylem

The materials upon which this comparison of secondary xylem is based are 89 wood slides of Ebenaceae, 90 of Sapotaceae, 1 of Sarcospermataceae, 1 of Lissocarpaceae, 6 of Styracaceae and 7 of Symplocaceae, all belonging to the Commonwealth Forestry Institute, Oxford. The Ebenaceae list is given in Table 1.4 and the rest in Appendix 5. Table 2.1 gives a comparative summary of all the families concerned.

Ebenaceae wood is extremely uniform and has been described in Part 1. The wood of Sapotaceae is equally uniform and, as has already been noted by other authors (e.g. Metcalfe & Chalk 1950), bears a close resemblance to Ebenaceae. The only consistent difference between the two is that vessel-to-ray and vessel-to-parenchyma pits in Ebenaceae do not exceed 8μ in diameter whereas in Sapotaceae, any 1 x 1 cm. specimen will show some pits 10 - 20μ in diameter. Such pits are best observed in radial sections (fig. 2.1).

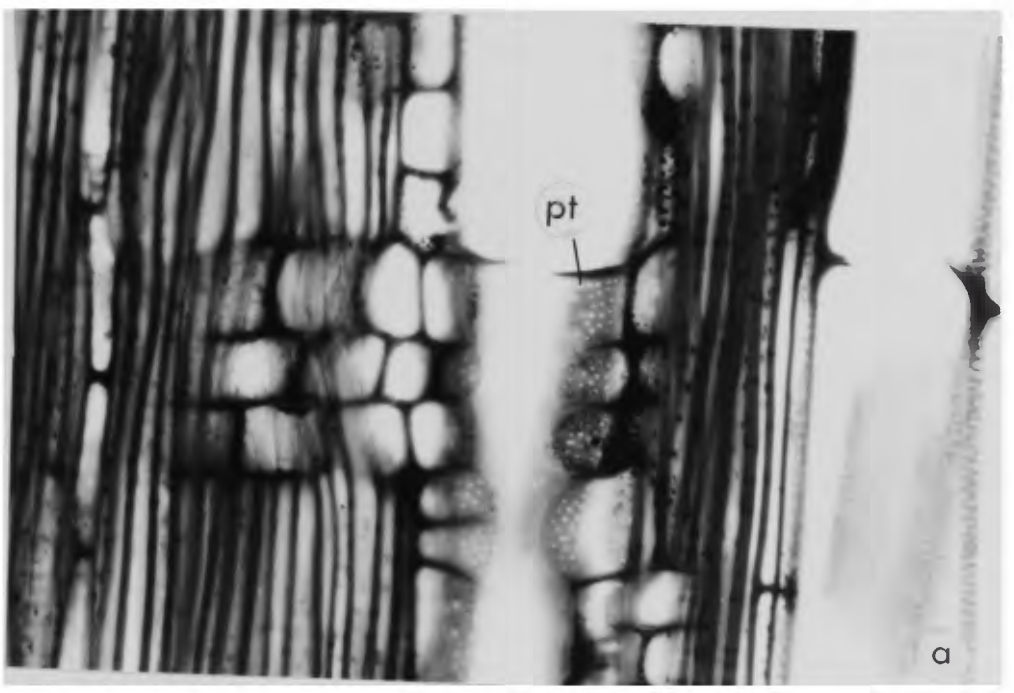
The wood of Sarcospermataceae (fig. 2.2) is identical to that of Sapotaceae (fig. 2.3).

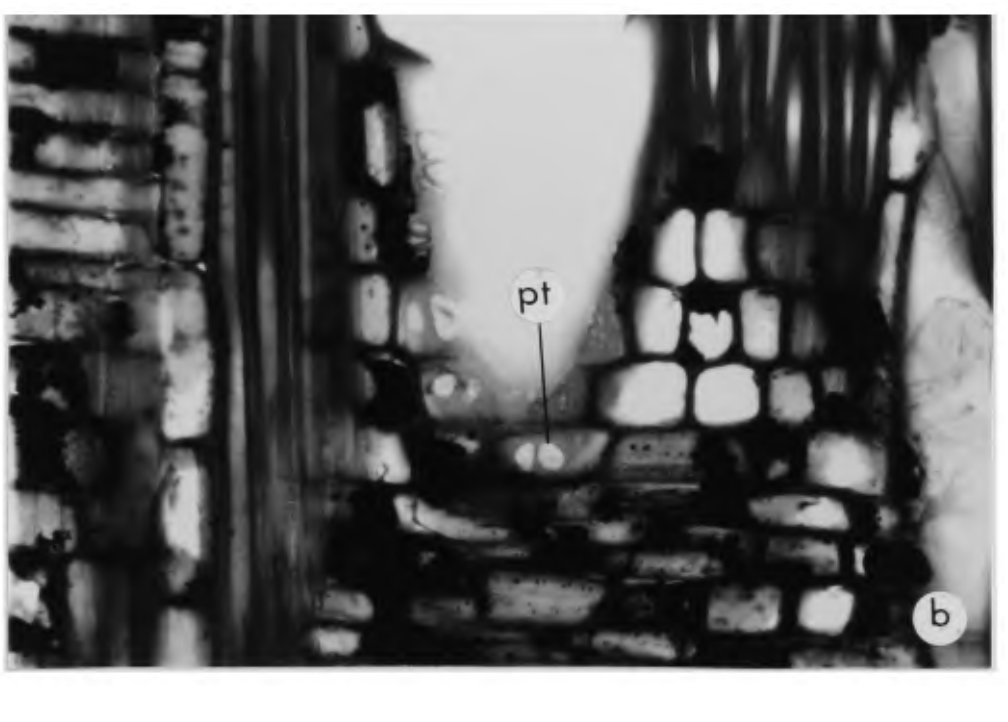
Lissocarpaceae (fig. 2.4) differs from Ebenaceae only in having taller rays (best observed in tangential sections), those in the former being predominantly over 1 mm. high while those in the latter are predominantly less than 1 mm. high in any given specimen.

Styracaceae (fig. 2.5) and Symplocaceae (fig. 2.6) differ strikingly from all the preceeding families in having scalariform plates rather than simple vessel perforations. The plates in Styracaceae have usually fewer than 20 bars whereas those in Symplocaceae have usually more than 20 fine bars.

Symplocaceae differs from all the other families in having exclusively solitary vessels and occassional spiral thickening in the fibres.

The evidence from wood structure is that each of the families is separable by constant differences except Sarcospermataceae which cannot be distinguished from Sapotaceae. The families with the fewest differences from Ebenaceae are Sapotaceae (including Sarcospermataceae) and Lissocarpaceae.





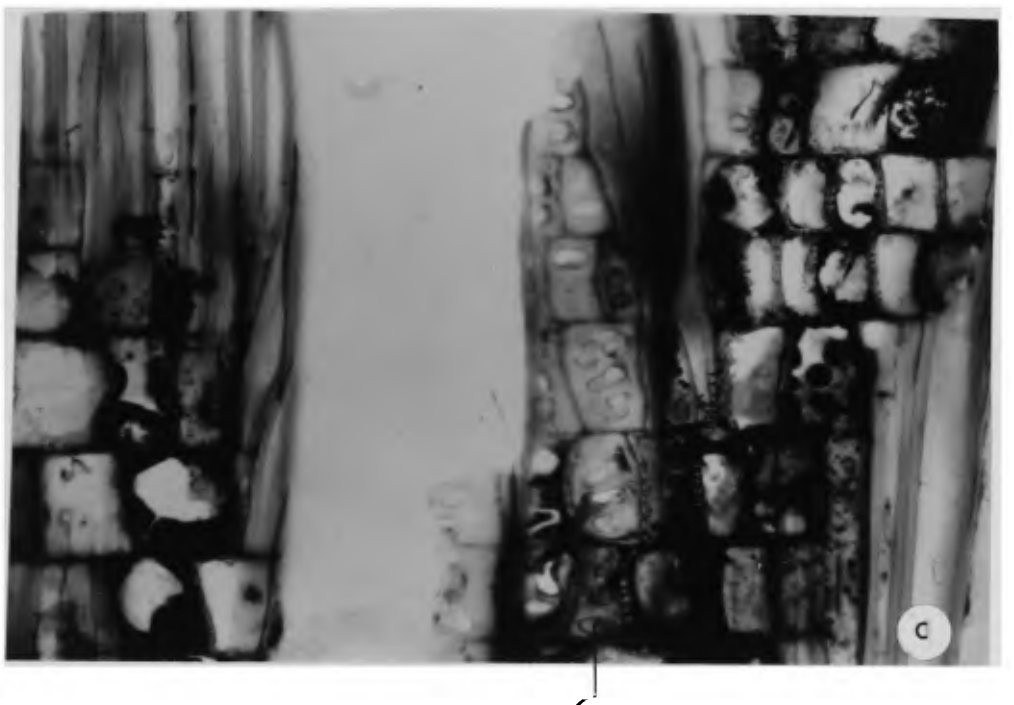
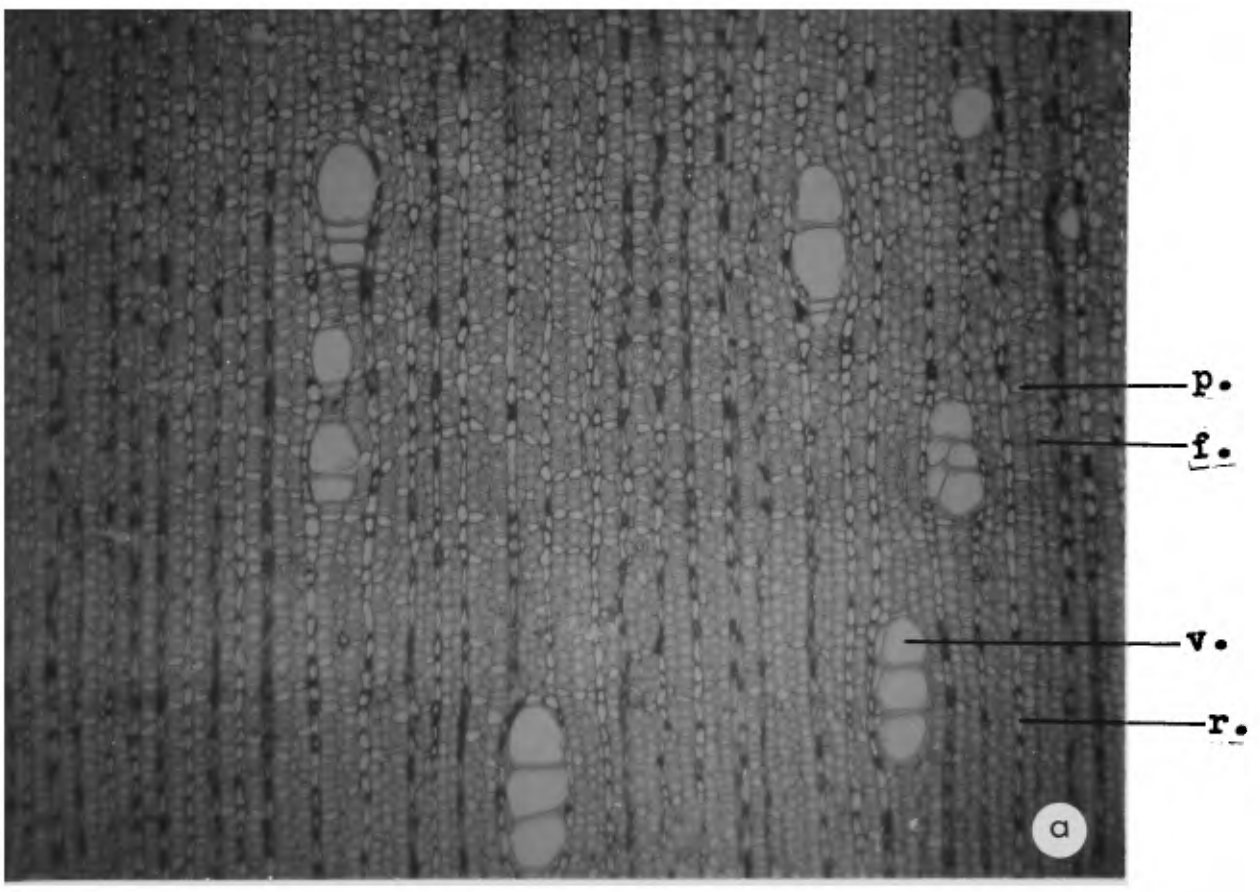


Fig. 2.1. Vessel-to-ray pitting in Ebenaceae, Sapotaceae and Sarcospermataceae at 150x: (a) Diospyros latisepala; (b) Palaquium hispidum; (c) Sarcosperma paniculatum.

pt: pit.



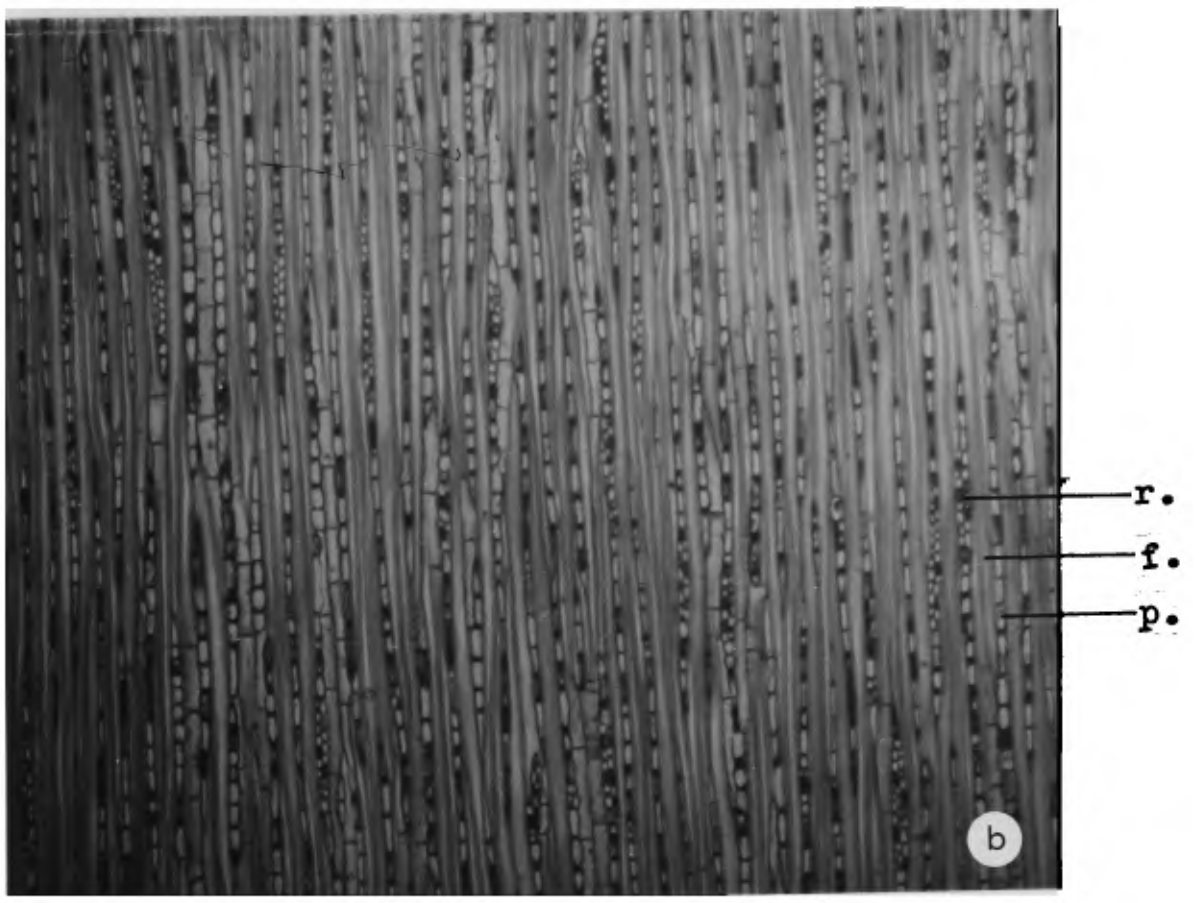


Fig. 2.2. Wood of Sarcosperma paniculatum 50x.
(a) transverse section; (b) tangential section.

f: fibre; p: parenchyma; r:ray; v: vessel.

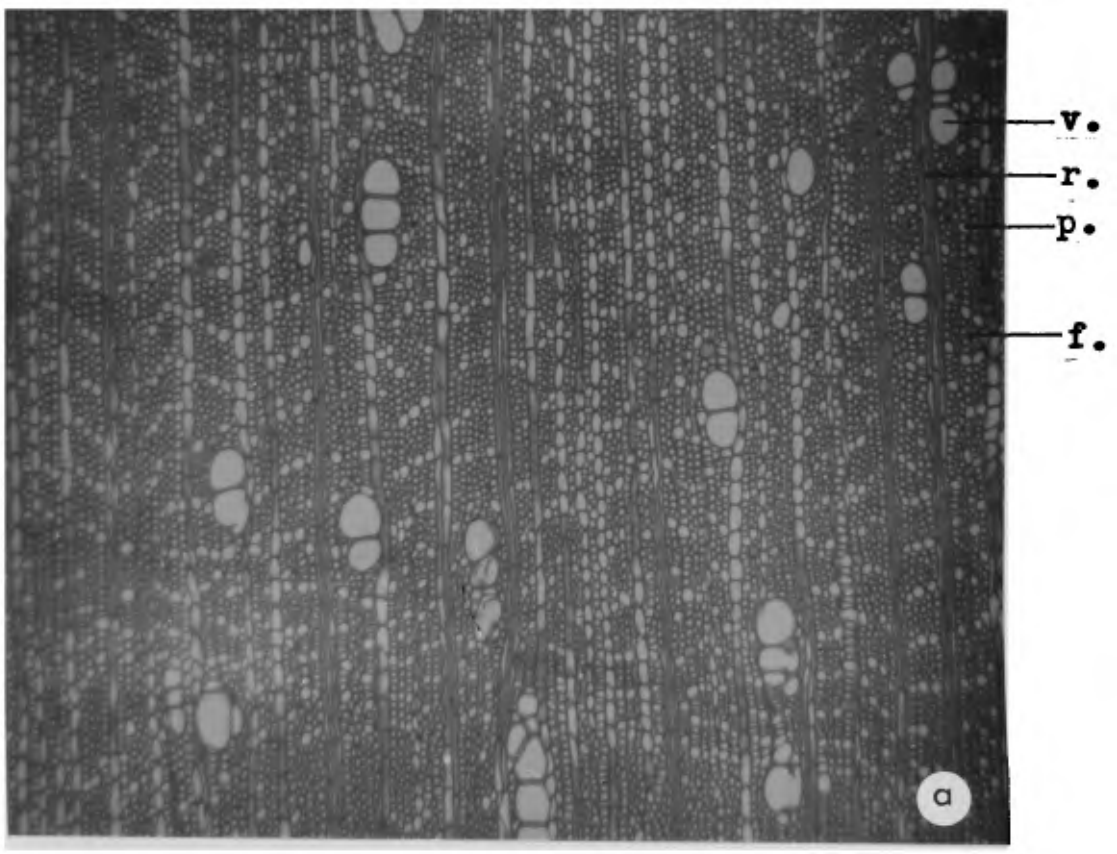


Fig. 2.3. Wood of Chrysophyllum lanceolatum (Sapotaceae) 50x. (a) transverse section; (b) tangential section.

f: fibre; p: parenchyma; r: ray; v: vessel.

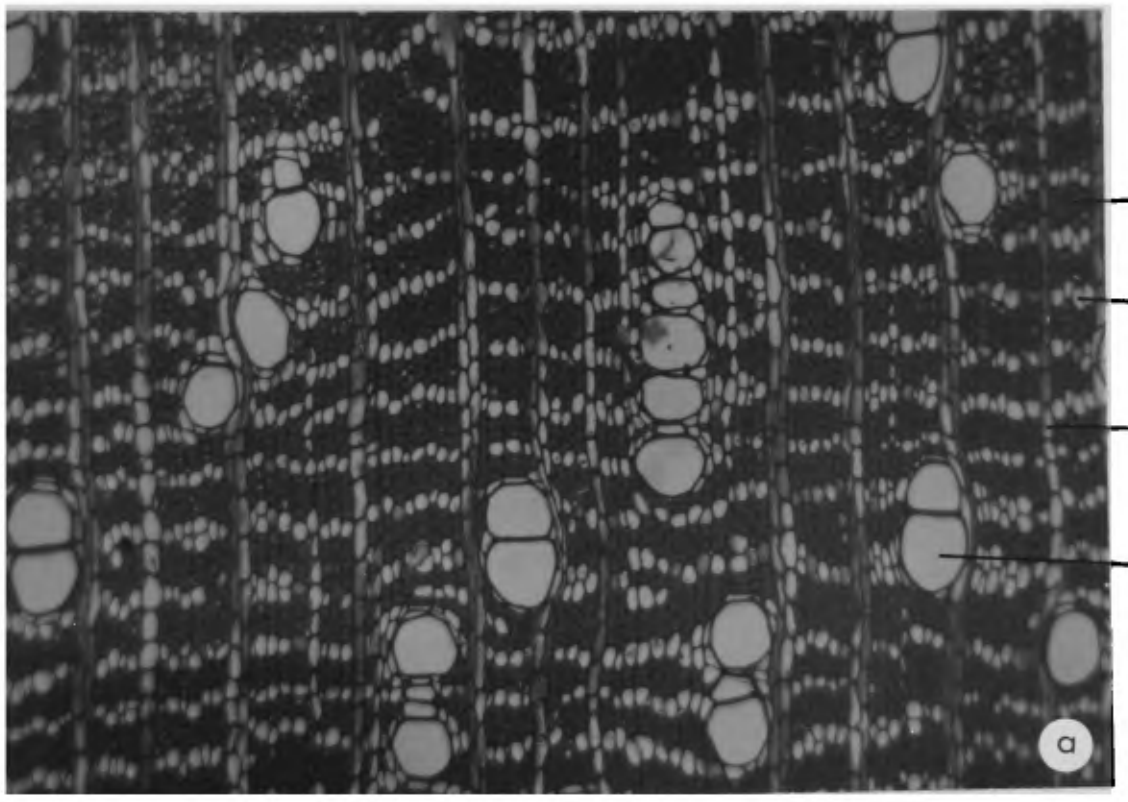


Fig. 2.4. Wood of Lissocarpa guianensis 50x. (a) transverse section; (b) tangential section; (c) radial section. Compare ray height in (b) with fig. 1.17c.

f: fibre; p: parenchyma; r: ray; v: vessel.

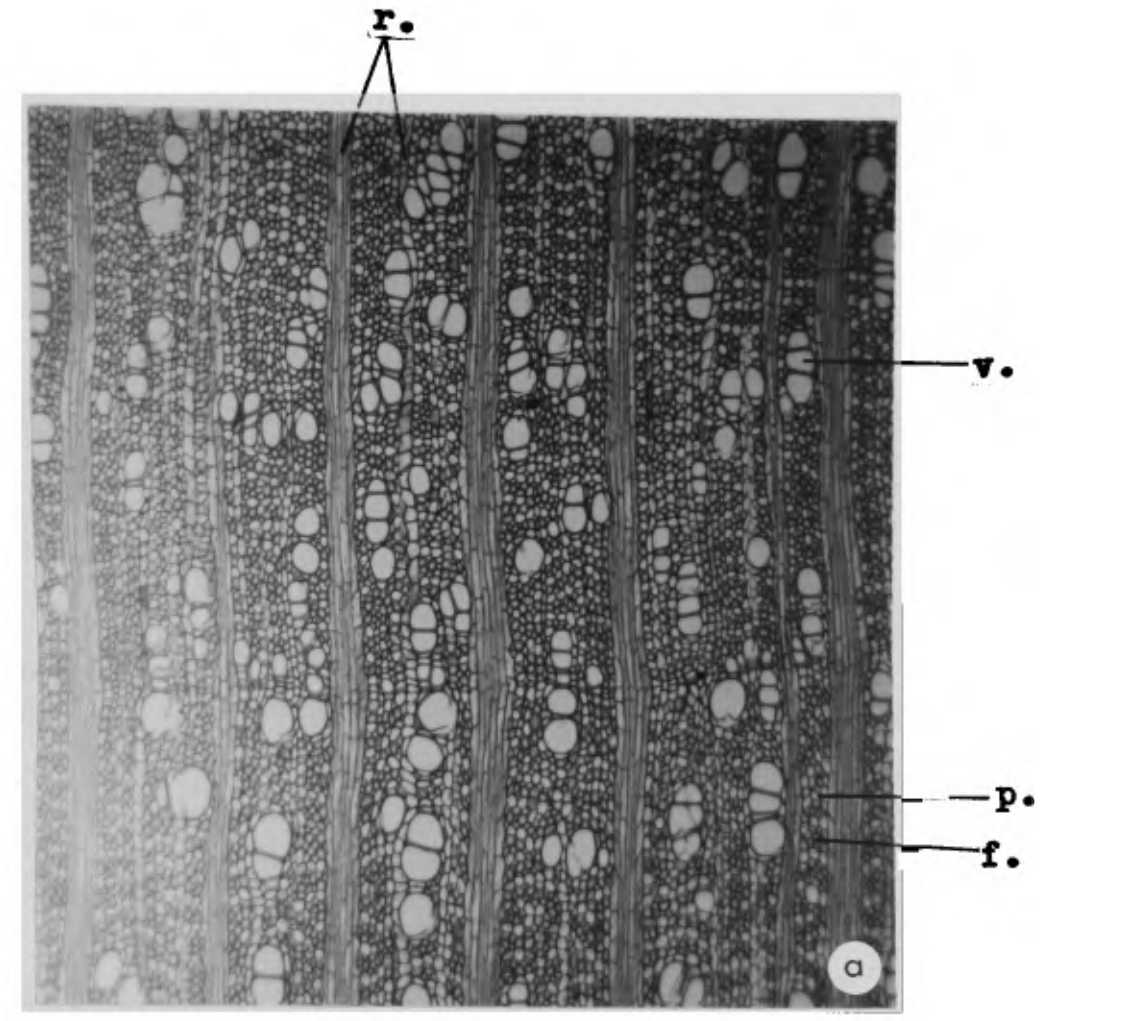
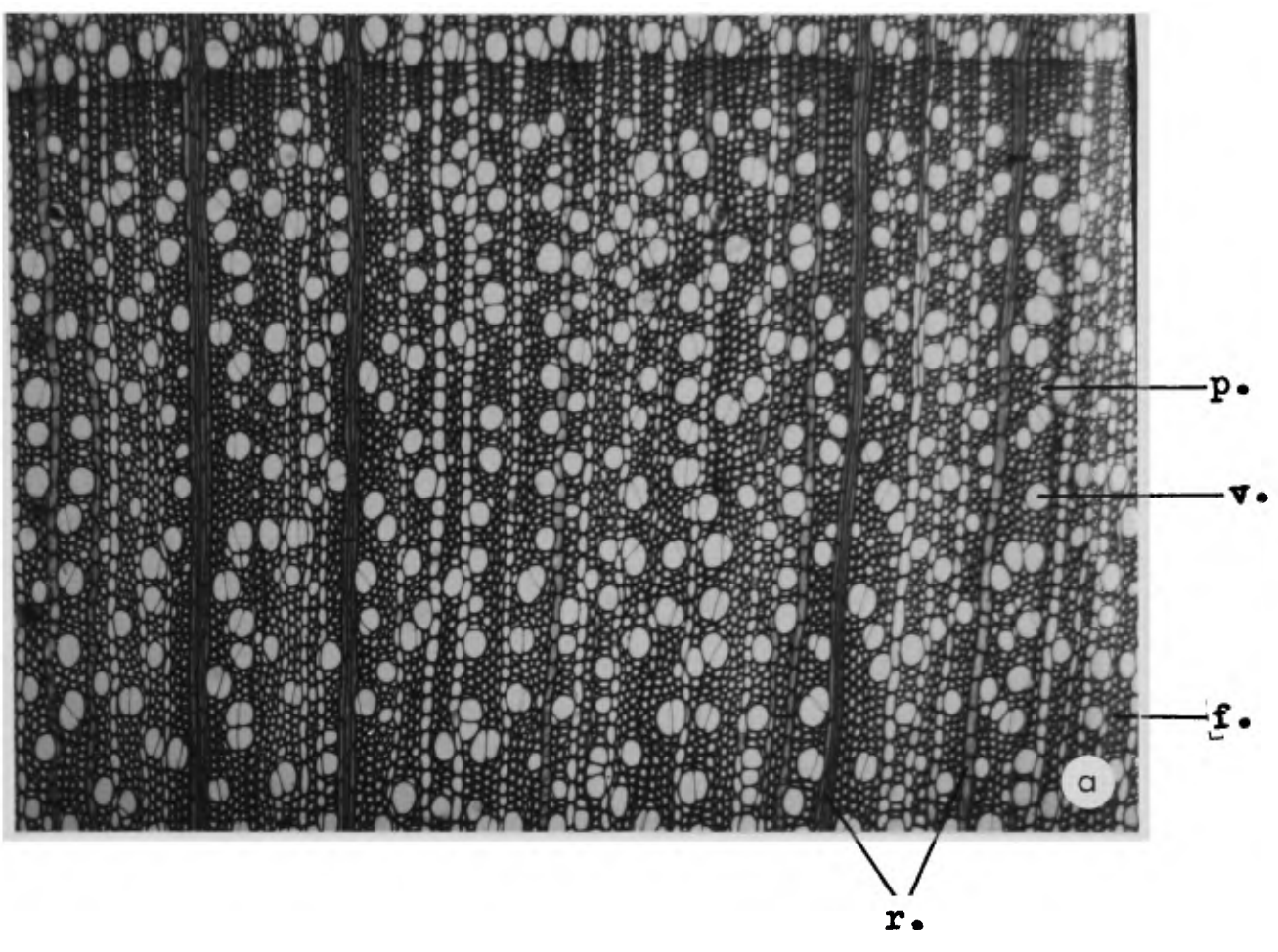


Fig. 2.5. Wood of Styrax officinalis 50x.
(a) transverse section; (b) tangential section.

f: fibre; p: parenchyma; r: ray; s.p: scalariform plate;
v: vessel.



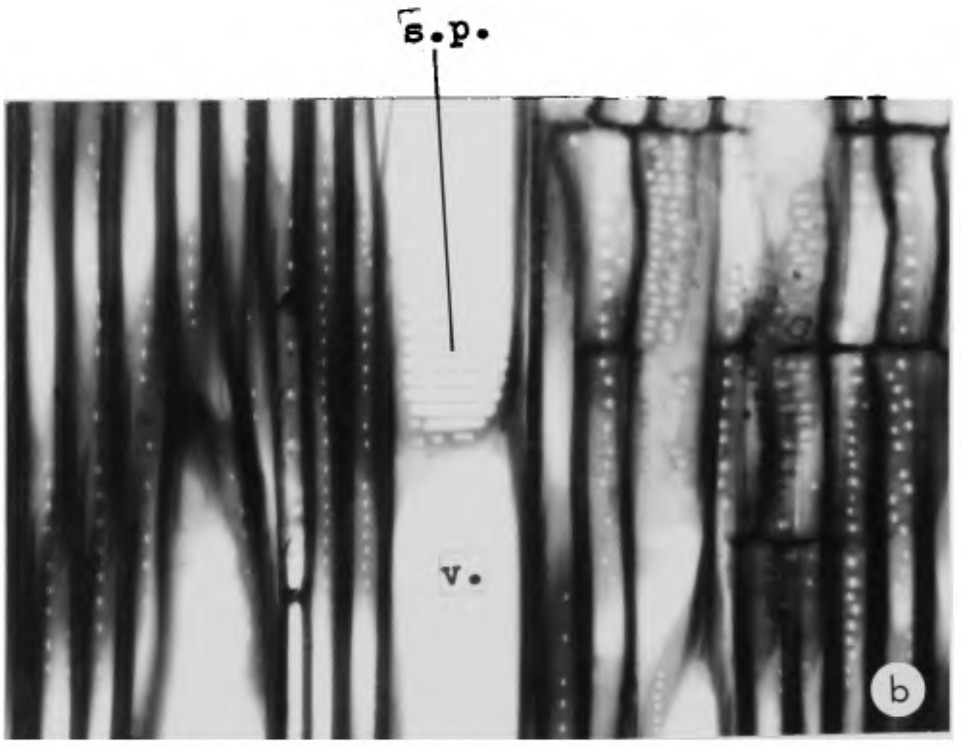


Fig. 2.6. Wood of Symplocos. (a) S. caudata 50x, in transverse section; (b) S. perakensis 150x, radial section.

f: fibre; p: parenchyma; r: ray; s.p: scalariform plate; v: vessel.

Table 2.1 Comparison of secondary xylem

	Ebenaceae	Sapotaceae & Sarcospermataceae	Lissocarpaceae	Styracaceae	Symplocaceae
1. Vessels (arrangement)	solitary and radial multiples of 2-4 or more cells	solitary and radial multiples of 2-4 or more cells	solitary and radial multiples of 2-4 cells	solitary and radial multiples of 2-4 or more cells	solitary except paired at overlapping ends
2. Vessel perforations	simple	simple	simple	scalariform plates with usually fewer than 20 fine bars	scalariform plates with usually more than 20 fine bars
3. Vessel-to-ray & vessel-to-parenchyma pits	small, to 8μ wide	large, to 10-20μ wide	small	variable	variable
4. Rays (width)	1-4 cells wide	1-4 cells wide	1-2 cells wide	1-6 cells wide, often in two well-contrasted sizes	1-5 cells wide, sometimes in two contrasted sizes
5. Rays (height)	predominantly less than 1mm high in any specimen	variable (<1->1mm)	predominantly more than 1mm high in any specimen	variable	variable
6. Fibres	without spiral thickening	without spiral thickening	without spiral thickening	without spiral thickening	sometimes with spiral thickening
7. Parenchyma (predominantly apotracheal in all families of the Order)	scattered cells and uniseriate lines; rarely sporadically biseriate	scattered cells and uniseriate lines; sometimes bi- or triseriate bands	scattered cells and uniseriate lines	scattered cells and uniseriate lines	scattered cells and uniseriate lines
8. Parenchyma	often tending to form vasicentric sheaths round the vessels	not forming vasicentric sheaths	tending to form vasicentric sheaths round the vessels	not forming vasicentric sheaths	not forming vasicentric sheaths

Pollen

(A list of material examined is given in Appendix 5)

Sapotaceae pollen is (3), 4, (5, 6) colporate, spheroidal to prolate (polar axis/equatorial axis = 1.0 - 2.0) and 21 - 75μ long. The ora are round to lalongate, and the surfaces are smooth to finely warty (scabrate), often appearing to be finely pitted (fig. 2.7a, b). Most of the species examined had 4, 5, 6-colporate grains which cannot be mistaken for the 3-colporate grains of Ebenaceae. However Chrysophyllum lanceolatum has smooth 3-colporate grains (fig. 2.7c) similar to Ebenaceae and may be noted as a possible link between the two families. Planchonella obovata has a mixture of 3- and 4-colporate smooth grains.

Sarcospermataceae pollen is 4-colporate (fig. 2.7d, e) and indistinguishable from Sapotaceae.

In contrast to Ebenaceae, Sapotaceae and Sarcospermataceae, in which the pollen grains are nearly always longer than broad (p/e 1.0 - 2.0), the next three families have pollen grains broader than long (p/e 0.7 - 1.0). This difference produces a very striking effect on the way pollen grains settle down on a slide. In the former case, the majority of grains settle on their side whereas in the latter, they settle on their ends.

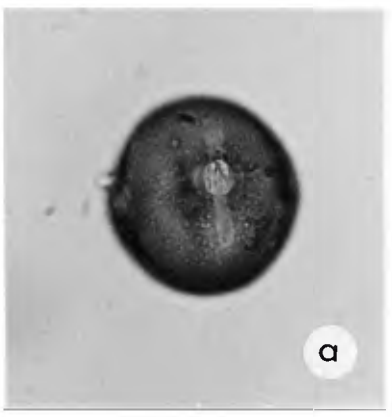
Lissocarpaceae pollen is 3-porate, has very prominent reticulate sculpturing, and is large, 46 x 53 - 65 x 70μ (fig. 2.8a, g, h).

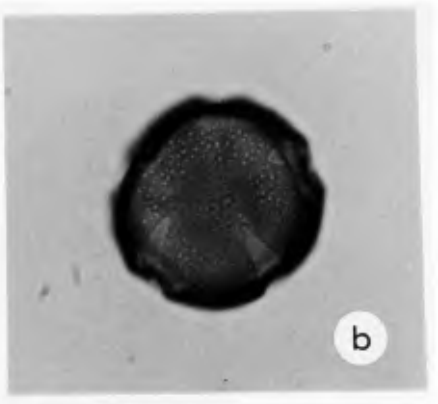
Symplocaceae pollen (fig. 2.8b, c) is likewise 3-porate (but Erdtman, 1966, describes it as 3-colporate, brevicolpate,

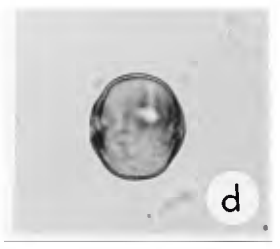
with era often more marked than colpi). They range from 20 x 26μ to 35 x 50μ and their surfaces are scabrous or reticulate.

Styracaceae pollen is 3-colporate except Afrostyrax 3-porate, with surfaces scabrous to reticulate (fig. 2.8d, e, f).

In summary, the only family in the Order with pollen which might be mistaken for Ebenaceae is Sapotaceae, but then only rarely. Pollen morphology reinforces the evidence from wood anatomy that Sarcospermataceae is indistinct from Sapotaceae. It supports the maintenance of Lissocarpaceae as a distinct family. Symplocaceae is fairly distinct but resembles Afrostyrax in the Styracaceae in being 3-porate.







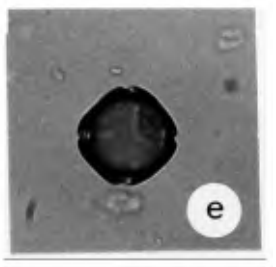
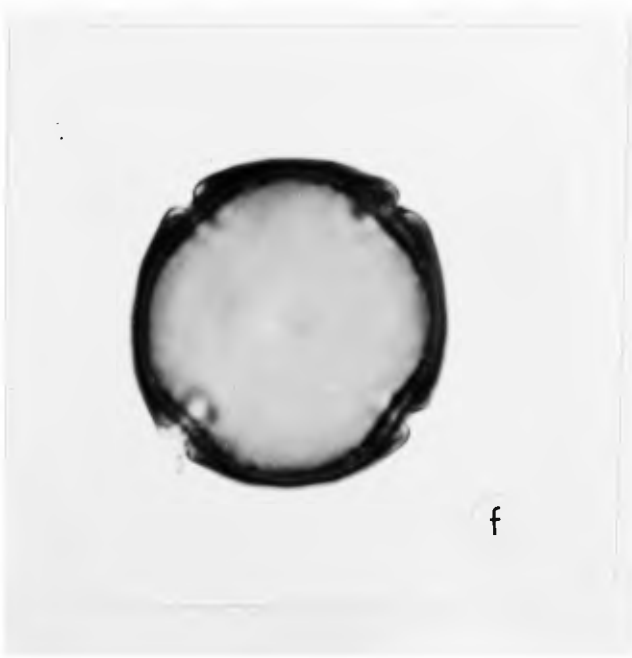
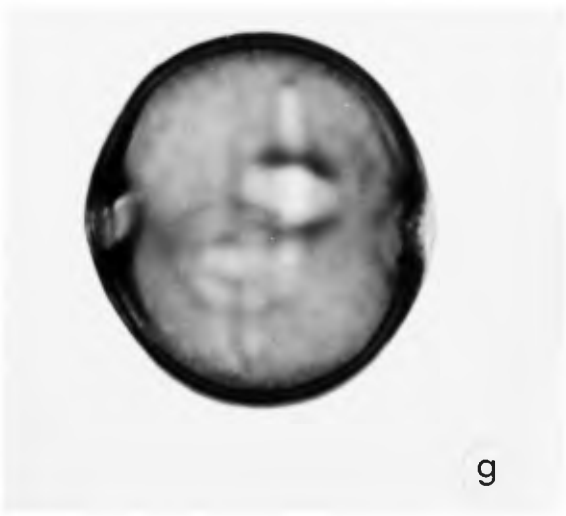


Fig. 2.7. Pollen of Sapotaceae and Sarcospermataceae at 375x: (a) Donella curtisii, in side view; (b) D. curtisii, in polar view; (c) Chrysophyllum lanceolatum, in side view; (d) Sarcosperma paniculatum, in side view; (e) S. paniculatum in polar view.

(f)&(g) Manilkara zapota at 750x, in polar and side view respectively.





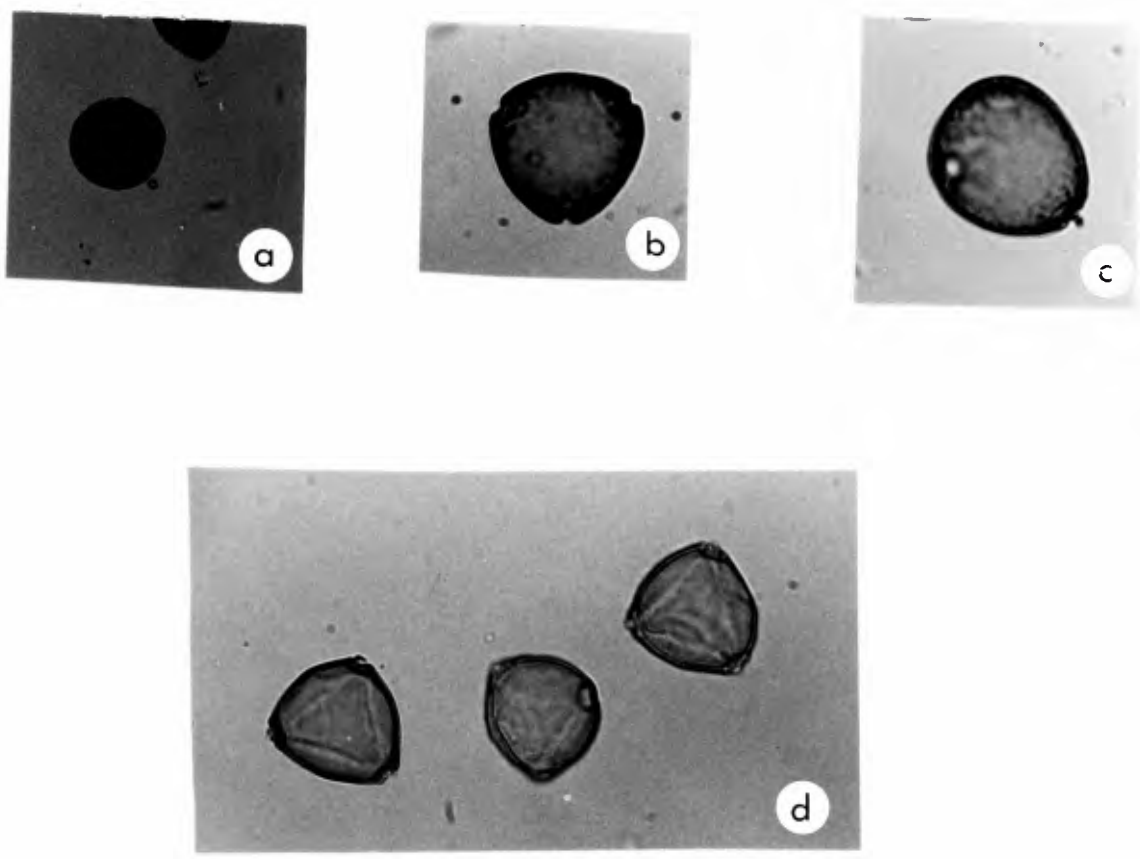
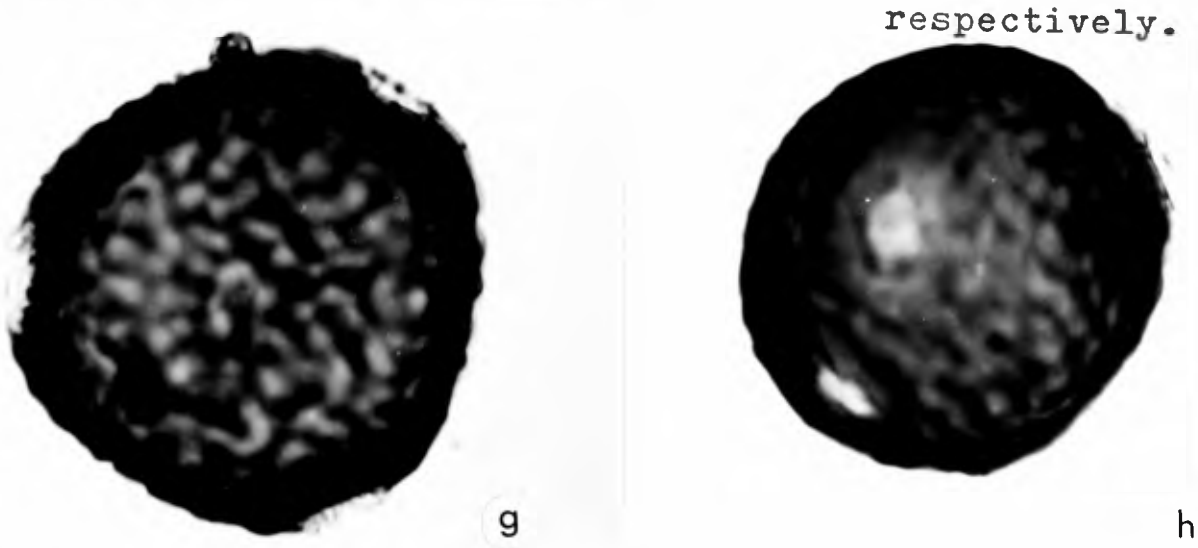


Fig. 2.8. Pollen of Lissocarpaceae, Symplocaceae and Styracaceae at 375x except (a) at 150x: (a) Lissocarpa guianensis, polar view; (b) Symplocos maingayi, polar view; (c) S. maingayi, oblique view; (d) Afrostyrax lepidophyllus, polar view; (e) Styrax benzoin, polar view; (f) Bruinsmia styracoides, polar and side view.

(g)&(h) Lissocarpa guianensis at 750x, polar and side view respectively.



Gynoecium

Pickled material of representatives (Appendix 5) of all families except Lissocarpaceae were embedded in paraffin wax and serial sectioned at 7.5 - 12.5μ in this study of gynoecial structure.

It soon became apparent that an error with rather serious taxonomic consequences for the Sapotaceae, is perpetuated in Engler's Syllabus from the 2nd (1898) to the 12th editions. In Engler's classification, the suborder Sapotineae is supposed to have the ovary completely divided into locules whereas in Ebenineae it is not chambered above.

In 1908 Dubard was led to describe the Sapotaceous genus Ganua as one whose most important features were, in the translation of van den Assem (1952) "the very low inserted ovules and the imperfectly closed cells of the conoidal ovary, the partitions of which ascend into the style like internal wings, thus leaving a central cavity above the placenta."

In 1946, Cronquist created the monotypic Sapotaceous genus Diploon with an ovary that was "unilocular by failure of partition." Cronquist took this to be an odd exception that did not invalidate Engler's rule.

It was left to Wood and Channel (1960) in a revision of the genera of Ebenales of the southeastern United States, to question the rule. They pointed out that in Sapotaceae, the ovaries "of at least some (e.g. species of Bumelia and Manilkara) are at anthesis septate below but are no more completely so above than those of Styrax, and in inferior ovaries in both Styracaceae and Symplocaceae a similar incomplete condition appears."

My study of longitudinal and transverse sections of 10 genera of Sapotaceae and of Sarcosperma convinces me that Engler's rule is completely without structural foundation. In fact in all species throughout the whole Order, the locules are in communication with one another by "failure of partition" in one way or another. The various ways will be described for each family below.

The significance of this communication has been pointed out by Carr & Carr (1961), in a paper on the functional significance of syncarpy. "The gynaecia of flowering plants may be classified as apocarpous, pseudo-syncarpous or eu-syncarpous. In the pseudo-syncarpous gynaeceum the carpels are fused to form a single structure, but in relation to the path of the pollen tube from the stigma to the micropyle they are functionally apocarpous. The eu-syncarpous gynaeceum is characterised by its possession of a compitum, a connection between the carpels which allows pollen tubes from grains germinating on any stigma or part of the stigma to fertilise ovules belonging to more than one carpel. In multilocular ovaries the compitum characteristically consists of pores, ducts or splits in the septa between loculi, through which the pollen tubes pass to the placentae."

In Ebenaceae, it has been shown in Part I that the gynoecium is 2 - 8 carpellate, each carpel bearing a pair of bitegmic anatropous ovules suspended from the apex of the ovary. A false septum is nearly always present to divide each carpellary chamber into two uni-ovulate locules. However it is important to note that at or above the placentae, all the locules open into a common chamber which is continued up the style as a single stylar passage, dividing into separate branches only to enter the separate style branches (fig. 1.3, 1.4, 1.5 & 2.9a). The size of the common chamber and its visibility varies

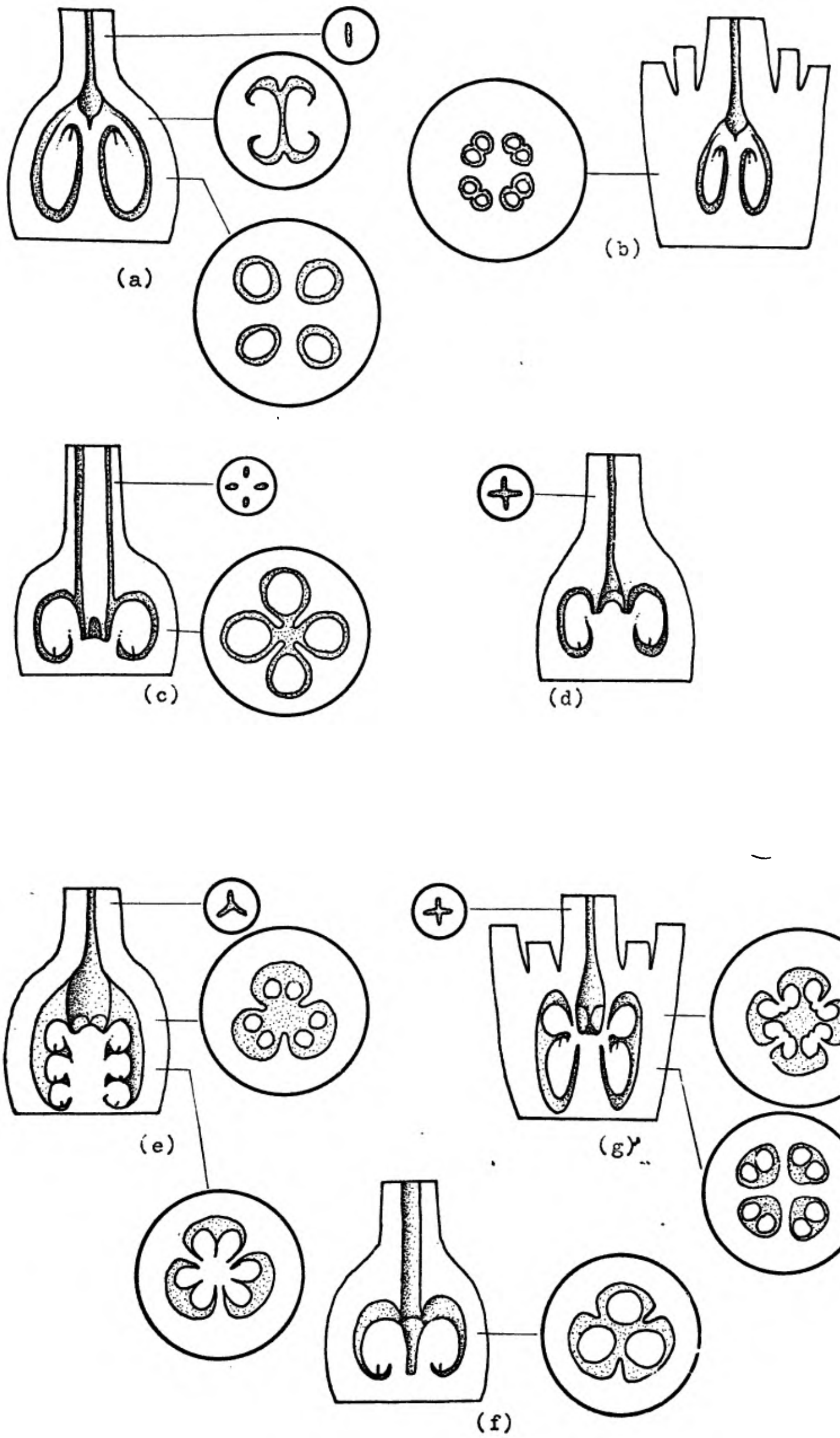


Fig.2.9. Diagrammatic comparison of gynoecial structures in Ebenales. (a)Ebenaceae (b)Lissocarpaceae (c)&(d)Sapotaceae (e)Styrax (f)Pamphilia (g)Symplocaceae

with the age of the flower and perhaps with the species but probably more with the microtechnical ability of the observer. A passage for a pollen tube needs only to be a narrow slit and this/it often is in the Ebenaceae.

In Sapotaceae, the ovary is 2 - 12 carpellate but each carpel contains a single ovule only. Placentation is axile (fig. 2.9c, d,, fig. 2.10) but the actual point of attachment may be high up on the axis (sub-apical) or lower, or near the base (sub-basal). Sometimes it may be described as basal. The ovule is hemianatropous if axile, anatropous if basal. In either case, the effect of ovule curvature is to bring the micropyle downwards to face the base of the ovary. This leads to the striking result that the embryo in Sapotaceae is erect (radicle inferior) whereas that in Ebenaceae is upside-down (radicle superior). A further difference is that the Sapotaceous ovule is unitegmic (fig. 2. 10f).

Above the placentae, there is an opening by which all the locules communicate with each other. At one extreme, this opening or compitum may be as little as 30μ high (Mimusops elengi, fig. 2.10) hence unlikely to be seen except in sections of 10μ or less. Each locule opens axially into the compitum and apically into its own stylar channel (fig. 2.9c; 2.10). At the other extreme, the compitum opens upwards into a single common stylar channel (e.g. Payena lucida, Pouteria malaccensis; fig. 2.9d). Since the lower limit of the compitum is determined by the position of the placentae, it may be apical, median, or basal along the ovarian axis. The condition in Diploon may be seen as a third extreme in which septae "fail" to "fuse" in any part of the ovary, resulting in a unilocular condition, which is the ultimate compitum.

The gynoecium of Sarcospermataceae is indistinguishable from Sapotaceae except that the ovary is 1 - 2 carpellate and the placentation consistently basal. However, it must be remembered that Diploon in the Sapotaceae is also 2 carpellate. Also, the basal placentation is only a slight shift from the sub-basal that is quite common in Sapotaceae. The compitum in Sarcosperma is a small basal connection between the two locules (absent of course where there is only one carpel), and the locules open independently into their own stylar passages at their apices (fig. 2.10A).

In Lissocarpaceae, the gynoecium is 4 carpellate and quite similar to Ebenaceae in structure except that the ovary is inferior and false septa are not developed (fig. 2.9b). Each of the four locules bear a pair of anatropous ovules at the apex of the ovary. The locules all open into a common stylar passage. As in Ebenaceae, the radicle of the embryo is superior.

In Styracaceae, which is 2 - 5 carpellate, the compitum is usually large enough for anyone with a razor blade and a hand lens to see. In Bruinsmia, Halesia, Pterostyrax and Styrax (fig. 2.9e; 2.11), it occupies the upper third or half of the ovary. In Pamphilia (fig. 2.9f), the septa extend at best only three-quarters of the way from the wall to the centre so that no part of the ovary is completely septate. In Afrostyrax even such partial septa are absent, and the 5-carpellate ovary is distinctly unilocular. In all the above genera, the compitum is extended upwards into a single stylar channel.

The ovules are 1 to many per loculus, hemianatropous or anatropous, mostly axile but basal in Pamphilia and Afrostyrax. According to Hutchinson (1967) the ovary is partly ($\frac{2}{3}$), or wholly inferior in 7 of the 12 genera. Of the remainder, I find that Afrostyrax and Bruinsmia have ovaries $\frac{1}{4}$ to $\frac{1}{2}$ inferior.

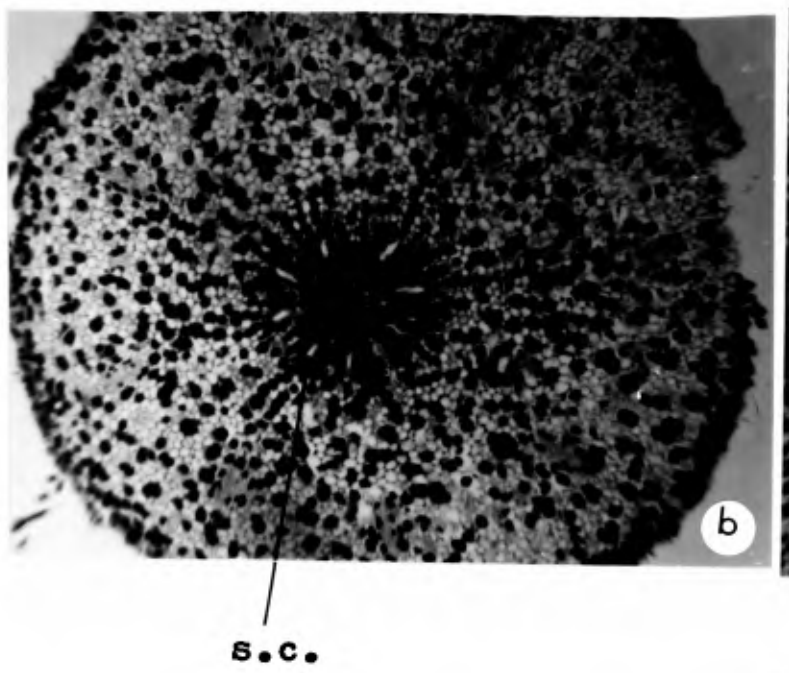
The ovules are bitegmic in Styrax (fig. 2.11).

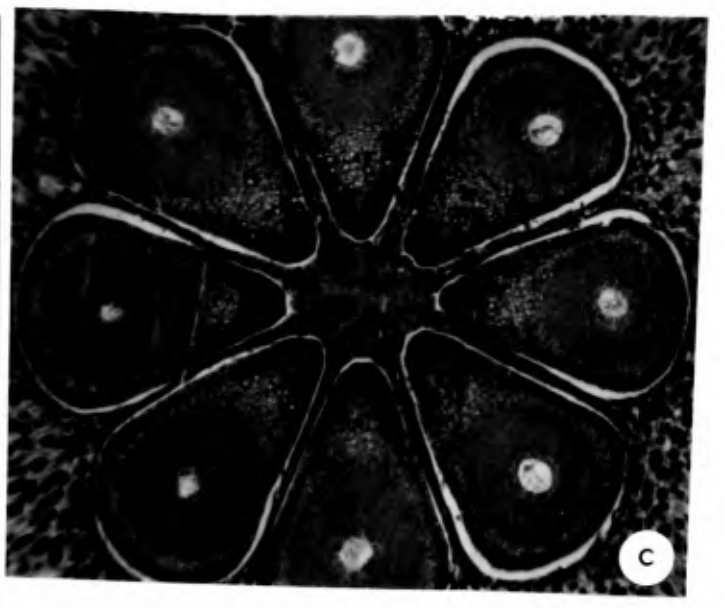
In Symplocaceae, the gynoecium is 2 - 5 carpellate with as many locules, and 4 (2?) ovules per locule. The ovary is wholly or partly inferior. Placentation is axile, and the ovules anatropous, unitegmic. The compitum occupies the upper half of the ovary (fig. 2.9g; 2.12) but may in transverse section appear only as a narrow slit. It opens upwards in a common stylar passage.

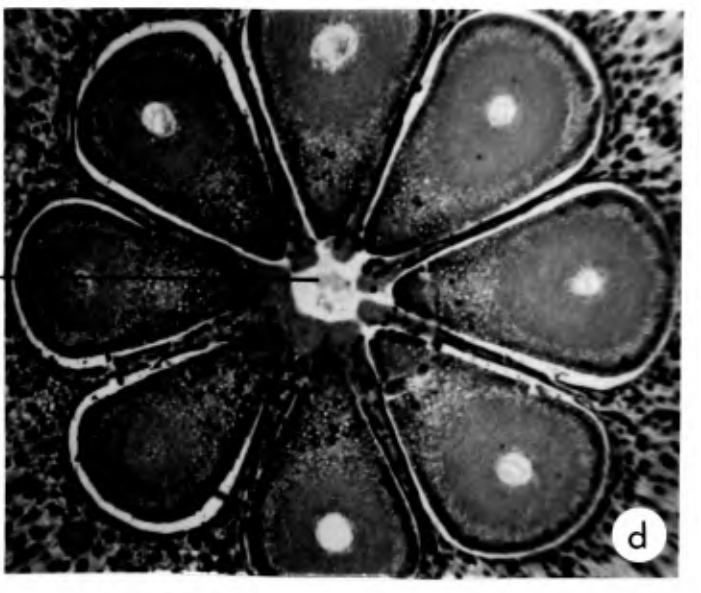
After surveying the whole Order, it appears that Lissocarpaceae is closest to Ebenaceae in gynoecial structure, differing only in the inferior condition of the ovary.

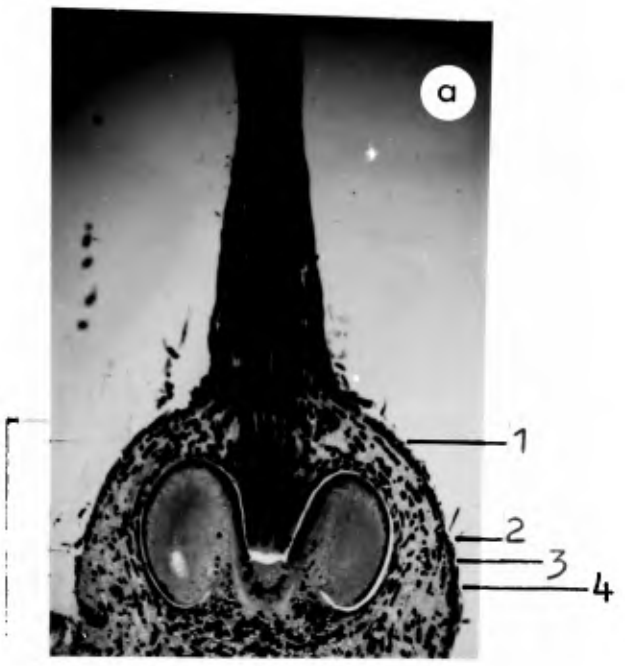
Sarcospermataceae fails the test once again and its gynoecium is best considered a case of extreme reduction of a Sapotaceous gynoecium to the 1 - 2 carpellate condition.

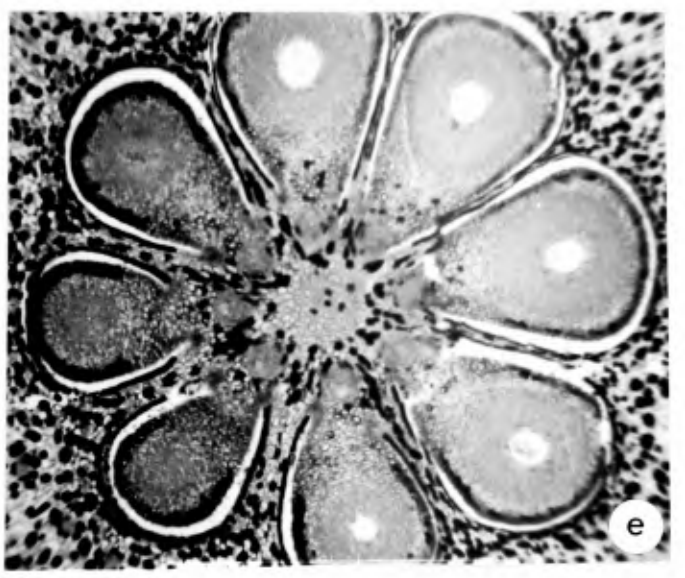
The difference between ovary "incompletely septate" and "completely septate" in the Ebenales turns out to be based on whether a compitum within the ovary is visible or not with a hand lens and simple dissection techniques. Under a microscope, the character disappears. The trouble with it is that it is a size difference, not a structural difference. The unfortunate consequence of it having been described as a structural difference is that other taxonomists have been misled to giving it more weight that it deserves, since structural differences usually indicate greater genetic and evolutionary divergence than size differences.











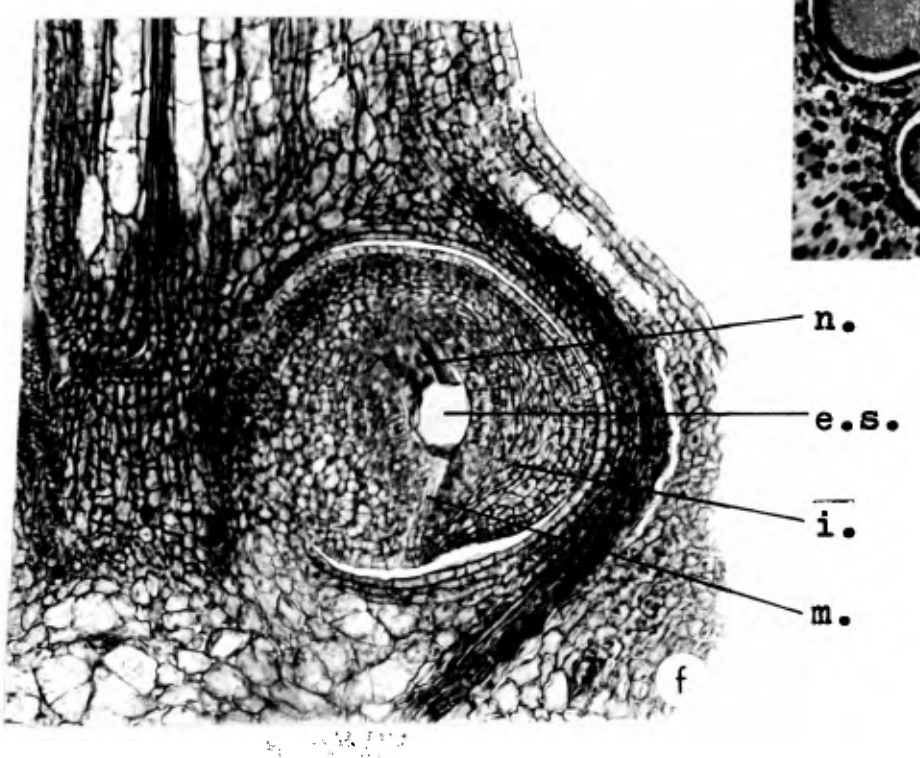


Fig. 2.10. Gynoecium in Sapotaceae. (a) - (e) Mimusops elengi: (a) median l.s. through two ovules, 20x; (b), (c) (d), (e) correspond to levels 1, 2, 3, 4 respectively, in t.s. at 50x. The plane of sectioning was slightly tilted so that in (d) only 4 septa are shown as free whereas all are actually free at this level, as other sections, not shown here, reveal. (f) Ovule of Chrysophyllum lanceolatum 150x.

c: compitum; e.s: embryo sac; i: integument; m: micropyle, n: nucellus; s.c: stylar channel.

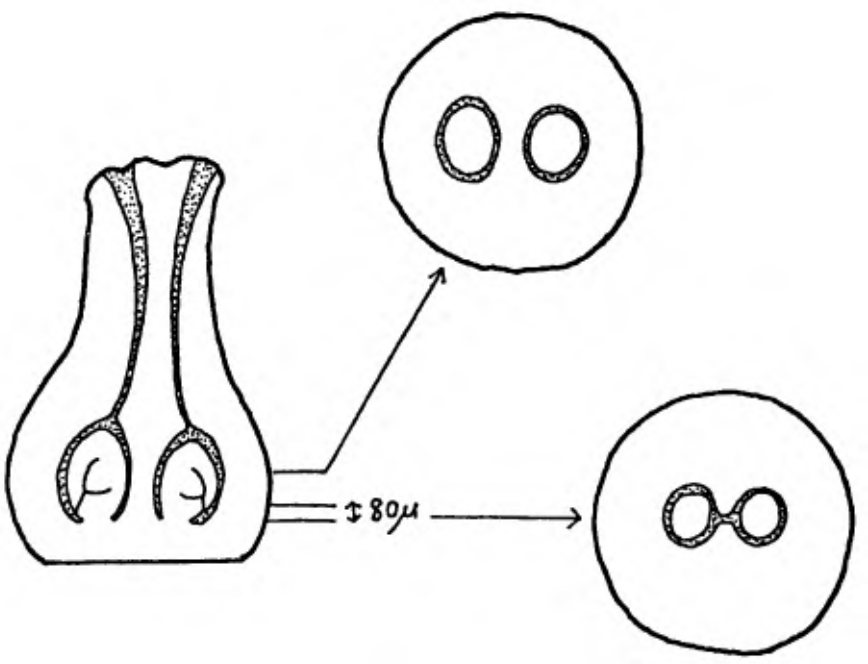
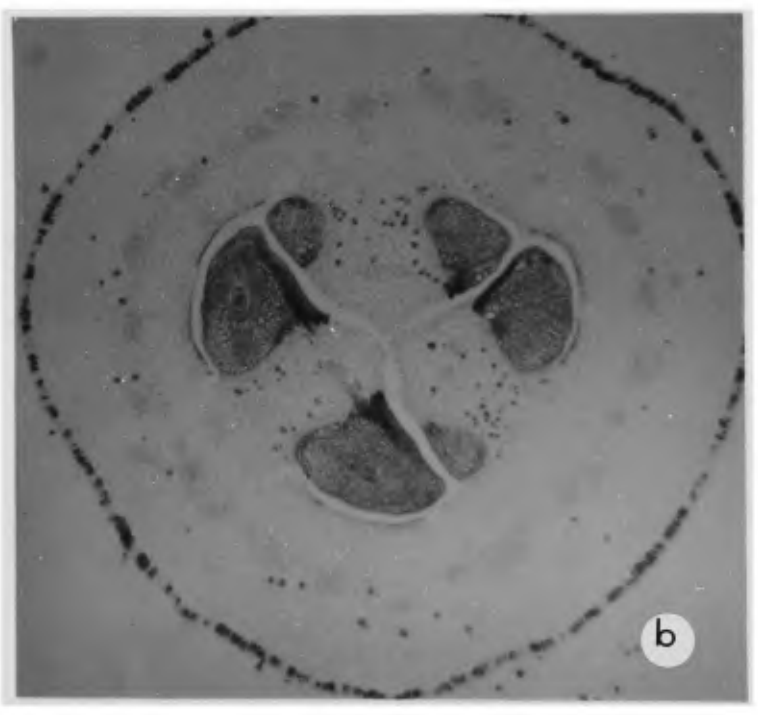


Fig. 2.10A. Gynoecium of Sarcosperma paniculatum, 20x. The compitum is only 80μ high, and too narrow to be seen in longitudinal section.

Fig. 2.11. Gynoecium of Styrax benzoin in median longitudinal section, 50x.



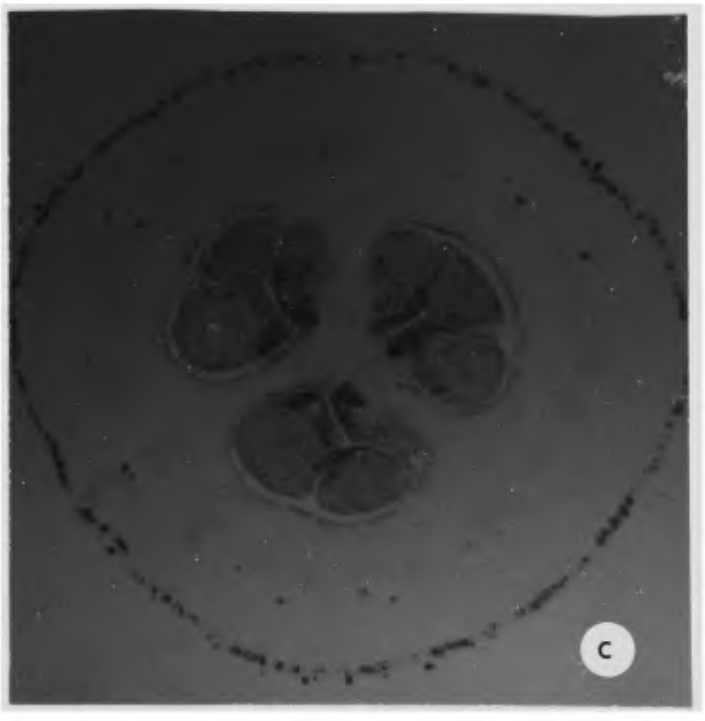


Fig. 2.12. Gynoecium of Symplocos adenophylla, 50x. (a) median longitudinal section; (b) transverse section through upper part of ovary showing compitum; (c) transverse section through lower part of ovary.

Trichomes

It is generally known (Solereder 1908, Metcalfe & Chalk 1950, Hummel & Staesche 1962) that the various families of the Ebenales have their own rather characteristic set of hair types. Ebenaceae has a broad range of types: (i) unicellular simple which by being grouped together become (ii) tufted, also (iii) unicellular two-armed, (iv) multicellular glandular, (v) peltate. Sapotaceae has two types, unicellular two-armed and unicellular simple. Styracaceae has tufted, stellate and peltate hairs, and Symplocaceae has unicellular simple hairs sometimes septate by development of thin cross walls.

These characters are given a very prominent place in Cronquist's (1968) Key to the families of the Order.

On checking the usefulness of trichome characters for family delimitation, I found them to be elusive; the closer one looks, the less sure one is of one's ground.

For example, two-armed hairs are often thought to be diagnostic of Sapotaceae. With a hand lens the Sapotaceae creates a strong impression because many species have a dense pubescence of unicellular hairs each bearing two long arms. The Ebenaceae rarely have hairs with two long arms but with careful teasing out of hairs and examination under a microscope, a large proportion of Ebenaceous species are found to have two-armed hairs, one arm of which is very short. The "difference" between the two families with respect to trichomes is based therefore on a superficial impression. The situation is similar to that of Engler's "incomplete" versus "complete" septation of the ovary. What looks very sound with a hand lens disappears when placed under a microscope. This character is useful for

rough sorting of specimens into their families but has no structural basis and must be taxonomically evaluated like any size character rather than as a structural character.

Another problem with trichomes is that many plants bear more than one type, and although one can say quite definitely which trichomes occur in which family, one cannot say which trichomes do not occur in any family without first examining every part of every species of that family - a time consuming enterprise for any family with more than a few dozen species, and yielding rapidly diminishing returns. I feel on the basis of a fairly large sample of the family that the five types of trichomes known to occur in Ebenaceae probably represent the full range in that family but it would be reckless to say categorically that other types cannot possibly occur. The other families have not been worked upon as fully.

A brief check on the Symplocaceae confirmed my worst suspicions that a great deal remains to be done before trichome characters can be confidently used in family delimitation. I examined 30 species of Symplocos and found without much effort two kinds not previously recorded in the literature: two-armed unicellular hairs on the calyx of S. maingayi and multi-branched unicellular hairs on the inflorescence of S. adenophylla (fig. 2.13).

It might be argued that enough is known for one to state quite confidently what the most common hair types in each family are and that the rarities need not be allowed to upset classification. This is true if such characters are used as secondary evidence to reinforce other lines of evidence rather than as a primary indicators of taxonomic status. The rarities nevertheless have a significance out of proportion to their

number as indicators of relationship e.g. the peltate hairs present on fewer than half-dozen species of Ebenaceae may indicate a link to other families with peltate scales.

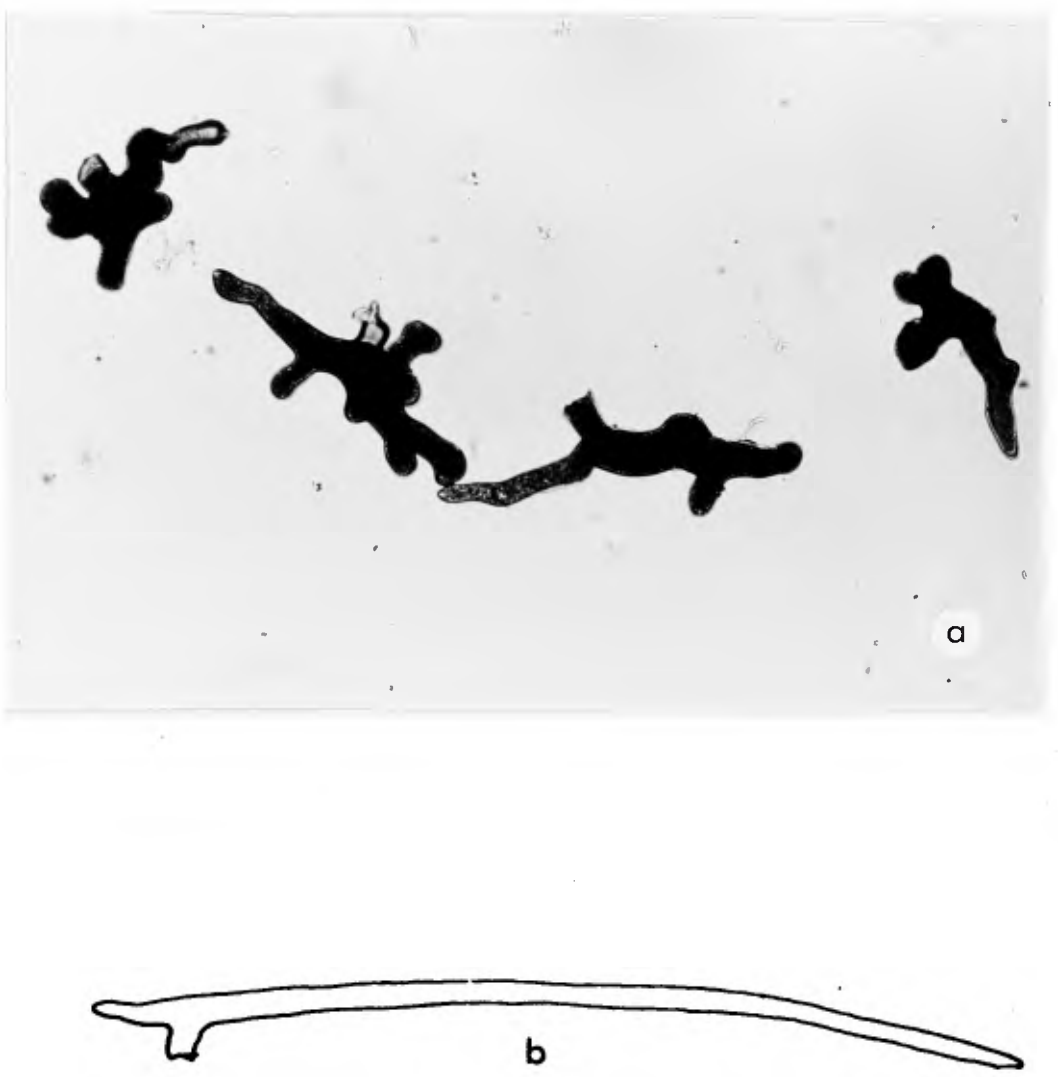


Fig.2.13. Trichomes in Symplocos, 150x; (a)multibranched, from inflorescence of S. adenophylla; (b) two-armed, from calyx of S. maingayi.

Inflorescence

Inflorescences are notoriously difficult to define. In his review of the terminology, Rickett (1944) found that the terms were "confused from the beginning" and current usage "unreliable". The Ebenaceous inflorescence is conventionally referred to in the taxonomic literature as a "cyme", that of Sapotaceae as a fascicle, that of Sarcospermataceae as a raceme and those of the other families variously as panicles, fascicles, racemes, cymes and spikes. These terms sometimes conceal more information than they convey, hence it is necessary to describe exactly what the situation is in each family before a proper critical comparison can be made.

The Sapotaceous fascicle (fig. 2.14a) is an axillary cluster of peduncles, each peduncle bearing a single terminal flower, and free of bracts along its length. Bracts occur only around and at the bases of the peduncles. In many species, the same axils produce flowers year after year and become swollen and knobbly while the subtending leaves drop and their scars are gradually distended and obscured, but there is no doubt the fascicles are axillary in origin. It is significant that as a general rule, all the twigs have a double role - vegetative and reproductive. An exception is seen in the aptly named Aningeria pseudoracemosa in which there are separate reproductive and vegetative shoots (fig. 2.14b). The reproductive shoots arise in the axils of leaves of vegetative shoots and bear an acropetal series of fascicles, each fascicle subtended by a common caducous bract. The whole reproductive shoot resembles a raceme but the apical bud resembles an ordinary vegetative bud and could probably revert to a vegetative condition although in practice it seems to pass into dormancy and abortion. Comparing Aningeria pseudoracemosa with other species of Aningeria and

with the rest of the Sapotaceae, there is no doubt that its raceme is a second-order inflorescence evolved from an ordinary reproductive-vegetative shoot by suppression of the leaves.

This interpretation has important consequences for the Sarcospermataceae. One of the main reasons given for maintaining it as a family is that its inflorescence is a raceme as opposed to the fascicle of Sapotaceae. Close examination of the Sarcospermataceous raceme reveals that it is a second order inflorescence, exactly as in Aningeria pseudoracemosa, consisting of a shoot ending in a vegetative bud and bearing lateral fascicles in the axils of bracts. Hence the real difference between the two families is not "raceme" versus "fascicle" but "shoots reproductive-vegetative" versus "shoots separately reproductive or vegetative." The basic (first order) inflorescence remains a fascicle throughout Sapotaceae and Sarcospermataceae.

In Ebenaceae, the inflorescence (fig. 2.15) is loosely described as a cyme. It is always axillary in position, at least in origin, and always bearing bracts along the peduncles. Each flower is articulated (fig. 1.2a) and, if lateral, subtended by a bract. If there is one flower only, it occupies a terminal position on a bracteate peduncle (fig. 2.15g). Quite often, the inflorescence is a dichasium, with the two lateral buds subtended by bracts (fig. 1.15d). Numerous variations are seen ranging between the three-flowered dichasium and a multiflowered multibranched paniculate condition, but in nearly all cases, the terminal units resemble dichasia i.e. the terminal flowers develop before the two immediately behind. In Euclea, where the inflorescence is unbranched and multiflorous, what results is a structure that looks like a raceme except at the apex which looks like a dichasium (fig. 2.15b). Alternatively, all the

buds seem to arrive at the same stage of development, and then bloom together.

The manner of development of the Ebenaceous inflorescence suggests that the terminal bud of the inflorescence inhibits the development of the axillary buds in a way analogous to the inhibitive hormonal influence terminal buds exert on axillary buds of vegetative shoots. Pursuing the same analogy, the hormone would diminish in effectiveness with distance from the apex hence the axillary buds would develop acropetally. At the apex, if the terminal bud continues to produce the hormone while being transformed into a flower, as seems to happen in Ebenaceae, this would ensure that the terminal flower has a developmental advantage over the penultimate flowers. If the terminal bud has a very strong inhibitive effect, it would suppress completely the development of the axillary buds hence producing a solitary terminal flower or a bracteate peduncle. This hypothesis of hormonal inhibition by the apical bud provides half the answer to the variations in inflorescence structure in the Ebenaceae. It might be added that if the terminal bud is only slightly inhibitive or non-inhibitive, or aborts, a raceme would result, but this does not happen in the Ebenaceae.

The other half of the solution concerns the behaviour of buds once development is initiated. In vegetative shoots, a bud, once it becomes active, produces a branch. In an inflorescence, a bud may either develop into an inflorescence-axis or a flower. It is a complete mystery how the 'decision' is made. A terminal bud, by postponing its change into a flower, prolongs the main axis of the inflorescence, producing many lateral bracts and axillary buds. The axillary buds may repeat the process, producing branches. A panicle results. If

all axillary buds develop immediately into flowers we have an unbranched inflorescence. If the terminal bud develops into a flower after producing only two laterals we have a dichasium. This unknown controlling factor, together with simple apical dominance, suffices to explain all inflorescence structures in the Ebenaceae, except that of Diospyros toposioides to be described later.

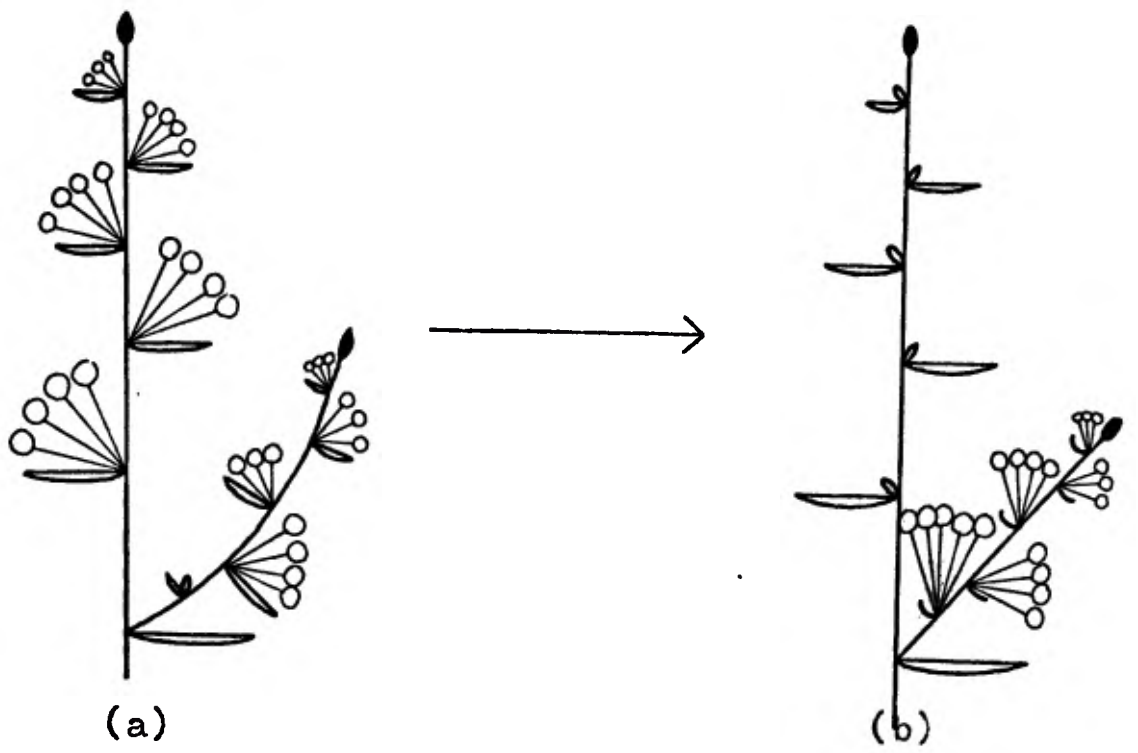
Synchronous blooming is not strictly a structural problem. To explain it, it is necessary to postulate the evolution of a system of physiological control whereby all flowers develop to a certain stage and then wait for some triggering process to set off flowering. Such devices are known to operate among species in other families (Holttum 1954), e.g. Dendrobium crumenatum (Orchidaceae), Coffea arabica (Rubiaceae), Pterocarpus indicus (Leguminosae), Murraya exotica (Rutaceae). However it still needs to be established in the field that synchronous blooming does take place in certain species of Euclea. An alternative explanation for apparent synchronous blooming as seen on herbarium sheets is that flowers may remain open long enough for the last ones to open before the first ones have been shed, in which case, it may be difficult to determine the order of opening.

In Diospyros toposioides, we see the development of a second order inflorescence along a pathway parallel to that described in Sapotaceae and Sarcospermataceae. As in Sapotaceae, the ordinary Ebenaceous shoot has a mixed vegetative-reproductive function. In Diospyros toposioides, there is a differentiation into separate vegetative and reproductive shoots. The latter develop from the axils of leaves on vegetative shoots, bear small dichasia (males) or solitary bracteate flowers (females) in the axils of caducous bracts, and terminate in a vegetative

bud instead of a flower (fig. 2.14d). In fact the terminal bud sometimes converts to vegetative status and produces a leafy shoot after producing flowers. The "raceme" then become "intercalary" (Parkin 1914). However, it is a second order inflorescence. The first order inflorescence is the individual axillary unit: a dichasium in the male plant, or a solitary bracteate flower in the female. I believe most of the intercalary inflorescences cited by Parkin are similarly second order inflorescences. The others may have evolved from ordinary first order racemes by the terminal bud somehow becoming vegetative instead of changing into a flower or aborting.

In Lissocarpaceae, the inflorescence is an axillary multibracteate multiflorous system with articulated flowers similar to that in Ebenaceae. The articulations are well hidden by the bracts, but as in Ebenaceae, old herbarium material tend to be left with flowerless peduncles, which is characteristic of inflorescences with articulated flowers.

The inflorescence in Symplocaceae (fig. 2.16) is also a bracteate multiflorous articulated system. The flowers seem to either open synchronously or in acropetal sequence indicating weak or absent apical dominance. In many species, especially in Malesia, the inflorescences are exclusively axillary. But in many temperate species, the inflorescences are terminal, hence different from all the preceeding families. The evolutionary relationship between the conditions in Symplocaceae seems to be as follows. In the primitive state, all the buds grew by producing a flush of leaves and terminating in an inflorescence. Continuation of growth was by axillary buds lower down repeating the same process each growing season. This condition may have been retained in temperate species as it fits into the stop-go regime of alternating winters and



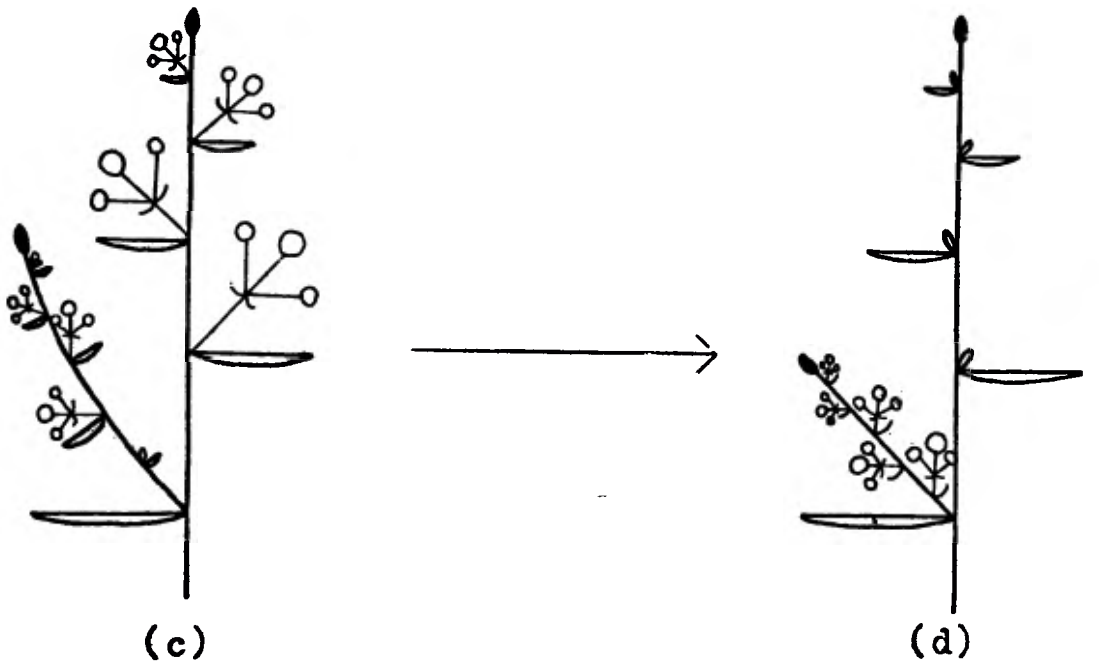


Fig.2.14. Evolution of second-order inflorescences in Sapotaceae (a&b) and Ebenaceae (c&d) by differentiation of reproductive shoots from mixed reproductive-vegetative shoots.

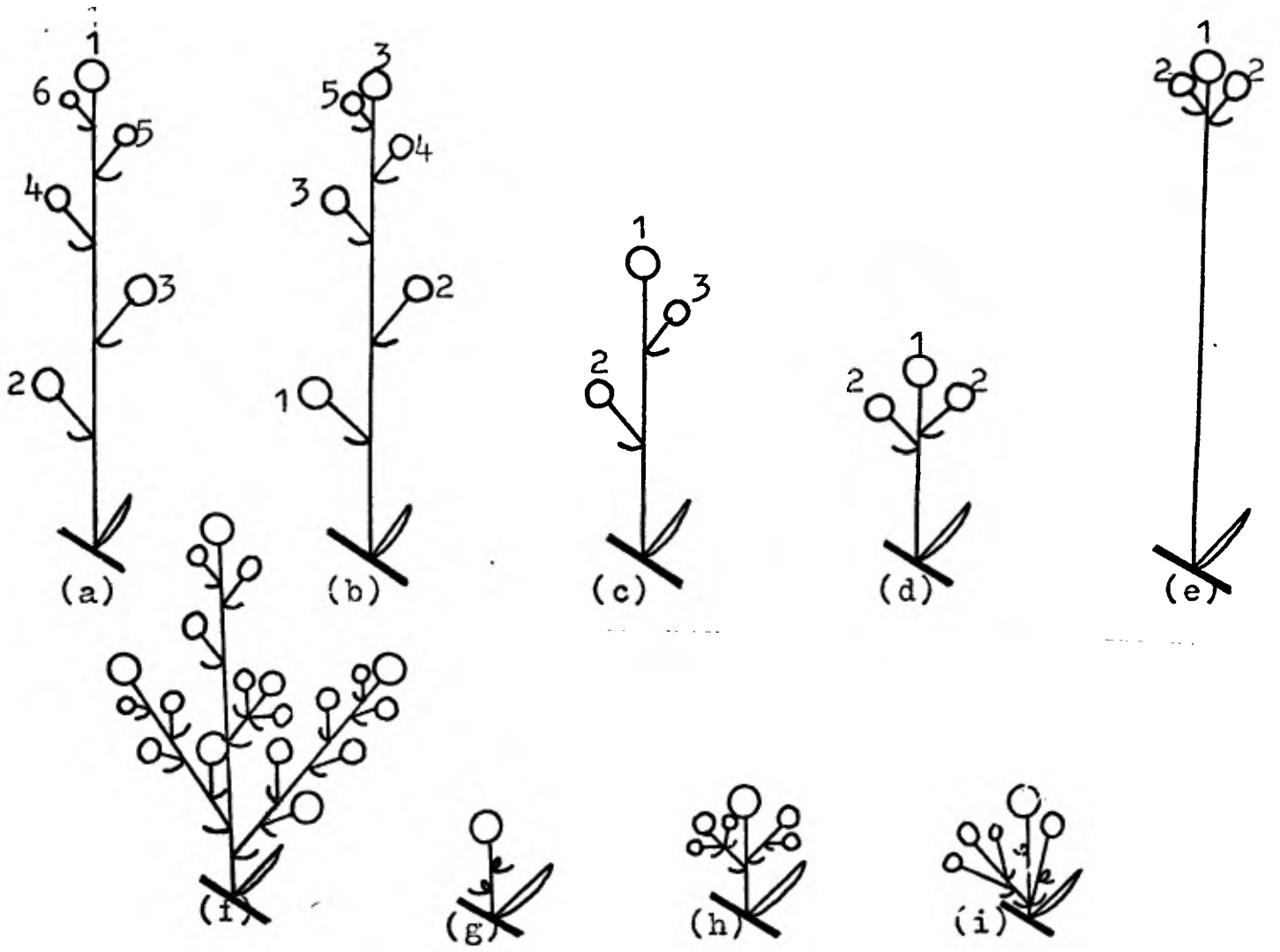


Fig.2.15. Inflorescences in Ebenaceae. Numbers refer to order of opening. Terminal parts cymose presumably because of apical dominance. (a)strong apical dominance (b)weak apical dominance (c)main axis bearing only two lateral buds (d)dichasium (e)flagelliflory by elongation of basal part of axis (f)panicle resulting from some lateral buds developing into branches instead of flowers (g)very strong apical dominance completely suppressing lateral buds (h)branched dichasium (i)fascicle.

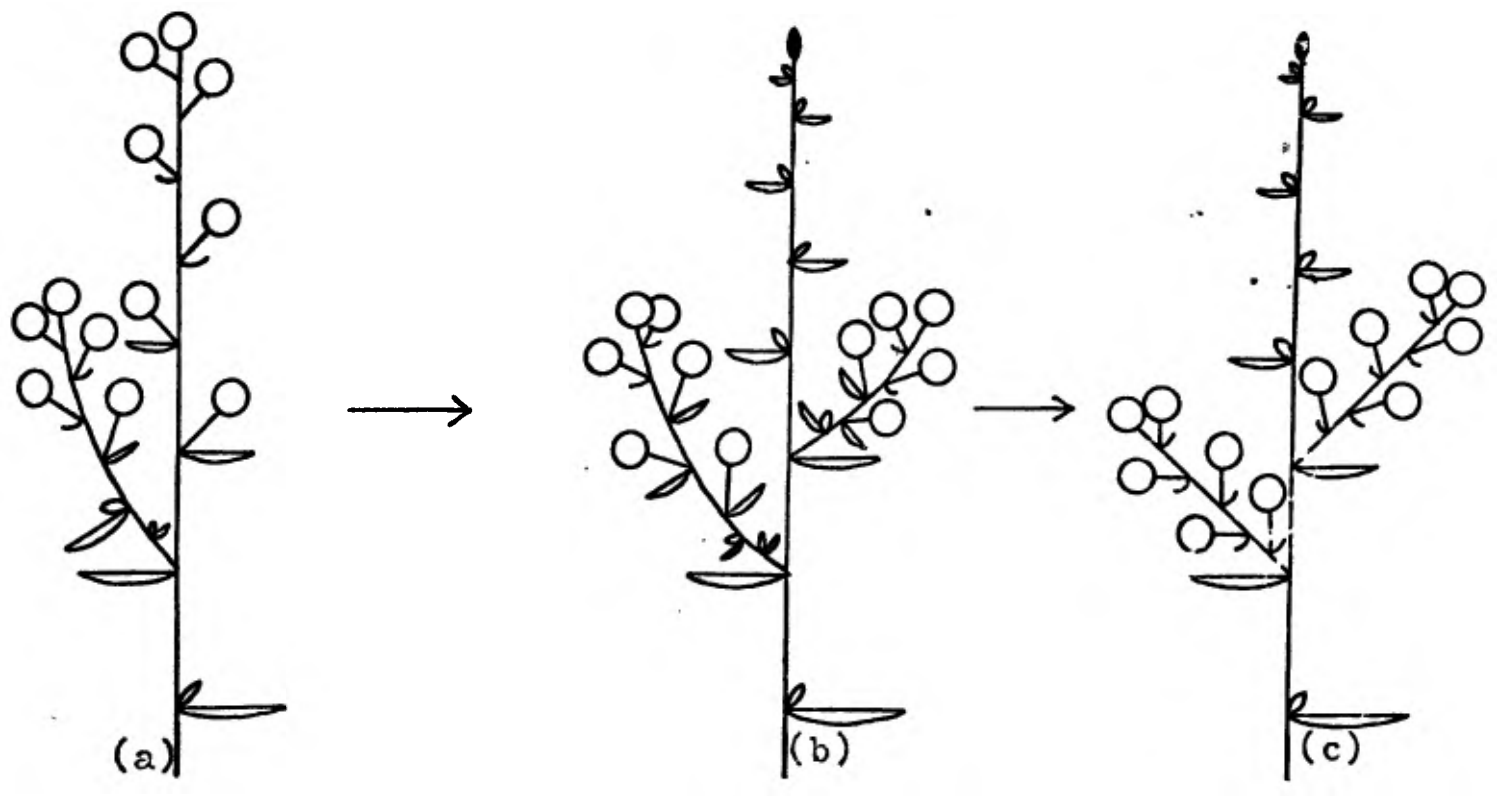


Fig.2.16. Inflorescences in Symplocaceae. (a)terminating all shoots (b)terminating short shoots (c)axillary. Arrows show presumed direction of evolutionary specialisation. Stage (c) resembles the Ebenaceous inflorescence and it is suggested therefore that the Ebenaceous inflorescence has had a similar evolutionary history but with stages (a) and (b) no longer extant.

summers. In the humid tropics there has been a differentiation of shoots, resulting in some buds growing out and remaining continuously vegetative while others are differentiated into short shoots producing a few leaves and terminating in inflorescences. Finally, all the leaves of such short shoots are suppressed and the result is an axillary bracteate inflorescence. Although this evolutionary series is hypothetical all the three stages are evident from an examination of herbarium material of the numerous species of Symplocos.

If the evolutionary sequence proposed to explain the inflorescence types in Symplocaceae is correct then the Ebenaceous inflorescence may also have had the same origin i.e. from a short shoot.

As for the Styracaceae, this is the only family for which it is impossible to generalise about the inflorescence. The flowers of Afrostyrax and Styrax are not articulated, but those of Pterostyrax, Bruinsmia and Halesia are. In Afrostyrax, the inflorescence is an axillary fascicle similar to that of Sapotaceae. The inflorescence in Halesia is axillary and almost a fascicle, but has a very short axis with leafy bracts subtending the flowers. It appears to be an axillary short shoot with a very condensed axis. Perhaps this is how the Sapotaceous fascicle began. The inflorescences of Styrax, Bruinsmia and Pterostyrax are multifloreus, multibracteate and in range of structure, parallel that in Symplocaceae; the terminal flowers are slightly dominant or non-dominant, resulting in mixed inflorescences (dichasia if only 3 flowers develop) or racemes respectively.

Summarising the above observations, the inflorescences in Sapotaceae and Sarcospermataceae are closely related to

each other; the inflorescences of Ebenaceae and Lissocarpaceae are structurally the same; those of Symplocaceae are in part structurally like Ebenaceae, but in part different because they may terminate leafy shoots. It is suggested that all inflorescences in the families of the Ebenales originated from leafy short shoots. Within Styracaceae, all the types of inflorescences met with in the other families are found in the various genera.

Comparison of Ebenaceae with Sapotaceae

Characters shared in common by Ebenaceae and Sapotaceae are: plants woody; leaves simple, alternate (rarely opposite in Ebenaceae); flowers regular; calyx persistent; corolla sympetalous; anthers opening by longitudinal slits; ovary superior, sessile, syncarpous, multilocular; ovules tenuinucellate; fruit a berry with persistent calyx.

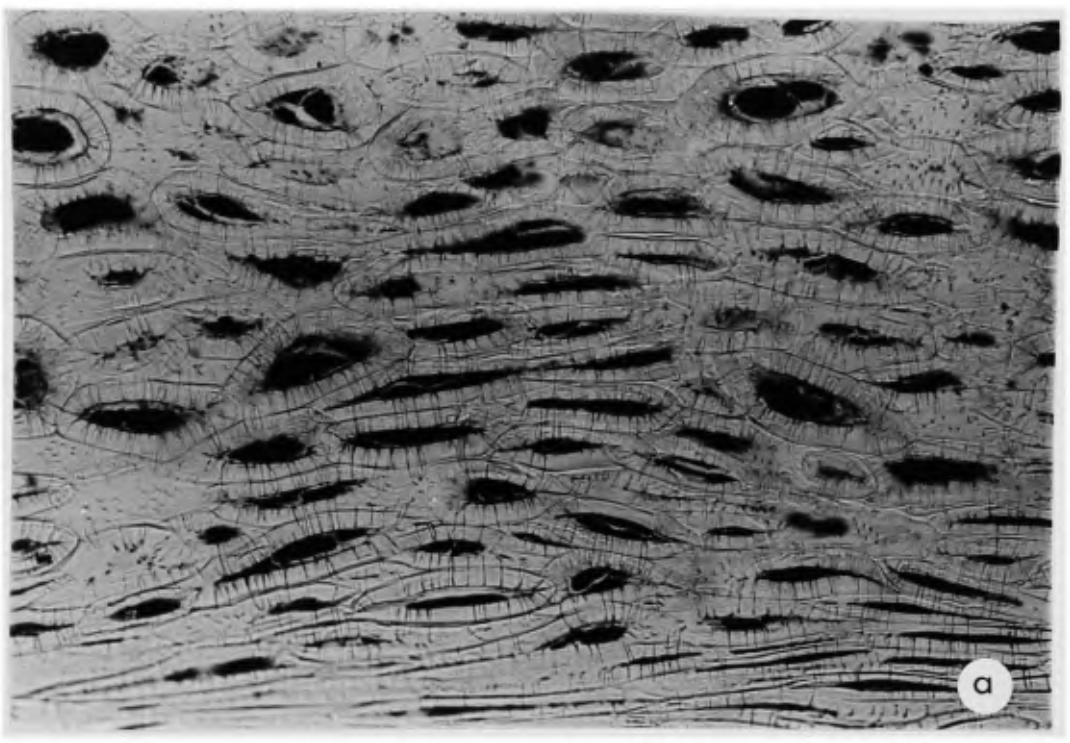
Differences between the two families are tabulated below, characters marked with an asterisk * are those which show the sharpest differences between the two families.

	Ebenaceae	Sapotaceae
1.	Latex absent.	White latex in bark, leaves, flowers, pericarp and embryos but absent in Mimusops elengi and possibly other species of Mimusops.
2.	Stipules absent.	Stipules in many, perhaps most, species.
*3.	Inflorescence a bracteate "cyme" sometimes reduced to a solitary flower on a bracteate peduncle.	Inflorescence a fascicle. Bracts restricted to base of fascicle.
*4.	Flowers articulated at base.	Flowers not articulated.
5.	Flowers nearly always unisexual.	Flowers nearly always bisexual.
6.	Calyx in one series, often cohering basally into a distinct tube.	Calyx in 1, 2 or more series, rarely cohering.
7.	Corolla ± isomerous with calyx.	Corolla isomerous or twice or more times as many lobed as calyx.

	Ebenaceae	Sapotaceae
8.	Stamens mostly adnate to base of corolla, sometimes free from corolla, rarely epipetalous towards neck of corolla tube.	Stamens epipetalous, often attached at neck of corolla tube.
9.	Staminodes, if present, completely replacing stamens (therefore such flowers female).	Staminodes if present, alternating with stamens (rarely completely replacing stamens; cf. 5).
10.	Pollen 3-colporate, smooth to very finely warty.	Pollen (3), 4, (5), (6)-colporate, smooth to finely warty.
11.	Styles distally or completely free, seldom completely united.	Styles completely united.
12.	Carpels bi-ovulate, but usually subdivided by false septa into uni-ovulate loculos.	Carpels uni-ovulate.
13.	Ovules with apical placentation.	Ovules with axile or basal placentation.
14.	Ovules bitegmic.	Ovules unitegmic.
15.	Ovules anatropous.	Ovules anatropous to hemianatropous.
16.	Fruits articulated at base (cf. 4).	Fruits not articulated.
17.	Seeds often with a distinct circum-peripheral vascular loop.	Seed vascular system invisible externally.
18.	Hilum small.	Hilum large.
19.	Hilum apical (cf. 13).	Hilum basal or lateral.
20.	Testa coriaceous (parenchymatous).	Testa crustaceous (sclerenchymatous).

	Ebenaceae	Sapotaceae
21.	Albumen abundant, horny, smooth or ruminate.	Albumen present or absent, if present, succulent, smooth.
22.	Radicle superior (embryo upside down).	Radicle inferior (embryo erect).
23.	Vessel-to-ray and vessel-to-parenchyma pits 8μ diam. or less.	Pits up to 20μ diam; at least some larger than 8μ on every 1 x 1 cm specimen.
24.	Trichomes unicellular-simple, unicellular-two-armed, club-shaped glandular, rarely peltate.	Trichomes unicellular-two-armed and unicellular-simple.
25.	Chromosomes x = 15, 2n = 30, 60, 90.	Chromosomes 2n = 20, 22, 24, 26, 28, 48, 52 (see Bolkhovskikh et al. 1969).

Of all the characters listed twelve sharply differentiate between the two families. Probably the most impressive differences are those of gynoecial structure, each family having its own highly distinctive construction. The number of sharp and partial differences between Ebenaceae and Sapotaceae is so large that unless the other families in the Order form a "bridge" between them, it is scarcely conceivable that they can be at all closely related.



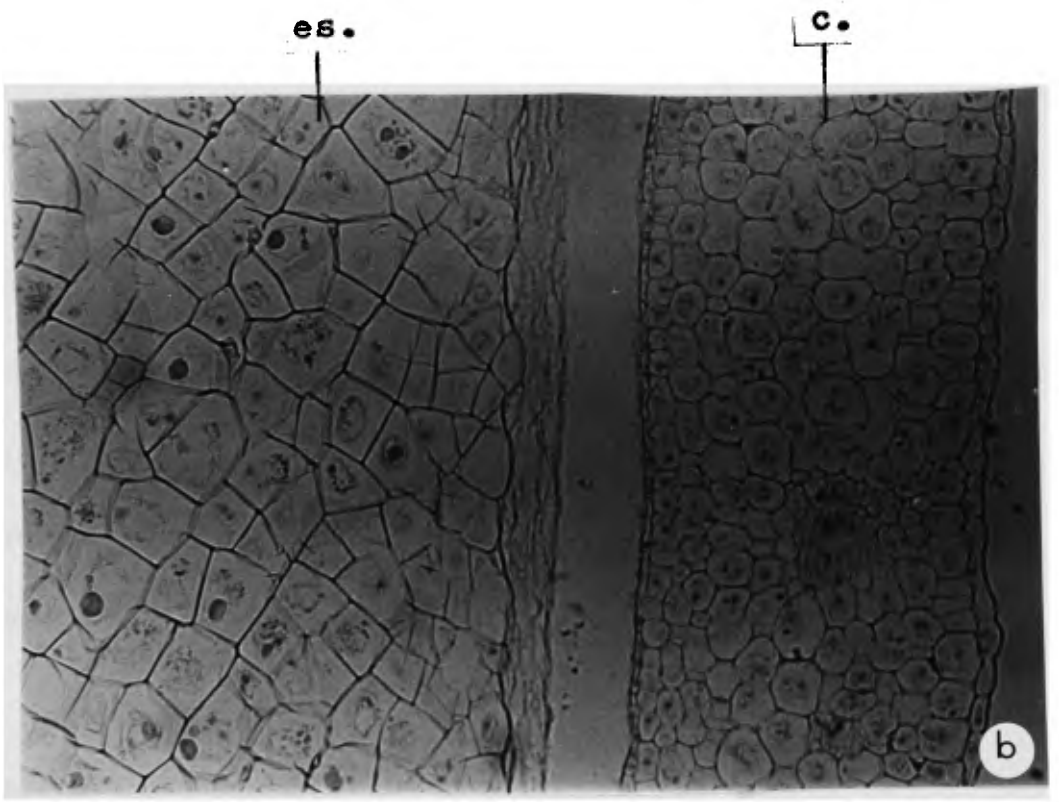


Fig. 2.14. Seed of *Manilkara kauki* (Sapotaceae) (a) Section of testa, 150x (b) section through endosperm and cotyledons, 150x.

es: endosperm; c: cotyledon.

The Taxonomic Position of Sarcospermataceae.

The monogeneric family Sarcospermataceae was established by Lam in 1925 and consists of 8 South-East Asian species (Lam & van Royen 1952). Previously, Sarcosperma had been a genus within the Sapotaceae. Cronquist and Takhtajan do not quite accept that it is distinct from Sapotaceae but Hutchinson and Engler have accepted it as distinct.

The family is said to differ from Sapotaceae only in the five characters tabulated below. The initials L, H and E refer to Lam (1925), Hutchinson, and Engler respectively.

	Sarcospermataceae	Sapotaceae	
1.	Flowers in racemes or panicles.	Flowers in fascicles.	H, L.
2.	Leaves opposite or sub-opposite.	Leaves alternate.	H, L.
3.	Fruit a drupe.	Fruit a berry.	E
4.	Ovary 1 - 2 (3) locular.	Ovary mostly 4 - 12 locular.	E, L.
5.	Testa coriaceous to crustaceous.	Testa crustaceous.	

The first character has been discussed in the section on inflorescences in which it was shown that the raceme in Sarcosperma is a second-order inflorescence consisting of a series of Sapotaceous fascicles on a twig, the leaves of which have been reduced. Such an inflorescence occurs in the Sapotaceous genus Anningeria also.

The second character, likewise, does not offer as sharp a distinction as it sounds. Some species of Sarcosperma actually have a mixture of alternate, sub-opposite and opposite leaves. In Sapotaceae itself, most genera have leaves clustered in spirals at the ends of upturned twigs but in Payena and

Chrysophyllum there has been a differentiation in the shoot system resulting in two kinds of shoots - upright shoots with spiral leaves and lateral shoots with leaves alternating on opposite sides in a horizontal plane to form applanate outward-growing sprays. Hence in Sapotaceae, we have both the poplar and willow habits of Corner (1964) which have evolved independently within many different families. The Sarcospermataceous phyllotaxy is such an unstable balance of alternate, sub-opposite and opposite conditions that in my opinion it is a derivative of the willow habit in which the alternate leaves have become more and more closely paired.

If an analogy is needed, it can be supplied from Ebenaceae in which we see exactly the same progression in parallel. All Malesian species have the willow habit but some African species have the poplar habit. A few Indian species, e.g. Diospyros tomentosa, D. melanoxylon, D. oppositifolia (see Clarke 1882) exhibit a mixture of the alternate, sub-opposite and opposite conditions.

A similar series is evident in the Symplocaceae in which nearly all species have the poplar habit, some have the willow habit, and a few have sub-opposite and opposite leaves in applanate sprays.

In neither Ebenaceae nor Symplocaceae is opposite and sub-opposite phyllotaxy considered strong enough evidence on its own to mark out species into separate genera or families.

The third character, used by Engler and probably taken from Hutchinson who might have taken it from King & Gamble (1905) is a mistake, which Lam (1925) has already pointed out. I rechecked the character and can confirm that Sarcosperma does not develop a hard endocarp.

As for the fourth character, the 1 - 2 (3) carpellate condition of Sarcosperma fits nicely to the 4 - 12 carpellate condition of Sapotaceae to form one natural series. But in fact Engler has overlooked the Sapotaceous genus Diploon with two carpels, so that even the arbitrary distinction he makes is obscured.

Excluding the third character as a bad error, we are left with the fact that in Sarcosperma, the ends of four evolutionary tendencies are found together in the same genus: from a first order to a second order inflorescence, spiral to alternate to sub-opposite to opposite phyllotaxy, reduction of carpel number to 2 and 1, loss of sclerification of the testa. Do these traits combined make a distinct family? Seen from the point of view of Sapotaceae, in which most genera are notoriously weak, the relative distinctness of Sarcosperma makes its elevation to a family of its own, understandable. But seen from the view point of the Order as a whole, the Sarcosperma-taceae is definitely not co-equal with the other families. It is scarcely distinguishable from the Sapotaceae and ought at best to be considered a sub-family.

Comparison of Lissocarpaceae with Ebenaceae.

Lissocarpaceae, established by Engler & Gilg in 1924, is a monogeneric family of two very closely related tropical American species. Previously, Lissocarpa had been included in the Styracaceae.

The family is sharply delimited from Ebenaceae by the following characters.

	Lissocarpaceae	Ebenaceae
1.	Ovary inferior.	Ovary superior.
2.	Corona of 8 lobes.	No corona.
3.	Pollen 3 porate, p/e 0.9 - 0.7, surface with very prominent reticulate sculpturing.	Pollen 3 colporate, p/e 1.5 - $1.2^{(0.9)}$, surface smooth to very finely warty.
4.	Rays (tangential wood sections) predominantly over 1 mm high in any specimen.	Rays predominantly less than 1 mm high in any specimen.
5.	Seed vascular system of 6 - 12 branches prominent as longitudinal ridges.	Seed vascular system a circumperipheral loop or if branched, the branches not prominently raised.

There are also a number of partial differences, which I think are irrelevant in a comparison between a large family and a very small one. For example, the two species of Lissocarpa have their styles completely united whereas such a condition is rare in Ebenaceae. This might be cited as a difference between the two families. However, the exceptions in Ebenaceae, with styles completely united, outnumber the total species in Lissocarpaceae. This is therefore surely a meaningless comparison.

Furthermore if Lissocarpaceae is compared with the sub-genus Hierniodendron (comprising 3 species of Diospyros), this difference would disappear because Hierniodendron has completely united styles.

Similarly, the two species of Lissocarpa have the following characters, which are uncommon in Ebenaceae: calyx of four imbricate retuse lobes, locules not divided by false septa , stamens 8 in one whorl, seeds 1 - 2 (by abortion). In every case, the exceptions in Ebenaceae outnumber the two species of Lissocarpa.

The distinction and hence the validity of small taxa when compared to large (and almost certainly more variable) ones must depend, in my opinion, absolutely on clear-cut characters. Lissocarpaceae is sharply delimited from Ebenaceae although the number of differences is relatively few. The two families appear to be closely related. The external morphology of Lissocarpa, the internal structure of the gynoecium, ovule and seed and the structure of the wood all point towards a close relationship, as can be seen from the following description of Lissocarpaceae, which should be compared with that of Ebenaceae given at the end of Part I.

Lissocarpaceae: Woody plants without latex. Leaves exstipulate, alternate, with entire margins. Inflorescence axillary, multi-bracteate, multiflorous, sporadically reduced to a single flower on a bracteate peduncle. Flowers articulated at base, unisexual (hermaphroditism erroneously presumed in all previous descriptions), probably dioecious, regular, 4 merous. Calyx imbricate, persistent in fruit. Corolla sympetalous, isomerous with calyx, with lobes contorted sinistrorsely, tube prominent, bearing a corona of 8 lobes. Male flowers with 8 epipetalous stamens in one whorl; anthers linear, erect, basifixed

dehiscing by longitudinal slits. Pistillode as pistil but devoid of ovules. Pollen 3-porate, prominently reticulate. Females flowers with ovary inferior, 4 carpellate, 4 locular, each carpel bearing two ovules. Ovules with apical placentation, oblong, anatropous, with raphe descending on outer side. Staminodes resembling stamens except anther lobes collapsed and devoid of pollen. Fruit a berry with persistent calyx at apex. Seeds 1 - 2 by abortion, penduleus, with prominent raised vascular system consisting of one vein descending from placenta to chalasa which then sends 5 - 11 branches back up to the apex (Hutchinson mentions only 3 "ribs" but in error). Hilum relatively small, apical; testa smooth, thin, coriaceous; albumen horny, abundant, smooth; embryo upside-down, with two small foliaceous cotyledons and a strongly developed radicle. Wood as Ebenaceae except rays predominantly over 1 mm high.

Comparison of Symplocaceae with Ebenaceae.

The monogeneric family Symplocaceae shares with Ebenaceae the following features: woody plants without latex; leaves exstipulate, alternate, rarely opposite or sub-opposite; inflorescence multibracteate, multiflorous; flowers articulated at base, regular; calyx persistent; corolla sympetalous, ± isomerous with calyx; anthers dehiscing by longitudinal slits; ovary syncarpous, multilocular; ovules anatropous to hemianatropous, tenuinucellate.

Differences are tabulated as follows, with the sharpest differences marked with an asterisk *.

	Symplocaceae	Ebenaceae.
*1.	Wood: vessels exclusively solitary.	Vessels not exclusively solitary.
*2.	Vessel perforations scalariform.	Vessel perforations simple.
*3.	Pollen 3-porate.	Pollen 3-colporate.
*4.	Pollen p/e less than 1.	Pollen p/e (0.9)1.2-1.5.
*5.	Pollen surface reticulate.	Pollen surface smooth to finely scabrate.
6.	Leaf margin usually glandular-serrate or glandular-crenate; seldom entire.	Leaf margin entire; one exception crenulate but non-glandular.
*7.	Stomata paracytic.	Stomata anomocytic or rarely cyclocytic.
8.	Leaves often yellowish.	Leaves rarely yellowish (e.g. Diospyros australis, D. pentamera).
9.	Flowers nearly always bisexual.	Flowers nearly always unisexual.

	Symplocaceae	Ebenaceae
10.	Corolla irregularly imbricate.	Corolla sinistrosely contorted.
11.	Carpels 2 - 5, with styles fully united.	Carpels 2 - 8, with styles usually not fully united.
12.	Carpels 4 (2?) ovulate.	Carpels 2 ovulate.
13.	Carpels without false septa.	Carpels usually with false septa.
14.	Ovary ½ to fully inferior.	Ovary superior.
15.	Ovules with axile placentation.	Ovules with apical placentation.
16.	Ovules unitegmic.	Ovules bitegmic.
17.	Anthers sub-globose, with narrow inconspicuous connectives not produced beyond anther lobes.	Anthers ovate, lanceolate or linear, with prominent connectives produced beyond anther lobes.
18.	Fruit with hard endocarp.	Fruit with endocarp not differentiated or sometimes differentiated as a pulpy pseudo-sarcotesta.
19.	Fruit surmounted by persistent calyx.	Fruit sitting on persistent calyx.
20.	Chromosomes: x = 11, 12. 2n = 22, 24. Based on 5 spp. (see Index of Plant Chromosome Numbers for 1969, Regnum Vegetabile 77).	Chromosomes: x = 15 2n = 30, 60, 90.

The Symplocaceae is a highly distinct family, very isolated from the Ebenaceae. Lissocarpaceae is closer on overall characters to Ebenaceae, but with 3-porate pollen and inferior ovary, it is to some extent is a bridge between the two families.

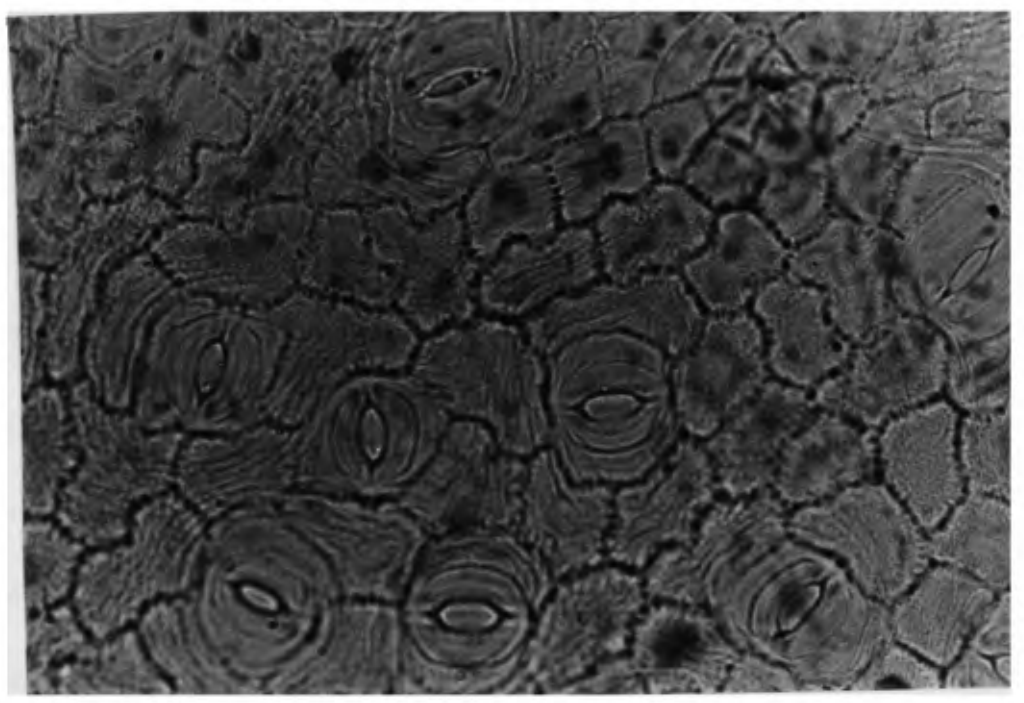


Fig. 2.15. Paracytic stomata in Symplocos adenophylla. 375x.

Comparison of Styracaceae with Ebenaceae

The Styracaceae is taxonomically in a highly unsatisfactory state. When the family was last monographed (Perkins 1907), there were only 6 genera, but the current (12th) edition of Engler's Syllabus lists 11 genera, while Hutchinson includes Afrostyrax to make the total 12.

But even with the exclusion of Afrostyrax, the family is far more variable than any others in the Order and possesses striking internal discontinuities. Owing to these complexities I am unable to treat this family as fully as the previous ones.

Collectively, the Styracaceae resemble Ebenaceae in the following: plants woody, without latex; leaves alternate, simple, exstipulate (except Afrostyrax); flowers regular; calyx persistent; corolla sympetalous, ± isomerous with calyx; anthers dehiscing longitudinally; ovary syncarpous, multilocular (rarely unilocular by failure of partition); ovules anatropous, bitegmic (at least in Styrax); albumen thick.

Differences are as follows (sharpest differences marked *):-

	Styracaceae	Ebenaceae
*1.	Wood: vessels with scalariform perforation.	Vessels with simple perforations.
2.	Rays often of two contrasting sizes.	Rays not in two contrasting sizes.
3.	Pollen 3-colporate to 3-porate.	Pollen 3-colporate.
*4.	Pollen p/e less than 1.	Pollen p/e (0.9)1.2-1.5.
5.	Gynoecium 3 - 5 carpellate.	Gynoecium 2 - 8 carpellate.
6.	Styles fully united.	Styles usually not fully united.
7.	No false septa.	Usually with false septa.

	Styracaceae	Ebenaceae
8.	Ovary inferior in most genera.	Ovary superior.
9.	Ovules axile or basal in placentation.	Ovules apical in placentation.
10.	Flowers nearly always bisexual.	Flowers nearly always unisexual.
11.	Leaf margin entire or glandular-serrate.	Leaf margins entire; one exception crenulate, not glandular.
12.	Peltate, stellate or tufted hairs very common, probably all species.	Peltate and tufted hairs on a few African spp. only.
13.	Chromosomes: <u>Halesia</u> & <u>Pterostyrax</u> 2n = 24. <u>Styrax</u> 2n = 16, >40. (Belkovskikh et al. 1969, Mehra & Bawa 1969).	Chromosomes: x = 15, 2n = 30, 60, 90.

If the genera are compared individually with <u>Ebenaceae</u>, more differences are highlighted e.g. <u>Styrax</u> has crustaceous testa, fleshy endosperm, non-articulated flowers; <u>Afrostyrax</u> has 3 porate pollen, stipules, Sapotaceous-type inflorescences (i.e. axillary fascicles the peduncles of which are devoid of bracts except at very base, and the flowers are non-articulated); <u>Alniphyllum</u> has winged seeds; and so forth. Hence whether the family is natural or not, it is collectively as well as the genera individually very distinct from <u>Ebenaceae</u>. Judging by the scalariform vessel perforations, pollen shape, and the tendency to inferior ovary, it is closest to <u>Symplocaceae</u>.

The Taxonomic Structure of the Order.

It has been demonstrated in the preceeding discussions that Ebenaceae is sharply distinguished from Sapotaceae, Sarcospermataceae, Lissocarpaceae, Symplocaceae and Styracaceae by several to numerous different characters. It also appears, although not as rigorously proven, that all the other families are sharply distinguished from each other, with the exception of the pair Sapotaceae-Sarcospermataceae which all lines of evidence, whether considered singly or together, suggest should be united in one family. We therefore really have five rather than six distinct families to consider. In the rest of this discussion, Sapotaceae will be treated in the broad sense, to include Sarcosperma.

Having shown that the five families are sharply distinct from each other, it now becomes very difficult to show how they can be closely related to each other as their association within the same Order implies.

The best proof of relationship is the existence of intermediates i.e. the presence of odd genera or species which have a mixture of the characters of two otherwise distinct families. Such intermediates are absent in the Ebenales. Each family is too distinctive. In fact, with the exception of Styracaceae, they are all almost monogeneric. Symplocaceae and Lissocarpaceae are actually monogeneric. As for Ebenaceae and Sapotaceae, patterns of infra-family discontinuity are so difficult to perceive that in Ebenaceae the trend in the past century has been toward lumping of genera accompanied by much splitting into sections whereas in Sapotaceae the trend has been excessive splitting and rearrangement at generic level. The two trends probably reflect historical precedent although

Sapotaceae, being much the larger and more variable of the two families, provides greater incentive for splitting at generic level. Essentially, the root of difficulty appears to be the strong degree of internal cohesion within each family.

However, if relationship between families cannot be proved by the existence of intermediates, it may be provable by considering the characters which all the families share in common, particularly if any of these characters are striking, rare, and unlikely to have arisen more than once in the evolution of the Angiosperms. This approach has been invoked by Davis & Heywood (1963) with regard to the continued retention of the Leguminosae as a unified family, "The Leguminosae have a unique fruit and seed and no close relatives. Surely it is more useful here to emphasise resemblances than difference....."

Unfortunately, the list of characters common to all families of the Ebenales reveals not a single character that does not also occur in at least a few dozen other families: plants woody, leaves simple, flowers regular, calyx persistent in fruit, corolla sympetalous, anthers dehiscing by longitudinal slits, ovary syncarpous, ovules anatropous to hemianatropous.

Expanding the list to include variable characters, we have: latex present or absent, leaves stipulate or exstipulate, alternate rarely opposite, with margins entire, crenate or serrate; flowers articulated or not, bisexual or unisexual; calyx in one or more whorls; corolla isomerous with calyx or not, valvate imbricate or contorted; stamens 3 - 100 or more or variously reduced to staminodes; ovary with 1 - numerous ovules per carpel; ovules unitegmic or bitegmic; fruit a berry,

drupe, capsule etc; seed winged or not; testa soft to crustaceous; and so forth. The list of variable characters is endless but perhaps enough have been cited to show that there is nothing to be gained in this approach.

The authors of phylogenetic classifications are usually obliged to favour a few characters above all others as indicators of evolutionary relationship. These are the conservative or "biological" or "constitutive" characters discussed by Davis & Heywood (1963). Sympetaly is one of these favoured characters and the Ebenales is one of the major sympetalous Orders. Another favoured character is epigyny versus hypogyny and this may be the main basis of Hutchinson's division of the families into two seperate Orders: Ebenales with superior ovary and Styracales with inferior ovary (or at least a tendency towards epigyny). Pollen shape favours Hutchinson's decision but wood anatomy suggests that Lissocarpaceae belongs with Ebenaceae rather than with Styracaceae and Symplocaceae. Gynoecial structure suggests three separate groupings: Ebenaceae + Lissocarpaceae; Styracaceae + Symplocaceae; Sapotaceae (including Sarcospermataceae). The problem is that these characters, together with other conservative characters e.g. integuments one or two, stipules absent or present, chromosome number etc. all offer conflicting lines of division, and when this happens, it is uncertain why any particular one should take precedence over the others.

Concerning the taxonomic affinities of Lissocarpa, two opinions have been offered which illustrate the problem. Oliver (1895) thought that Lissocarpa was closer to Ebenaceae than Styracaceae by its "general facies and horny albumen". Gleason (1926) rejected Oliver's opinion and declared the reverse because in his opinion epigyny links Lissocarpa to Styracaceae. In neither case were the reasons for weighting stated.

The conservative character, upon which so much phylogenetic thinking is based, seems to be a rather nebulous concept. Basically it appears to be a character which is found from experience to exist in states which are constant throughout higher taxa (family rank and above) for most taxa. If this is the case, the conservative character may be considered as a statistical measure for which a value can be calculated. It should be possible, for example, to work out an "index of conservatism" for each character at family level by counting the number of families in which it exists as a constant state divided by the total, and hence to build up a scaled ranking of all characters. An interesting punched card system devised by Hansen & Rahn (1969) for the determination of Angiosperm families, can be used to calculate such an index for the characters they have recorded. For example, it can be calculated that the character sympetaly versus polypetaly has an "index of conservatism" of 0.67 or 67% :-

Number of families with polypetalous corollas = 250

" " " " gamopetalous " = 186

" " " " both states = 109

" " " exclusively polypetalous = 250-109 = 141

" " " exclusively gamopetalous = 189-109 = 77

$$\text{Index of conservatism} = \frac{141 + 77}{141 + 77 + 109} = 0.67 \text{ or } 67\%$$

A similar calculation gives the character stipules absent versus present the much higher value of 78%. These calculations demonstrate better than any description, that no matter how conservative a character is, and how highly regarded by a concensus of taxonomic opinion, it has no more than a fair to good probability of being constant throughout a family. Indeed, if the states of each character have evolved and are evolving from each other or from intermediate states, then all characters

must break down somewhere or other. The procedure of arbitrarily selecting one or two such characters upon which to base major taxonomic decisions is difficult to justify.

Hutchinson's creation of two separate Orders seems to be based on one or two characters which have, on unspecified grounds been weighted above all others. If all characters are treated equally without weighting, then Hutchinson's treatment is the worst possible because the differences between Ebenaceae and Sapotaceae are far more numerous than between Ebenaceae and Lissocarpaceae. In fact, if number of differences, unweighted, is the sole criterion, then of all the gaps isolating the families from each other, that between Sapotaceae (including Sarcosperma) and the rest is the greatest and hence Engler's subdivision of the Order into Sapotineae and Ebenineae is the best of the classifications offered.

It may well be that the Order is best broken up and better relationships sought elsewhere, with other families in other Orders, but such a study would be outside the scope of the present project.

PART 3 : GENERIC and INFRA-GENERIC LIMITS

Introduction

Character analysis

Characters in Diospyros

Part III Generic and Infra-generic Limits in Ebenaceae.

Introduction

The genera Royena and Diospyros were described by Linnaeus in 1753. These were followed by Euclea (Murray 1774) and Maba (J. & G. Forster 1776).

The family Ebenaceae itself, was not proposed until 1799, by Ventenat, who placed in it six genera, four of which were subsequently excluded:

Diospyros L.
Royena L.
Styrax (Tourn.) L. (now in Styracaceae)
Halesia L. (now in Styracaceae)
Camellia L. (now in Theaceae)
Hopea L. (=Symplocos, now in Symplocaceae).

Hence as initially proposed, the Ebenaceae was a very heterogeneous group.

The circumscription of the family as we know it today, dates back to de Candolle (1844) who recognised eight genera:

Euclea Murr.	Macreightia A. DC.
Royena L.	Diospyros L.
Gunisanthus A. DC.	Maba J. & G. Forst.
Rospidios A. DC.	Cargillia R. Br.

De Candolle's monograph was superseded by Hiern's of 1873 which remains the most recent world-wide treatment of the family. In it, de Candolle's eight genera were merged into four, and a new genus, Tetraclis, was added to make five:

Royena L.
Euclea Murr.
Maba J. & G. Forst. (including Macreightia).

Diospyros L. (incl. Gunisanthus, Rospidios, Cargillia).

Tetraclis Hiern

The genus Rhaphidanthe was proposed, with some doubt, by Gurke in 1890. Since then, the trend has been towards reduction of genera in favour of Diospyros:

Maba (Bakhuizen 1933, 1936, Standley 1935, White 1956)

Royena (White & Barnes 1958, de Winter & White 1961, White 1963).

Rhaphidanthe (White 1963)

Only three genera are now left, of which Tetraclis cannot be maintained and is due to be reduced (White, personal communication). Effectively therefore, the family Ebenaceae consists of only two genera, i.e. the world-wide, mostly tropical, Diospyros of about 500 species and the east- and south-African Euclea of only 14 species.

In Malesia (sensu Flora Malesiana, van Steenis 1948, 1964) there are 150 - 200 species of Diospyros. These were monographed by Bakhuizen (1936 - 1941) who also included species from Australia and Oceania in his treatment.

Bakhuizen initially (1936) divided the genus in Malesia into four subgenera: Maba, Hierniodendron, Cargillia and Eudiospyros. Maba was in turn subdivided into three sections and Eudiospyros into 31 sections. A very extensive "addenda et corrigenda" was published in 1941 which added greatly to the complexity of the monograph. In it, a new subgenus Mabacea was created and one more section each were added to Maba and Eudiospyros.

It is noteworthy that Hiern was unhappy about generic limits in the Ebenaceae for on p. 63 of his mongraph he wrote "The diagnostic characters of the genera of this family are not well

defined; indeed it has been proposed to unite all into one genus." As for sectional limits, doubts were expressed by Bakhuizen in the preface to his monograph "These sections are mainly founded on characters of the principal species belonging to them. Several of these sections should be considered to be provisional ones which will have to be suppressed when the plants will be more fully known." In fact sectional limits in Diospyros have undergone very drastic changes between de Candolle, Hiern, Clarke (1882) and Bakhuizen.

In this part of my thesis, it was intended to put Bakhuizen's classification to the test and to suggest how improvements might be made. A classification can be tested in many different ways. Do the keys work? Does the classification look logical on paper? Does it have any predictive value? Can it absorb new information or new species without needing drastic revision? Would another trained observer have arrived at the same classification independently? Does it help users to understand better the group that has been classified? And so on. These are the traditional ways in which a classification is put to the test by users and a concensus gradually develops about its general quality.

The approach chosen here has only very recently been developed (Estabrook 1967, Hawkesworth, Estabrook & Rogers 1968, Bisby 1970) and involves the direct testing of characters by a taximetric procedure "character analysis".

Character Analysis

In orthodox practice, the taxonomist usually takes into consideration a large number of characters of the group under study - perhaps as many characters as he can think of. Most of these are soon rejected for various reasons, and the classification is finally presented on paper as being based on a relatively small number of "good" characters. If the taxonomist's choice of characters for subdividing the group has been quite arbitrary, it will soon become apparent to others that the classification is artificial. Other characters will simply not fall into line. But if those few characters have been chosen because they correlate best with other characters, then the classification will appear natural because other characters will tend to fall into line. Hence in a good natural classification, the number of characters actually used in presentation of the classification, though only a small sample of the total, represent the best correlated of a very large number assessed mentally, nearly always informally, but as far as humanly possible, objectively. The taximetric procedure of character analysis was developed in the hope of simulating the process of objective character assessment and weighting.

In the technique described by Bisby (1970) in a study involving 52 characters and 273 species of Crotolaria, each character was compared with every other character in turn. For each comparison, a value of correlation called the "fractional information in common" was computed on a scale of 1 to 0. For example if character "a" divides up the species in exactly the same way as character "b" then the correlation between them is absolute and a value of 1 is assigned. If correlation is less than absolute, a value smaller than 1 is assigned, according to a predetermined formula. The computations are carried out

by computer using the programme CHARANAL, details and references of which are given by Bisby.

After character "a" has been compared in turn with "b", "c", "d" and so on for all the characters, the values of "fractional information in common" are summed up and this sum or "information contribution of the character" is a measure of the degree of correlation between the given character "a" and all other characters. Similar values are calculated for all the other characters, and the characters can then be ranked on a numerical scale. The result is a ranking by correlation-weighting.

Crotolaria was chosen because it had recently been revised by Polhill (1968). Hence Polhill's assessment of characters could be used as a standard for comparison. The degree of agreement was extremely good. Characters that Polhill had used for his major divisions ranked high in Bisby's list. In contrast, characters used by Baker (1914) in an earlier classification of Crotolaria and which Polhill had criticised, were found, "with one exception, to have very much lower information contributions than those of Polhill".

It appears therefore that we now have a powerful tool for assessing characters, which might be used to test existing classifications or to help create new ones. The application of this tool to the infrageneric classification of Diospyros became a very attractive idea.

Characters in Diospyros.

As earlier stated, Bakhuizen grouped Malesian and Australasian species of Diospyros into five subgenera to which he provided a conspectus (1936 - 1941, p.6 & 454). If the gynoecium is reinterpreted in term of carpels (Part I), the conspectus may be rewritten, somewhat more concisely, as follows:-

A. Ovary 3 carpellate, with or without false septa. Flowers 3 (4 - 5)* merous; calyx lobes valvate or subvalvate, sometimes accrescent. Albumen smooth or ruminate. Maba

B. Ovary 2 - 3 carpellate, without false septa. Flowers 4 - 5 merous; calyx lobes suborbicular or reniform, contorted-imbricate, not or slightly accrescent. Albumen ruminate. Hierniodendron

C. Ovary 4 carpellate, without false septa. Flowers 4 merous; calyx lobes triangular, valvate. Albumen smooth. Cargillia

D. Ovary 2, (3), 4 - 10 carpellate, with false septa. Flowers 4 - 10 merous; calyx lobes very variable in shape (rarely absent), valvate or imbricate. Albumen smooth or ruminate. Eudiospyros

E. Ovary 2 carpellate, with false septa. Flowers 4 (5) merous; calyx lobes triangular, probably valvate. Albumen ruminate. Mabacea

It might be stated at the outset that there does not appear to be any logical basis for maintaining the monospecific Mabacea from the very large and variable Eudiospyros. Also, carpel

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* Floral merism refers to the two perianth whorls only.

merism is unstable; 4-merous ovaries are known in Maba and Hierniodendron, 3-merous ovaries in Cargillia and Eudiospyros, hence the character as formulated Bakhuizen is true only in a very general sense.

From the conspectus, the following five characters may be extracted that can be put to the test:-

a) Ovary predominantly 3-carpellate versus not.
b) False septa present versus absent.
c) Flowers predominantly 3-merous versus not.
d) Calyx lobes valvate versus imbricate versus variable.
e) Albumen smooth versus ruminate versus variable.

These then are the characters to which Bakhuizen has given most weight. It will be noticed that for characters (d) and (e), variability is treated as a state in its own right. This is necessary because for use with CHARANAL, each character has to be defined so that there should be absolutely no doubt into which of its states every species belongs. Hence species which have e.g. both ruminate and smooth albumen cannot be entered twice, under smooth, and again under ruminate. They would have to be placed in the state 'variable'. It may be argued in support of this procedure that variability with respect to any character is as much a property of a given species as constancy, and deserves to be taken into account in character analysis.

For sectional delimitation Bakhuizen used a very large number of characters e.g. depth of calyx lobing, degree of accrescence of fruiting calyx, size of fruits, petiole terete or not, hairiness of parts, shape of corolla, density of lateral nerves, texture of leaves.

It might appear to be a relatively simple matter to extract the sectional characters, process them with the subgeneric characters and obtain a ranking by information contributions. Unfortunately this turned out to be extremely difficult and usually impossible. What Bakhuizen appears to have done has been to associate his species into sections first, dealing with a few species at a time, arranging them around certain "principal" or marker species, and then writing a key around the whole scheme. This is classification <u>from below.</u> It allows for considerable flexibility in the use of characters because the characters can be changed from one part of the classification to the next, the choice being determined by the actual subset of species being compared at any one time. It is unnecessary that the characters should be formulated so as to apply to the whole set. However, for this very reason, such characters are difficult to extract for use in taximetric analysis.

Most taximetric models demand that the characters should be formulated for the complete set of species or operational taxonomic units. This introduces a considerable constraint on the selection of characters.

To illustrate this point, we might consider the character leaf length. <u>Diospyros buxifolia</u>, with leaves 0.6 - 8 cm. long is sharply distinguished from <u>D. argentea</u> with leaves 15 - 45 cm. long. If we want to characterise these two species, this character can be used with great effect, because it exhibits two distinct states as far as this particular comparison is concerned.

However, if leaf length is considered for the genus <u>Diospyros as a whole</u>, it would be absolutely impossible to see any internal discontinuities in the character i.e. it simply does not divide

up into states. The gap between *D. buxifolia* and *D. argentea* is completely obliterated by other species and no other gaps can be perceived. Hence in selecting characters from above, by considering all species together, the character leaf length will immediately be discarded.

It so happens in *Diospyros* that most characters behave like leaf length in being so continuously variable when the species are considered *en masse* that it is virtually impossible to detect discontinuities in them, although the species themselves are quite distinct from each other. The *Crotolaria* situation in which a relatively large number of characters exist in sharply contrasting states, certainly does not apply here. I considered 102 species (Appendix 7) and after considering all sorts of characters - size of structures, degrees of pubescence, numbers of floral parts, shapes, presence and absence of structures, I arrived at 28 characters (table 3.1) which exhibit fairly distinct states. However, even this number may be over-optimistic because certain characters appear as related pairs, viz.

1. Male inflorescence on old or current wood
4. Female inflorescence on old or current wood

2. No. of flowers on male inflorescence
5. No. of flowers on female inflorescence

3. Male inflorescence flagelliflory
6. Female inflorescence flagelliflory

52. Male floral merism
53. Female floral merism

54. Male calyx aestivation
55. Female calyx aestivation

31. Male calyx hairiness

33. Female calyx hairiness

22. Male corolla hairiness

26. Female corolla hairiness

In a genus with only bisexual flowers such as Crotolaria, this situation does not occur, but in Diospyros, sexual dimorphism presents us with separate male and female versions of certain floral and inflorescence characters. The two versions do not always coincide, otherwise there would be no sexual dimorphism, but they often coincide to a considerable degree. For example character 6 has an information contribution of 3.44, of which 0.74 is contributed by character 3 alone. If there had been complete correlation, character 3 would have contributed a value of 1.00. Because such pairs of characters tend to support each other to mutually boost up their information contributions, it may be considered that there is an unfair bias and that such pairs are equivalent more or less to certain characters being scored twice. In order to see what would happen if the bias is removed, table 3.2 was prepared, in which the male characters 1, 2, 3, 22, 31, 32, and 34 were deleted. After re-adjustment of information contributions, it was found that the rankings of many characters were altered, but the three top characters remained unchanged relative to each other since characters 6 and 3 are almost equivalent to each other. The drop in information contribution is steepest between the first three characters.

The rest of this discussion is based on table 3.2, in which Bakhuizen's sub-generic characters are indicated by an asterisk*. The character at the top of the list is a modified Bakhuizen character. The original formulation: endosperm ruminate/smooth/ variable, scored only 0.99 because it hardly correlates with

any other character. In its new formulation, it is strongly correlated with characters 48, 11, 51, 14, (see table 3.3) and coincides clearly with the division between subgenus Hierniodendron and the rest.

The second character, no. 48, strongly correlates with two other characters, no. 55 and no. 9, and coincides with the divisions between subgenus Hierniodendron, section Brachycylix, and the rest.

Next, character 6 picks out very weakly, section Phyllosepala and D. mutans (of sect. Basithrix) from the rest.

Character 10 picks out mixed assemblages of species which cannot possibly be closely related to one another. In fact, from the third character downwards, all the characters are very low in information contribution whether compared to the first character or compared to the theoretical maximum of 21 for a 21-character analysis. Support for subgenus Maba is extremely weak (character 53, information contribution 1.92). None of the other subgenera or sections stand out, although it must be re-emphasized that most of Bakhuizen's diagnostic characters for sections could not be directly analysed in this way.

While selecting and scoring characters for the analysis, I had, quite independently from the computer study, been testing the limits of Bakhuizen's sub-genera and sections by orthodox visual comparison of specimens. I came to the following conclusions:

(a) Sections 3, 7 - 31 of Bakhuizen's Eudiospyros cannot be distinguished from each other nor from Maba, Cargillia, and Mabacea except quite arbitrarily, by single characters. Maba

is an excellent example of an arbitrary taxon based on the single character, trimery. The absence of false septa (locules bi-ovulate) is another character that has been overrated, probably because it is rare and striking in Ebenaceae. It has been responsible for the maintenance of Cargillia for these species without false septa and which could not be fitted into Maba nor Hierniodendron. Ebenus seems to be based entirely on the presence of an internal elevated rim on the female calyx. Most of the other sections seem to lack distinguishing features and merge smoothly into each other. Some of the sections e.g. Kurzella, Eriantha, Ebenus, Nesindica, Glutinosa appear to consist of species so very closely related that they may prove conspecific to some considerable degree. If Maba, Cargillia, Mabacea and sections 3, 7 - 31 of Eudiospyros are merged as I think they should be, the result would be a very large and variable section (or sub-genus, but see below) to which the name Diospyros would have to be given (instead of Eudiospyros) according to the International Rules, since it would include D. lotus, the type of the genus.

(b) Of the seven taxa left out, viz. Hierniodendron, Brachycylix, Cavanillesastrum, Podophora, Ebenaster, Basithrix and Gaudifera I have always considered Hierniodendron to be the most distinct, and this opinion is now strongly supported by the character analysis. Hierniodendron differs from the rest of the genus in being vascular-ruminate (see Appendix 6 for definition), with a staminal tube formed by union of all filaments (fig. 1.1k), bi-ovulate loculos, sepals imbricate, free or nearly free, and a unique mode of germination (fig. 1.13d-f).

(c) Brachycylix is much less distinct than Hierniodendron but has a unique staminal morphology (fig. 1.1d), bicarpellate gynoecium of four uni-ovulate loculos, sepals imbricate, free

or nearly free, and small fruits generally less than 2 cm. diameter. It gets some support from the character analysis. All these characters except the first are individually found elsewhere but they form a rather constant syndrome in Brachycylix.

(d) I am at this stage undecided about the status of Cavanilleastrum, Podophora, Ebenaster, Basithrix and Caudifera. Cavanilleastrum (especially D. poncei) seems very close to Ebenaster. Podophora is almost certainly a bad mixture, one of whose members, D. insidiosa undoubtedly belongs to sect. Diospyros close to D. borneensis. Basithrix will probably also have to be broken up, with some members assigned to Brachycylix and others to sect. Diospyros. Unfortunately the character analysis does not give any positive guidance for these six doubtful groups.

As an interim measure, pending a complete world-wide assessment of the infra-generic structure of Diospyros, I would propose that the rank of sub-genus be abandoned, since the use of both sub-genus and section suggests a degree of objectivity in decision making between species and genus, that cannot be justified by our present state of knowledge. What appears to happen in the genus Diospyros is that we have one large variable section Diospyros from which a few groups such as sect. Hierniodendron, sect. Brachycylix and possibly a few others yet to be decided, stand out by possession of small syndromes of unusual characters. The use of a single intermediate rank, viz. the section, appears to be quite adequate for expressing the taxonomic situation.

Table 3.1. Information Contribution of Characters
(For definitions of characters, see Appendix VI)

*Character Information Number	Contribution	Description
44	6.33	Endosperm: vascular-ruminate/not.
48	4.57	Stamens: "normal"/maingayi-type/clavigera-type .
3	4.35	♂ inflorescence: not flagelliform/ flagelliform/ variable.
52	3.64	♂ floral merism: predominantly 3/not.
53	3.53	♀ floral merism: predominantly 3/not.
6	3.46	♀ inflorescence: not flagelliform/ flagelliform/variable.
10	2.88	Ovary: glabrous/hairy-glandular/hairy non-glandular/var. 1 or 3 .
54	2.78	♂ calyx lobes: imbricate/valvate or absent/variable .
55	2.69	♀ calyx lobes: imbricate/valvate or absent/variable.
33	2.38	♀ calyx inside: glabrous/hairy/variable.
11	2.38	False septa : present/absent .
15	2.29	Pistillode: glabrous/hairy/both .
26	2.23	♀ corolla outside: exclusively glabrous/ glabrous to simple-hairy/glabrous to forced-hairy/glabrous to glandular hairy.
34	2.14	♀ calyx: with internal elevated rim/ without.
51	2.10	Carpel merism: predominantly 3/not.
31	2.01	♂ calyx inside: glabrous/hairy/variable.
19	2.01	Stamens: glabrous/hairy/variable.
14	1.95	Pistillode: absent/present.
22	1.92	♂ corolla outside: excl. glab./glab. to simple hairy/glab. to forked-hairy/glab. to glandular hairy.
2	1.84	No. flowers on ♂ inflorescence: 1/1-4/ 1-20/3-4/3-∞ .
20	1.82	Staminodes: glabrous/hairy.
9	1.61	Gynoecium: reduced/not reduced/variable
37	1.60	Fruiting calyx: reflexed/erect/split/ spreading.
1	1.58	♂ inflorescence: on old wood/current wood/variable.
4	1.54	♀ inflorescence: on old wood/current wood/variable.

Table 3.1 (Cont'd.)

*Character Number	Information Contribution	Description
13	1.51	Styles: free/united/variable.
36	1.22	Fruit: hairy/glabrous or nearly.
5	1.22	No. flowers on ♀ inflorescence: 1/ 1-4/1-20/3-4/3-∞ .

*These are the actual numbers allocated to each character formulation. Numbers not listed are those that have either been replaced or abandoned.

Table 3.2. Information Contribution of Characters after deleting 1, 2, 3, 22, 31, 52, 54.

Character Number	Information Contribution	Description
**44	5.02	Endosperm: vascular-ruminate/not.
48	3.31	Stamens: "normal"/maingayi type/ clavigera type.
6	2.30	♀ inflorescence: not flagelliform/ flagelliform/variable.
10	2.21	Ovary: glabrous/hairy-glandular/hairy non-glandular/variable 1 & 3.
*53	1.92	♀ floral merism: predominantly 3/not.
*11	1.85	False septa: present/absent.
*15	1.74	Pistillode: glabrous/hairy/variable.
51	1.54	Carpel merism: predominantly 3/not.
14	1.53	Pistillode: absent/present.
19	1.53	Stamens: glabrous/hairy/variable.
20	1.51	Staminodes: glabrous/hairy.
33	1.49	♀ calyx inside: glabrous/hairy/variable.
34	1.46	♀ calyx: with internal elevated rim/ without.
*55	1.39	♀ calyx: imbricate/valvate or absent/ variable.
9	1.12	Gynoecium reduced/not/variable.
13	1.10	Styles: free/united/variable.
37	1.06	Fruiting calyx: reflexed/erect/split/ spreading.
26	1.02	♀ corolla outside: exclusively glabrous/ glabrous to simple hairy/glab. to forked hairy/glab. to glandular hairy.
36	0.83	Fruit: hairy/glabrous or nearly.
4	0.82	♀ inflorescence: on old wood/current wood/variable.
5	0.71	No. of flowers on ♀ inflorescence: 1/ 1-4/1-20/3-4/3-∞ .

* Character used by Bakhuizen in sub-generic delimitation.

** As above but modified. The original formulation: Endosperm ruminate/smooth/variable, has an information contribution of only 0.99.

Table 3.3. Fraction of information in character i also contained in character j. (i characters to be read across, and j characters down the table).

i \ j	1	2	3	4	5	6	9	10	11	13	14	15	19	20
1	0.00	0.11	0.08	0.47	0.15	0.10	0.04	0.10	0.04	0.05	0.05	0.04	0.02	0.03
2	0.14	0.00	0.08	0.16	0.17	0.09	0.13	0.19	0.22	0.17	0.05	0.16	0.09	0.09
3	0.01	0.00	0.00	0.01	0.01	0.27	0.02	0.00	0.00	0.03	0.13	0.00	0.01	0.02
4	0.49	0.13	0.09	0.00	0.13	0.10	0.05	0.11	0.06	0.03	0.07	0.07	0.01	0.18
5	0.24	0.22	0.31	0.19	0.00	0.13	0.05	0.18	0.10	0.07	0.09	0.07	0.05	0.06
6	0.02	0.02	0.74	0.02	0.01	0.00	0.06	0.08	0.10	0.02	0.26	0.00	0.03	0.03
9	0.04	0.09	0.24	0.04	0.03	0.25	0.00	0.06	0.06	0.04	0.09	0.10	0.05	0.03
10	0.08	0.11	0.03	0.08	0.07	0.26	0.05	0.00	0.05	0.15	0.06	0.52	0.13	0.19
11	0.01	0.06	0.02	0.02	0.02	0.02	0.02	0.03	0.00	0.02	0.02	0.02	0.04	0.07
13	0.06	0.14	0.23	0.03	0.05	0.06	0.05	0.20	0.05	0.00	0.04	0.15	0.10	0.12
14	0.01	0.01	0.50	0.02	0.02	0.38	0.07	0.03	0.02	0.01	0.00	0.00	0.02	0.06
15	0.02	0.09	0.00	0.04	0.03	0.04	0.09	0.42	0.06	0.10	0.00	0.00	0.13	0.01
19	0.02	0.08	0.15	0.01	0.03	0.16	0.06	0.18	0.12	0.10	0.07	0.22	0.00	0.39
20	0.02	0.06	0.07	0.11	0.02	0.08	0.02	0.16	0.11	0.07	0.11	0.01	0.29	0.00
22	0.03	0.04	0.12	0.03	0.06	0.58	0.08	0.09	0.01	0.05	0.14	0.05	0.09	0.08
26	0.14	0.10	0.13	0.08	0.09	0.49	0.06	0.06	0.04	0.05	0.26	0.05	0.14	0.05
31	0.07	0.04	0.17	0.03	0.07	0.07	0.10	0.18	0.22	0.06	0.02	0.18	0.16	0.04
33	0.02	0.06	0.25	0.03	0.03	0.04	0.07	0.28	0.07	0.04	0.01	0.44	0.09	0.05
34	0.01	0.04	0.00	0.02	0.01	0.01	0.00	0.02	0.02	0.02	0.01	0.05	0.02	0.03
36	0.02	0.05	0.36	0.00	0.01	0.06	0.01	0.06	0.05	0.06	0.00	0.06	0.02	0.01
37	0.02	0.15	0.17	0.06	0.06	0.11	0.08	0.10	0.09	0.11	0.01	0.12	0.17	0.02
44	0.01	0.06	0.01	0.01	0.01	0.01	0.06	0.04	0.32	0.05	0.15	0.00	0.03	0.04
48	0.04	0.06	0.02	0.03	0.03	0.02	0.11	0.07	0.16	0.06	0.14	0.03	0.08	0.02
51	0.00	0.02	0.03	0.01	0.01	0.03	0.06	0.06	0.31	0.05	0.00	0.03	0.01	0.07
52	0.00	0.01	0.01	0.01	0.04	0.01	0.04	0.03	0.02	0.01	0.02	0.04	0.01	0.02
53	0.00	0.01	0.01	0.01	0.04	0.01	0.04	0.03	0.02	0.01	0.02	0.04	0.01	0.01
54	0.02	0.04	0.26	0.01	0.01	0.04	0.08	0.08	0.02	0.04	0.01	0.08	0.10	0.03
55	0.04	0.04	0.27	0.01	0.01	0.04	0.11	0.04	0.04	0.04	0.02	0.06	0.11	0.07
Total	1.58	1.84	4.35	1.54	1.22	3.46	1.61	2.23	1.38	1.51	1.95	1.29	1.01	1.82

PART 4 : SOME SPECIFIC PROBLEMS in DIOSPYROS

Introduction

D. ehretioides, D. sylvatica,

D. hermaphroditica, D. fasciculosa,

D. holttumii, D. ruminata and D. putii.

D. kaki, D. roxburghii, D. glandulosa.

D. kika and D. oldhamii.

D.lotus and D. brideliifolia.

Part IV. Some specific problems in Diospyros

Introduction

Bakhuizen recognised 190 species in his revision of Malesian and Australasian Diospyros. From citations following each species description, it is possible to work out that 44 of the species were known from single specimens, i.e. their types, only. A total of 103 species were known from 1 - 5 specimens each. Only 48 species were represented by over 15 specimens each. Compared with van Steenis' (1957) informal estimate that in the Malesian flora, 15 - 30 specimens per species more or less evenly spaced as to origin, are required for a good assessment of the range of infra-specific variation, and to White's (1969) more formal estimate of 30 - 40 specimens under African conditions, it is clear that Bakhuizen's revision was on the whole based on samples much too inadequate for a proper distinction to be made between infra- and inter-specific variation.

Table 4.1. No. of specimens on which Bakhuizen's species were based.

No. of specimens per species	1	2-5	6-10	11-15	15
No. of species	44	59	31	14	48

While working on the limits of the family (Parts 1 & 2) and again when selecting characters for taximetric analysis (Part 3), I became aware that some species are highly distinct while others fall into clusters which might, in extreme cases, be single highly polymorphic species. Decisions involving members of such complexes have always been difficult to make. If specimens are scarce, it is inevitable that many "paper species" will be created as a result of isolation by sampling

error, as opposed to the biological species, resulting from reproductive isolation, which is the task of the taxonomist to discover. There are still many species of Diospyros in Malesia which are poorly collected but fortunately many others have become much better collected since 1941 and for these latter, the time may be just about right for a balanced analysis to be made.

In this part of the thesis, I have attempted to analyse some of these complexes, taking into account all available morphological, geographical and ecological evidence simultaneously. However, the human mind is normally, as Anderson (1949) has pointed out, inefficient in analysing more than one variable at a time. To overcome this limitation, it is necessary to resort to graphical methods, of which some very ingenious ones have been devised by Anderson himself. The method which I have adopted involves the use of ideograms on a distribution map.

First, the whole complex is examined and a selection of characters is made to be subjected to further analysis. Such characters show more or less discontinuous variation within the complex and are the diagnostic and differential characters (sensu White 1962) that have either actually been used or may potentially be used to characterise taxa within the complex. Each ideogram represents a single specimen and contains all the morphological information about it that is relevant to the analysis. The ideogram I favour is basically a circle divided into parts. Each part represents one character and is variously inked-in or left blank to represent the particular state of that character which is seen on the specimen. The completed ideogram is then plotted on a map according to the locality given by the collector's label.

The completed distribution map shows the way the characters are associated with each other over the whole geographical range of the complex. Such maps are an excellent means of displaying variation patterns. I have been able to draw important conclusions from them, taxonomic as well as, in some cases, evolutionary.

Diospyros ehretioides, D. sylvatica, D. hermaphroditica, D. fasciculosa, D. holttumii, D. ruminata and D. putii.

The unity of this complex was partially recognised by Bakhuizen, who placed D. fasciculosa, D. ruminata, D. holttumii and D. hermaphroditica within the same section Rhipidostigma (Hasak.) Bakh. He also placed D. confertiflora in the same section but this is a highly distinct species that cannot be confused with anything else and is hence excluded from this discussion. Bakhuizen did not include D. ehretioides, D. sylvatica and D. putii in his revision presumably because they lay outside his geographical limits.

Variation within the complex is particularly noticeable in floral merism, because the complex lies on the controversial boundary between Maba and Diospyros in Hiern's classification. I examined the calyces of all available flowers on 69 specimens, and obtained frequencies of 1 : 315 : 258 : 6 for dimery, trimery, tetramery and pentamery respectively. Most of the specimens showed a mixture of trimerous and tetramerous flowers. Owing probably to accidents of sampling, Hiern had placed D. ehretioides and D. sylvatica in Diospyros but D. hermaphroditica, D. fasciculosa and D. ruminata in Maba, completely disregarding the overall similarity between them.

In fact, floral merism is so unstable, even among flowers on the same twig, that it cannot be considered as a character for subdividing the complex, although different populations may have different modal values. For example D. ehretioides appears to be predominantly tetramerous while D. hermaphroditica appears to be predominantly trimerous when a large number of representatives are considered. Given a specimen with a few flowers (most specimens have only a few flowers), it would be

satistically improper to say whether it belonged to one state or the other because the samples would be far too small.

I was able to find six characters that can be used in an overall analysis, and a seventh that can be used at a somewhat later stage, to be explained later. These characters, and their coded symbols are :-

1. Largest petiole bases (or their scars).
   - broad : 4 - 7 mm
   - narrow : 1 - 3 mm
2. Female cymes uniflorous
   - multiflorous
   - 1 - 3 florous
3. Ovary hairy all over
   - hairs concentrated in a basal ring
   - glabrous
4. Length/breadth ratio of largest well-formed leaf
   - $\leqslant$ 1.86
   - > 1.86
5. Endosperm *ruminate
   - smooth
6. Male flowers in dry state
   - large, 3 - 4.5 mm diam. •
   - small, 1 - 2.9 mm diam. o
7. (not incorporated in the ideograms)
   - Midrib depressed on upper leaf surface
   - Midrib prominent on upper leaf surface

The number 1.86 of character 4 was obtained by plotting length against width of the largest well-formed leaves of a

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*Recorded only for fruiting specimens. The endosperm is considered ruminate if ingrowths from testa exceed 2x thinnest part of testa.

large sample of specimens (fig. 4.1). A line passing through the origin and having a slope of 1.86 was found to separate D. ebreticoides from the rest, with few exceptions. The others could not be separated from each other by their length/width ratios.

Fig. 4.2 shows the geographical distribution of 104 specimens. The complex occupies a large area from the Deccan to Fiji but is curiously absent from the Philippines and Eastern Malesia (Celebes to New Guinea). Another curious gap is from E. Bengal to W. Burma. Oceanic barriers cannot be invoked to explain the gaps because representatives are found in N.E. Australia, New Caledonia and Fiji despite the vast mileage of salt water between.

There appear to be four allopatric taxa occupying the regions marked S, E, H, F on the map, corresponding to the epithets sylvatica, ebreticoides, hermaphroditica and fasciculosa.

In region F, comprising N.E. Australia, New Caledonia and Fiji, the specimens are uniform with respect to the six characters analysed although as earlier stated, the three loci are widely separated by ocean. Two names are current, D. fasciculosa and D. ruminata. D. ruminata (actually Maba ruminata at the time) was created by Hiern on a New Caledonian specimen because of its alleged ruminate endosperm as opposed to D. fasciculosa (Maba fasciculosa) with smooth endosperm. I have examined the type of D. ruminata (Deplanche 311) and find that Hiern was badly mistaken. The endosperm is smooth, hence D. ruminata is indistinguishable from D. fasciculosa to which it must be united.

D. fasciculosa differs from D. hermaphroditica in only two characters. The ovary is totally glabrous instead of having a basal ring of hairs and the midrib is prominent on the upper

surface of the leaf instead of sunken. The latter character was not brought into the overall analysis because although it sharply differentiates between D. fasciculosa and D. hermaphroditica, the distinction is completely obscured if D. sylvatica and D. ehretioides are also considered. In these last two species, midrib appearance is neither distinctly nor constantly one state or the other.

D. hermaphroditica occurs on the lands of the Sunda Shelf (region H), comprising Malaya, Borneo, Sumatra, Java and the southern coastline of Thailand, Cambodia and Vietnam. The region is one of tropical ever-wet rain forest. Characteristically, the ovary bears a basal ring of hairs, the leaves are narrow (length/breadth ratio greater than 1.86), and the petiole bases small. Yet exceptions are known to each of these three states. The variant specimens are marked "h" on the map. Each of these shows a departure from the "typical" specimens in only one character. Such variants are rare. There is no evidence that they form self-perpetuating populations, hence the best hypothesis is that they are members of the same D. hermaphroditica population.

D. hermaphroditica is rather abruptly replaced by D. ehretioides (region K), along a line running roughly between Tavoy and the Mekong Delta. In the Mekong Delta, the region of change is very indistinct and a field investigation is desirable to determine the precise zone in which replacement occurs, and the ecological factors associated with it. It is significant that there appears to be no hybridisation along the zone of replacement. I have not seen any specimen that might be intermediate between the two taxa. D. ehretioides is adapted to severe monsoonal conditions. The leaves are shed once a year. New growth takes place in the form of flushes

from axillary buds of the previous season. The earliest leaves of a flush are small, and bear inflorescences in their axils. The later leaves are progressively larger, with thicker petioles and consequently, they leave larger scars on the twigs. In the axils of these large leaves are formed the resting buds for next season's growth. D. putii, based on a Thai specimen (Put 2834) is absolutely indistinguishable from D. ehretioides to which it must be united.

A gap of about 500 miles separates region E from S. The latter is occupied by D. sylvatica, with about as much internal variation as D. hermaphreditica, but for the same reasons, D. sylvatica must be considered as a single taxon which would be meaningless to subdivide. D. sylvatica resembles D. hermaphroditica in having narrow leaves and narrow petiole bases, but it resembles D. ehretioides in the ruminate endosperm and solitary female flowers.

The ideal pattern of four geographically replacing taxa as so far described, is however, complicated by the specimens marked "s" and "f" in region E.

Specimen "s" occurs in Langkawi Island, off the N.W. coast of the Malay Peninsula, and is the type of D. holttumii. No other specimen has ever been collected in Langkawi that matches this although many have been collected which belong to D. hermaphroditica. On the morphological evidence available, this one and only specimen of D. holttumii is indistinguishable from D. sylvatica of India. It has solitary female flowers (actually young fruits) and ruminate endosperm. Bakhuizen records the endosperm as being smooth. This is a somewhat difficult point because the seeds are immature and hence very shrunken on the specimen. However, the young testa already has

ingrowths into the endosperm, and in my experience, a seed that is ruminate at this stage, will remain ruminate when ripe. Hence I disagree with Bakhuizen's interpretation.

Specimen "f" occurs in monsoon forest of S.W. Java and is one of a colony of such plants. Morphologically, it is, by the glabrous ovaries and prominent midrib, indistinguishable from D. fasciculosa although separated from N.E. Australia by some 2,000 miles. It is a significant fact that D. hermaphroditica also occurs in Java but the two taxa are ecologically mutually replacing (Backer 1965), with D. fasciculosa in monsoon forest, and D. hermaphroditica elsewhere.

The question arises as to what the origin of these "anomalous" specimens might be. Several hypothesis may be advanced. One is that they are intruders introduced by some unknown means from their "home" regions S and F. A second hypothesis is that they have evolved independently from the parent D. hermaphroditica population. The evidence available does not enable me to resolve the problem.

One ecological factor does, however, emerge. Region H is a region of evervet tropical rain forest but within it are pockets of monsoon forest with annual periods of severe drought. Langkawi is one such pocket and S.W. Java is another. To the north, region H gives way to region M, the monsoon interior of Burma, Thailand and Indo-China, with a very hot and dry season every year. The replacement of D. hermaphroditica by D. ebracteoides in the north, by D. fasciculosa in S.E. Java, and the occurrence of one specimen of D. sylvatica in Langkawi is strong evidence that typical D. hermaphroditica is non-resistant to drought and that under conditions of drought, it must either evolve a drought-resistant form or give way to

better-adapted species.

A review of taxonomic status can now be made. D. ehretioides has strong claims to being a good species because it shows the greatest number of morphological differences between itself and all the others. It is in geographical contact with D. hermaphroditica only but there is no evidence of hybridisation between them along the narrow zone of replacement.

D. hermaphroditica and D. fasciculosa differ from each other only by the midrib sunken or prominent, and the ovary hairy or glabrous. They both differ from D. sylvatica in having multi-flowered female cymes and smooth endosperm. On the evidence, they could be either three sub-species or three very closely related allopatric species. The differences between them appear to be less than the differences between the whole complex and other species outside the complex, hence I favour reducing them to sub-specific status. One further fact supporting the reduction is that if the status quo i.e. three separate species, is maintained, the well-known and common D. hermaphroditica will have to suffer a name change to the obscure D. venosa Wallich ex G. Don. Bakhuizen was well aware of this possibility (Bakhuizen 1937 p 89) and argues that venosa should be rejected as a nomen nudum on the grounds that de Candolle, Hiern, Clarke and King & Gamble had disagreed over the generic and even family identity of the specimen. Bakhuizen did not see the specimen himself. I have done so and have no doubt whatever that it is the same as D. hermaphroditica. Unfortunately it bears the older epithet and the International Rules do not support Bakhuizen's attempt to reject it. However, the epithet hermaphroditica can be maintained at sub-specific level.

Key

1. Largest petiole bases 4 - 7 mm wide, female cymes 1 - 3 florous, ovary hairy all over, leaf length/breadth ratio smaller than 1.86, endosperm ruminate, male flowers 3 - 4.5 mm diam. in the dry state.....*D. ehretioides*

1. Largest petiole bases 1 - 3 mm wide, female cymes 1 - ∞ florous, ovary glabrous to hairy, leaf length/breadth ratio greater than 1.86, endosperm smooth or ruminate, male flowers 1 - 2.9 mm diam. in the dry state.....2

2. Female cymes uniflorous, ovary glabrous to hairy, endosperm ruminate.....*D. sylvatica* subsp. *sylvatica*.

2. Female cymes multiflorous, ovary glabrous to hairy, endosperm smooth.....3.

3. Ovary with basal ring of hairs or rarely hairy all over. Midrib depressed above.....*D. sylvatica* subsp. *hermaphroditica*.

3. Ovary glabrous. Midrib prominent above.....*D. sylvatica* subsp. *fasciculosa*.

Fig.4.1. Length / breadth of largest well-formed leaf on specimen.

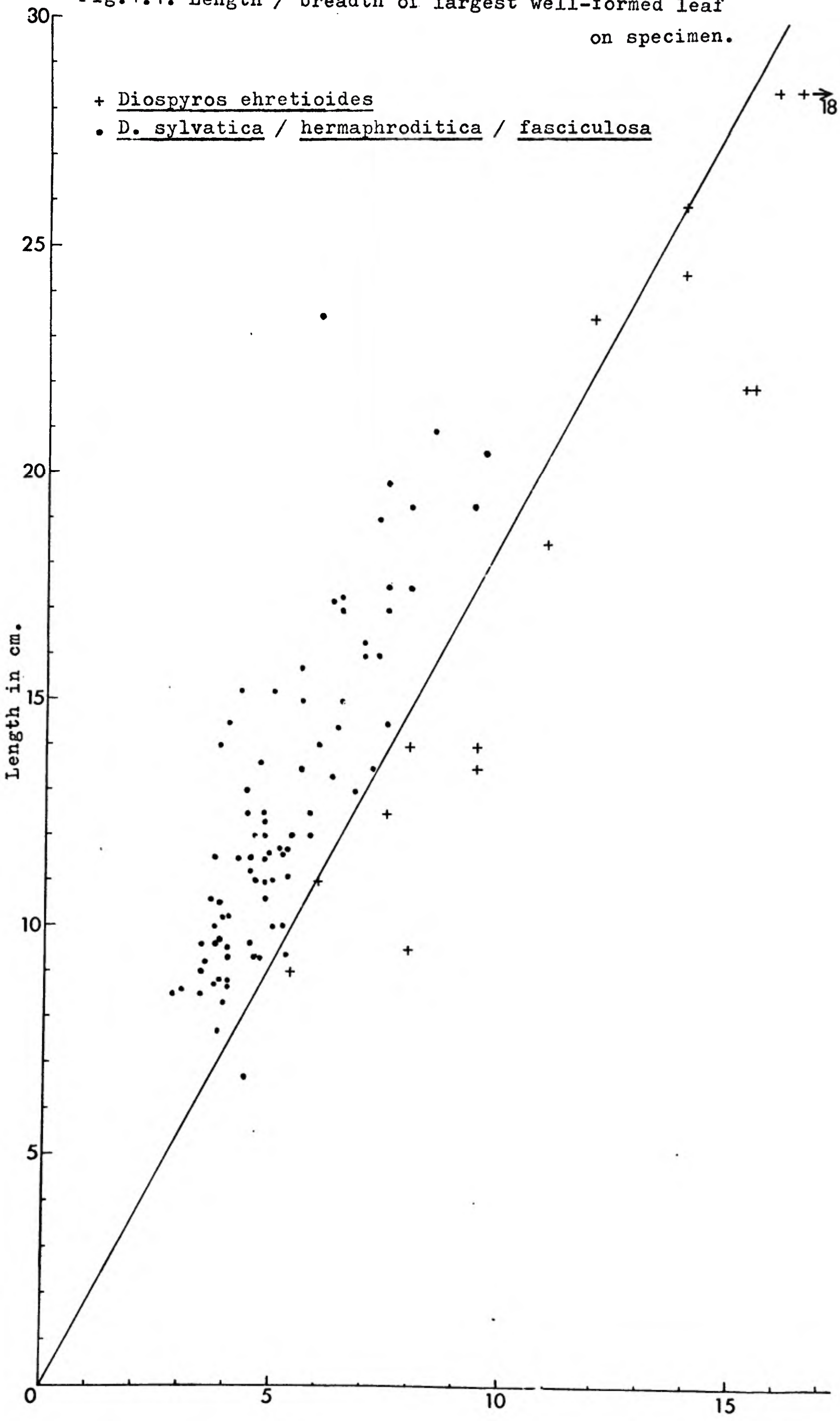

Fig.4.2. Geographical variation in six characters of Diospyros ehretioides, D. sylvatica, etc.

For explanation, see text.

Diospyros kaki, D. roxburghii, D. glandulosa, D. kika and D. oldhamii.

Diospyros kaki, the oriental persimmon, is economically probably the most important species in the Ebenaceae. It is one of the major fruit trees of Japan, China and Korea, although it seems to have first become known to Europeans only after the arrival of Jesuit missionaries in China in the mid-sixteenth century (Bretschneider 1898). The Jesuits found it commonly grown throughout the country. The Portuguese called it the Chinese Fig, because the fruits are often steamed, flattened, and dried for off-season consumption, when it resembles the fig in appearance and taste.

Not surprisingly for an intensively and widely cultivated species, a very large number of cultivars have been developed, of which many have been raised to the rank of species by uncritical workers, only to be reduced again (see Bakhuizen 1938 for synonymy). All these synonyms are best forgotten, but one of them turns out to be surprisingly durable - D. roxburghii, described by Carriere (1872), reduced by Hiern (1873), restored by Hemsley (1911), reduced by Bakhuizen (1938), and which I propose to restore again.

I have come to the conclusion that the relationship between D. kaki and D. roxburghii is of great biological interest and deserving of more attention than the monographers Hiern and Bakhuizen have given it. Rather than being a cultivar of D. kaki, there is abundant evidence that D. roxburghii is a naturally wild species which might well be ancestral to the cultivated plant. The historical background to the problem is briefly as follows.

In 1832 Roxburgh, in his Flora Indica, wrote of D. kaki "I find it not only a native of Japan but also of China, and the

mountains of Nepal, to the northward of Bengal". He also added that trees introduced and grown in Calcutta gave poor yields of fruit. Roxburgh's view of the distribution of D. kaki, from eastern India to Japan was adopted by workers in the field e.g. Clarke (1882) who actually collected wild specimens in the Naga Hills and noted "Nagas can eat the fruit", and Ferrars (1875) who noted in the forested Karenee country of Burma that "large areas are covered almost exclusively with Teh (Diospyros kaki) and an undergrowth of some cyperaceae". In 1921, Troup wrote "D. kaki.....is much cultivated in China and Japan and occurs wild in the Khasi Hills and Upper Burma".

D. roxburghii was described by Carriere based on specimens of unknown origin, cultivated in France and Algeria. Carriere, a horticulturist rather than a taxonomist, described the fruit as being tomentose, with soft sweet pulp. He observed that the species, as grown in France, was non-resistant to frost and seldom bore fruit. Hence, he argued, it could not possibly be the true D. kaki, which survives the cold Japanese winter and bears abundant fruit. Seizing on Roxburgh's remarks about the trees in Calcutta being unfruitful, Carriere argued further that his plant must be the same species as Roxburgh's and probably came from Nepal or Bengal. The implication here is, of course, that Roxburgh had mistakenly combined two species in his description.

Notwithstanding Hiern's rejection of Carriere's case, this heresy was taken up by Hemsley, who made a comparison of a set of French specimens, with specimens from India, China and Japan. He came to the conclusion that there were morphological and geographical grounds for recognising two species, "D. kaki is apparently confined to Central and Eastern China and Japan whereas D. roxburghii is a native of Eastern India and Western China".

Bakhuizen rejected Hemsley's conclusion without comment. Retracing Hemsley's footsteps, I find that he had no clear idea what the differences are between D. kaki, D. roxburghii and D. lotus. His set of French material of D. roxburghii includes three specimens from Thuret's collection of plants cultivated at Antibes, which Carriere had cited and which may therefore be taken as types of D. roxburghii. Two of these specimens have male flowers in separate envelopes and the third is in fruit. The fruit is tomentose, as described by Carriere, and may be taken to be the lectotype in the absence of a designated holotype. Hemsley rejected the flowers, which he thought to be male and female, and wrote that they might possibly belong to D. lotus. In fact they are all male and they definitely do not belong to D. lotus. I see no reason to doubt that they belong to Thuret's plant (see fig. 4.4 and the keys on p 181 and 190). Hemsley's diagnostic descriptions were also poor. Of D. roxburghii he wrote: "species ex affinite D. kaki, a qua differt imprimis folia crassiora fere coriacea lanceolata vel lanceolato-oblonga utrinque attenuata venis primariis prominentibus et corollae lobi latiores quam longi." These 'differences' are in my opinion non-existent. On paper, Hemsley's case is extremely weak as also was Carriere's. But Bakhuizen had not taken notice of two further developments, which might have caused him to pause and reconsider.

In 1915, Lace published the new species D. glandulosa based on six Burmese specimens. In 1937 Debbarman & Biswas published another new species, D. kika, based on four specimens, from Assam, Manipur and Burma. The name "kika" was coined "to indicate its affinity with D. kaki."

Putting together specimens of D. glandulosa, D. kika and D. roxburghii, I can find no differences between them. In fact

one specimen, Kurz 1008, is cited as a type of both D. glandulosa and D. kika. The authors of these last two names had quite inadvertently stepped into the muddle. It is apparent that to Debbarman & Biswas, it was inconceivable that a plant wild in Burma and E. India could be conspecific with the cultivated D. kaki of China and Japan.

To resolve this problem, I made a study of 118 specimens that belonged to either D. kaki or D. roxburghii after first satisfying myself that D. lotus is an absolutedly distinct species in its own right (see next section).

I sorted out two sets of specimens from the total: (a) specimens from E. India, Burma and Thailand and (b) cultivated specimens from China and Japan. For class (b), only specimens which had been explicitly described as cultivated, on the collectors labels, were included. This is necessary because D. kaki is said to occur in China and Japan, both under domestication and in the wild (Thunberg 1784, Makino 1908, Rehder & Wilson 1916, Lee 1935, Ohwi 1965). Makino had formalised the situation in Japan by naming the wild plant D. kaki var sylvestris and the cultivated one D. kaki var domestica. Var sylvestris he distinguished as having smaller, strongly astringent fruits. Such differences cannot be detected on herbarium specimens. Furthermore all authors since and including Makino consider D. kaki to have been introduced into Japan from China and hence the wild form as known to Makino must have been an escape from domestication, and not primitively wild. In China itself, we are in no position to judge whether wild plants are primitively or secondarily wild. Rehder & Wilson have followed Makino in making a taxonomic distinction between wild and domesticated plants, but gone one step further to equate D. roxburghii with D. kaki var sylvestris. No evidence was presented for this merger.

My approach is that a priori the only plants that can be considered cultivated are those collected from orchards and villages and specifically noted as being cultivated, by the collector. The only plants that can be considered primitively wild are those growing in countries where D. kaki is completely unknown in cultivation. From the collecting labels, and from correspondence with Forest Botanists in Burma and Thailand, I gather that D. kaki is not cultivated in E. India, Burma and Thailand.

Comparing the two classes (a) and (b) the only differences I could find were in degree of hairiness in flowers and fruits. The plants of India, Burma and Thailand (and also the types of D. roxburghii) have calyx lobes, ovaries and *fruits completely covered with dense hair (fig. 4.4). The cultivated plants of China and Japan (and also cultivated specimens introduced into Malaya and Java) have calyx lobes sparsely hairy, ovaries glabrous or with hairs restricted to base or apex, and fruits similarly glabrous or with hairs restricted to base or apex.

Having detected the differences between primitively wild, and domesticated plants, all the 118 specimens were scored for these characters and displayed on a map (fig. 4.5). What emerges is that hairy plants corresponding to D. roxburghii occur not only in E. India, Burma and Thailand but also in Laos, N. Vietnam and S. & W. Yunnan. A few specimens occur in W. Hupeh, Kwangtung and Chekiang. Specimens corresponding to the cultivated D. kaki occur in China, N. Vietnam, Korea and Japan. Some of the latter were recorded as being cultivated, others as apparently wild but

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*In deciding the distribution of hair, the herbarium specimens are examined carefully paying particular attention to the edges of the pressed fruits and the protected parts of puckered areas. Hairs on flat upper or lower surfaces tend to be rubbed off on herbarium sheets, and give misleading information.

morphologically they are indistingushable. I think therefore that although a distinction can be made between D. roxburghii and D. kaki on consistent differences in hairiness and in geographical distribution, no clear distinction can be made between D. kaki var domestica and D. kaki var sylvestris.

As for the relationship between D. roxburghii and D. kaki, the hypothesis advanced here is that the former is the ancestral species out of which D. kaki has arisen through centuries of cultivation and selection. There are several independent observations that the fruit of D. roxburghii is sweet and edible, e.g. Carriere's original description, Clarke's observation that Nagas eat the fruit, a Burmese forester's collecting label (U Tha Hla 1999) describing the plant as a wild fig tree with sweet edible fruits, a Thai collection (Somkhit 255) noting that the tree is medium to large, in evergreen forest, with sweet edible fruits. Hence D. roxburghii provides an incentive for cultivation. From North Vietnam comes evidence that the Muong tribes in the foothills of the interior (Poilane 1627, and Bon 353) do plant the species or at least have them growing in their villages. I had also five specimens of D. kaki from N. Vietnam which were definitely cultivated, according to their labels. North Vietnam is therefore an area of interest, where D. roxburghii is still being taken into cultivation while D. kaki has perhaps been introduced from China. Or could the latter have arisen from the former within N. Vietnam itself and then taken into China? This seems unlikely because the presence of D. roxburghii as rare individuals in Kwangtung, N. Hupeh and Chekiang suggests a former very extensive range for the species within China which may have broken up into pockets and become extinct in vast areas even as individuals were being taken into cultivation and evolving into D. kaki. I suggest that the main selection pressure was towards the production of smooth-skinned fruits from the original

bristly hairy condition. This might have affected not only the ovaries but also the general hairiness of the flowers and the whole plant.

Diospyros oldhamii

This is a poorly known species endemic to Formosa which differs from the preceeding two in having glabrous instead of hairy male pedunoles. The fruits are said to be glabrous (Li 1963). I have not seen the female flowers or fruits. That this species could have contributed to the origin of D. kaki is unlikely as Formosa had very little contact with the mainland, from which it is separated by 100 miles of sea, until after the arrival of the Europeans (Stamp 1967), by which time D. kaki was already in cultivation throughout China.

Cytological and histological considerations.

The discovery by Nemikawa & Higaski (1928) that D. kaki has a chromosome complement of 2n = 90 suggests that the problem of the origin of the species may be soluble by cytotaxonomic means. Nemikawa & Higashi examined 9 cultivars of D. kaki in Japan and all had the same number. We know now that the normal diploid number for Ebenaceae is a remarkably constant 2n = 30, hence D. kaki is a hexaploid. If the increase in ploidy has occurred in cultivation, then D. roxburghii as the putative parent species should have 2n = 30 while wild specimens of D. kaki (i.e. var sylvestris), as escapes according to this hypothesis should have 2n = 90. If it were possible to produce a chromosome map for the whole range of D. kaki - D. roxburghii, some very illuminating deductions could be made, and the hypothesis presented here, put to the most rigorous test. Such a project would need far more organisation than can be contemplated at present.

But if the size of cells is proportional to the chromosome complement, then it may be possible to infer the level of ploidy by direct measurements of the size of cells such as mature pollen grains or stomatal guard cells (Stebbins 1950 p 302 - 303). A pilot survey was conducted to test the feasibility of this scheme using three specimens of D. kaki, two of D. roxburghii, one of D. oldhamii and a number of specimens of other species of known ploidy, three of them being the actual voucher specimens on which counts had been made viz. D. confertiflora, D. wallichii and D. mairgayi (Appendix 4).

The results were disappointing (fig. 4.6). Although one might expect a large size difference between hexaploid and diploid cells, this in fact was not found to be so. In the nine species examined, cell size is not proportional to level of ploidy. Also, D. roxburghii is not distinguishable from D. kaki in pollen size nor stoma size. The volume of chromosomes varies not only by total number of chromosomes, but also by thickness of individual chromosomes, of which there is considerable variation between species (fig. 1.21), probably sufficient to obscure any simple relationship between ploidy and cell size. Hence there is really no alternative to mapping actual chromosome numbers.

Another consideration is whether a successful hexaploid could have arisen from a single diploid ancestor. In the paper by Namikawa & Higashi, six of the nine cultivars were studied in meiosis. In all cases 45 bi-valents were formed. Some cytologists would expect that three diploid species have contributed to D. kaki. Against this is the fact that D. kaki closely resembles D. roxburghii but no other species except possibly D. oldhamii. The last is unlikely to have played a part, as earlier explained, in the origin of D. kaki. It would be necessary to postulate two extinct ancestral species which,

hybridised with D. roxburghii, produced a plant indistinguishable from it except by being less hairy. This seems to be rather far-fetched. Lewis (1967) has shown that many species in nature consist of two or more chromosome races in which the polyploids must be autoploids, and which are quite able to hold their own, being, contrary to expectation, of good fertility and vigour. An example within Diospyros itself is D. virginiana with two chromosome races 2n = 60 and 2n = 90 (Baldwin & Culp 1941). In any case, D. kaki in cultivation is often propagated by bud-grafting so that any reduction in fertility would be of no great consequence.

Taxonomic consequences

The morphological differences between D. kaki and D. roxburghii are so slight, though constant, that if morphology and geographical distribution were the only criteria, it would be logical to consider them as being of sub-specific status. Against this is the fact that D. kaki, so far as is known, is a hexaploid and since D. roxburghii may be a diploid, there may be a reproductive barrier between them. It would be better to be cautious at this stage and keep up the two at species rank until a thorough cytotaxonomic study has been made.

As for D. oldhamii, it must be left as a full species simply because we know too little about it at present.

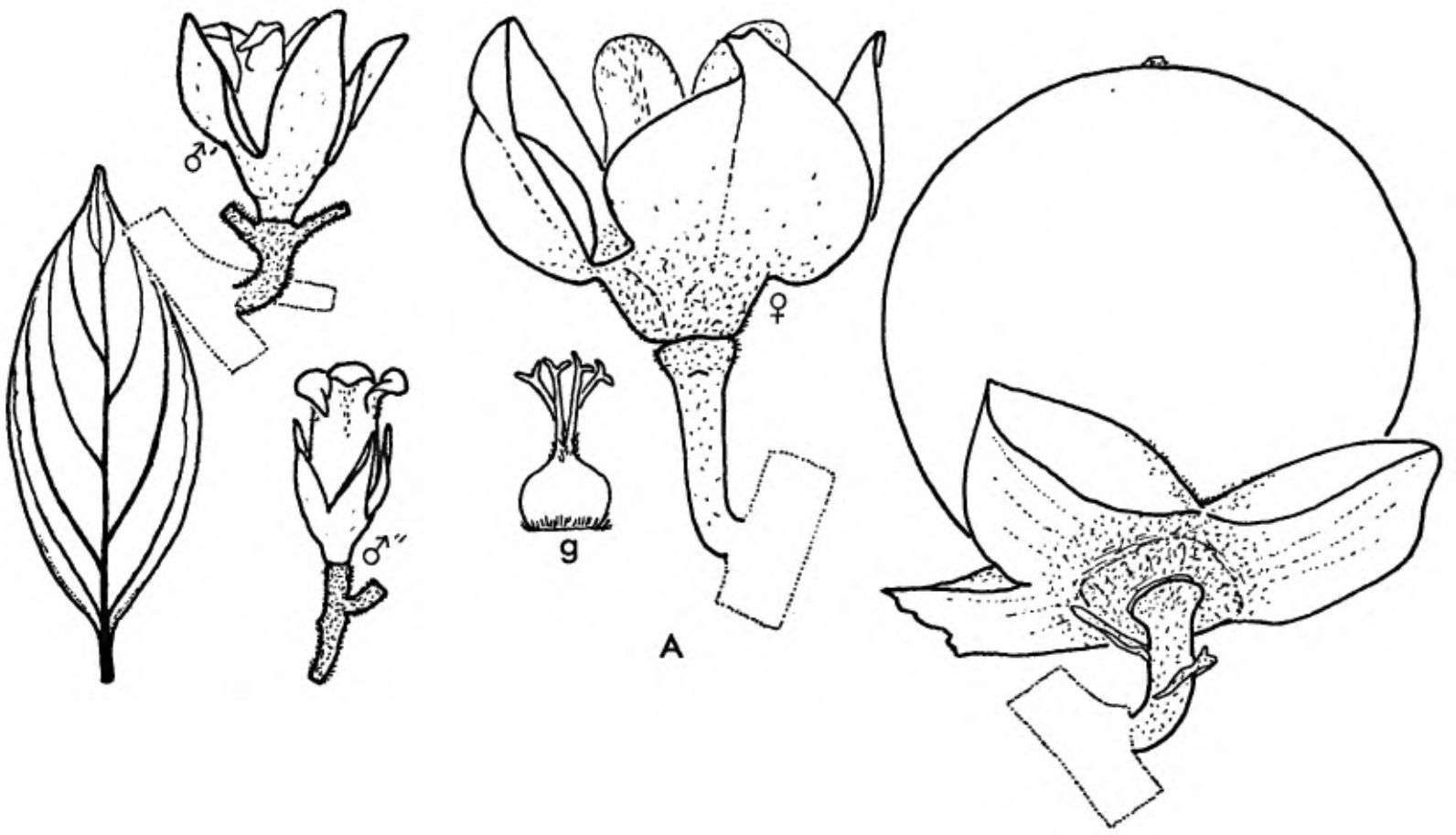
Key

1. Male peduncles and pedicels wholly or partly hairy 2

1. Male peduncles and pedicels glabrous..... D. oldhamii

2. Ovary completely densely hairy. Fruit hairy. Calyx lobes of both male and female flowers densely hairy outside.....D. roxburghii.

2. Ovary totally or partially glabrous, in the latter case with hairs restricted to apex or base. Fruits likewise totally or partially glabrous. Calyx lobes of both male and female flowers glabrous to scantily-hairy....D. kaki.



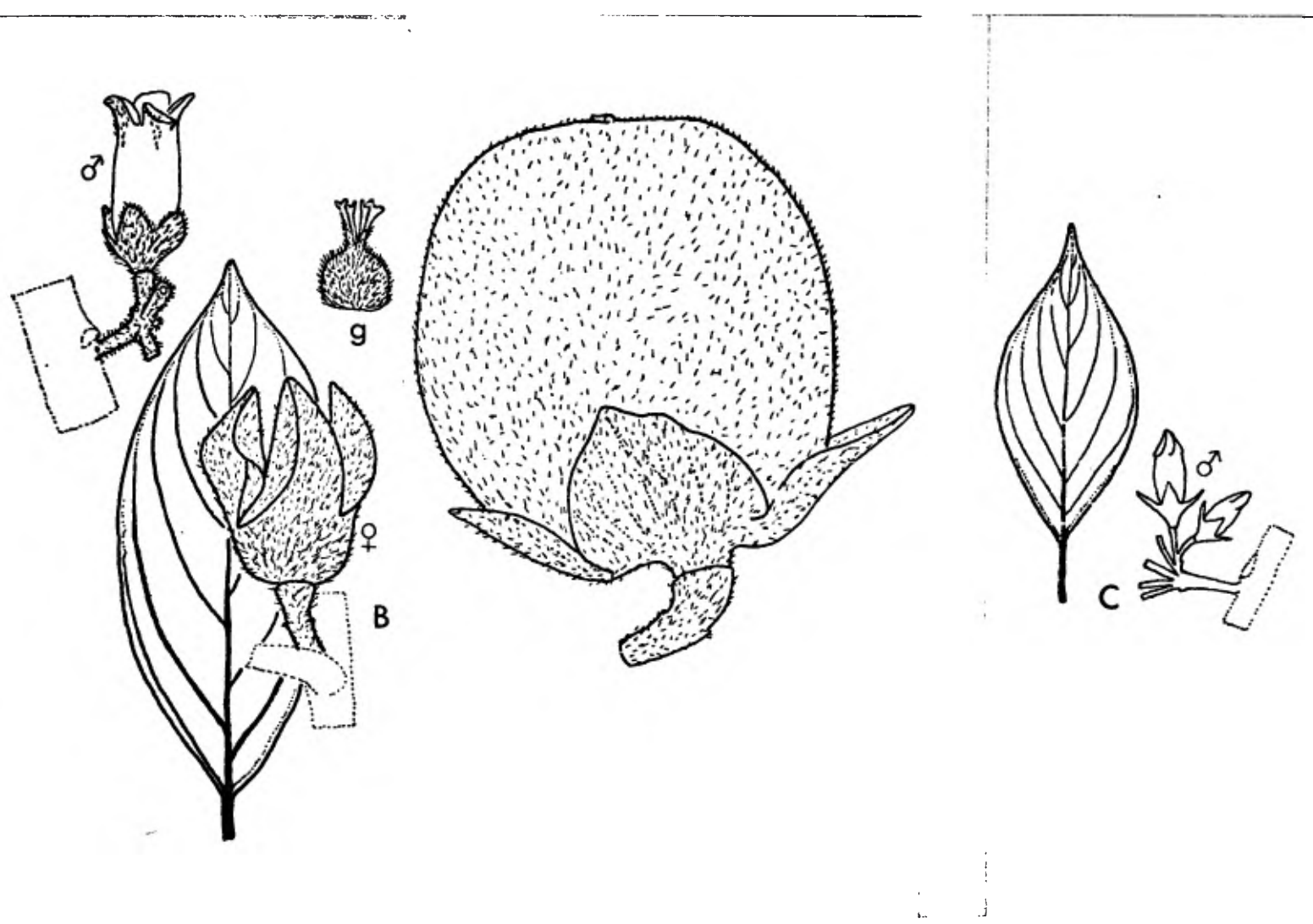


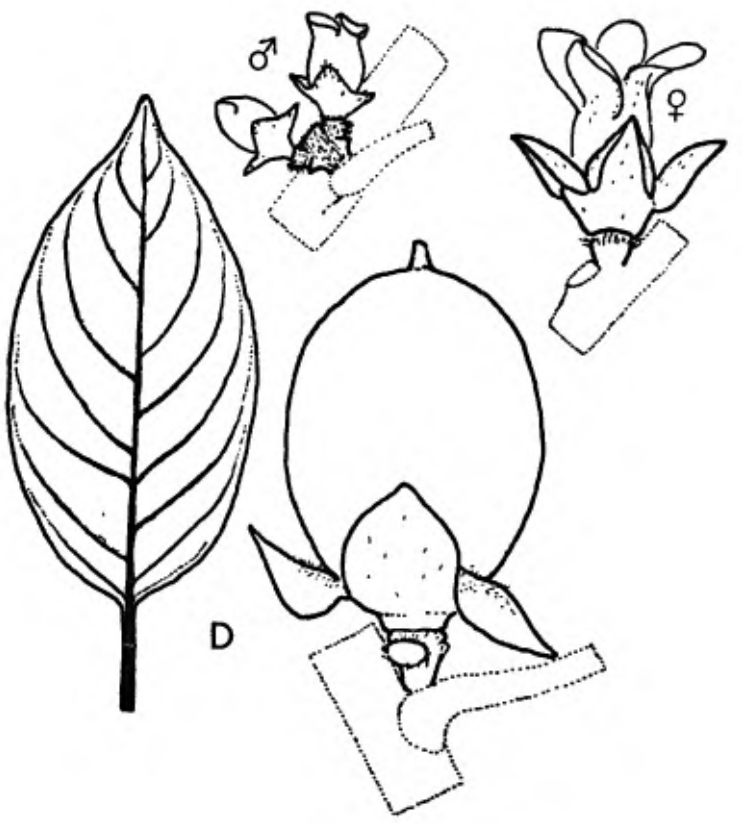
Fig. 4.4. Flowers and fruits at 2x; leaves at 0.5x.
(A) D. kaki (B) D. roxburghii (C) D. oldhamii.

♂: male flowers; ♀: female flowers; g: gynoecium.

A: ♂′ and leaf, Wilson 2914; ♂″ Savatier 809; ♀ Forrest 13815; fruit Fan & Li 156.

B: ♂ Saw Maung Mya 5400; ♀ Forrest 5537; fruit Kerr 6265; leaf Kerr 8851.

C: ♂ and leaf, Wilson 10262.



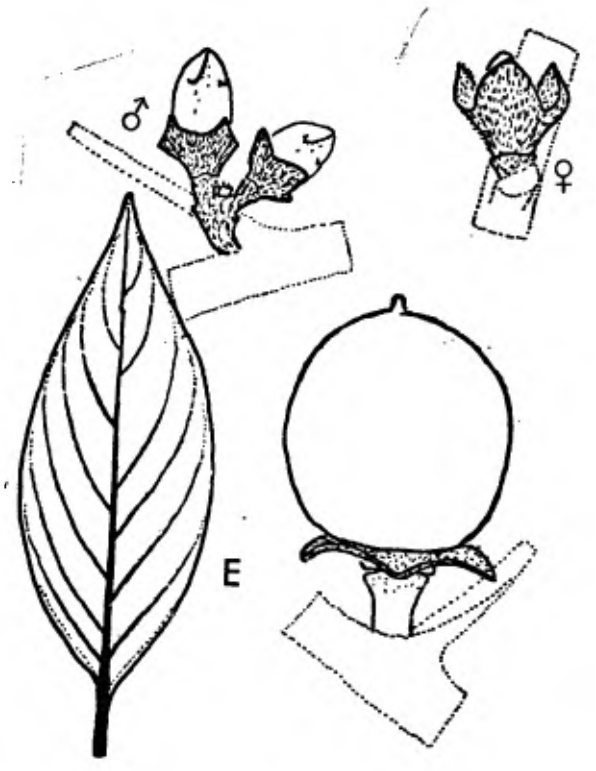
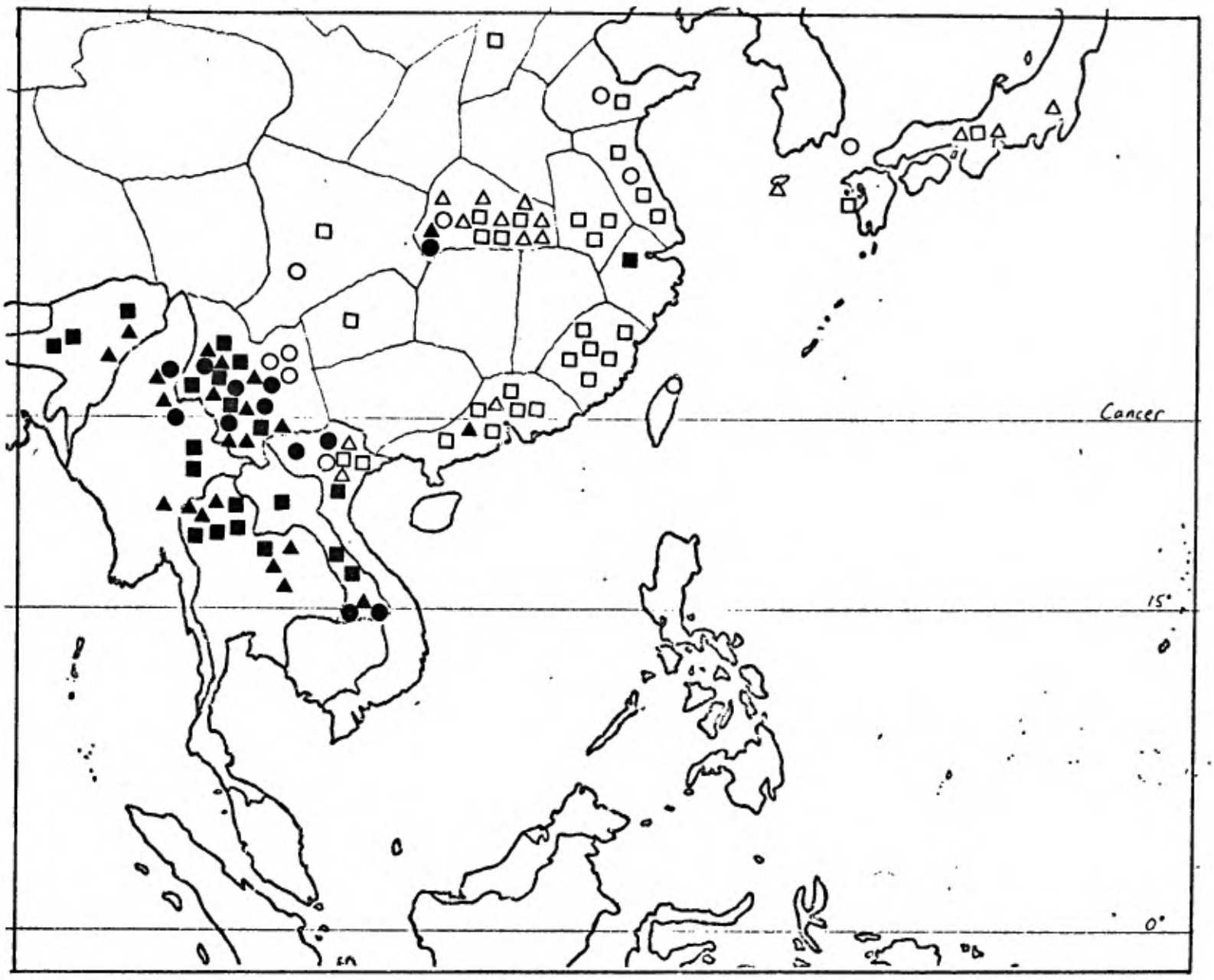


Fig. 4.4 cont'd. (D) D. lotus subsp. lotus (E) D. lotus subsp. brideliifolia.

♂: male flowers; ♀: female flowers.

D: ♂ Schneider 1650; ♀ Forrest 7599; fruit Oldham 529; leaf Wilson 429.

E: ♂ Santos (Bur. Sci.) 31801; ♀ Conklin & Buwaya (PNH) 80459; Fr. Elmer 14203; leaf Ocampo (BS.) 27969.



▲ ♂ calyx lobes densely hairy on outside.

△ ♂ calyx lobes sparsely hairy to glabrous on outside.

◓ ♀ calyx lobes densely hairy on outside.

◒ ♀ calyx lobes sparsely hairy to glabrous on outside.

◓ Ovary hairy all over.

◒ Ovary glabrous, or hairy at base or apex only but glabrous in middle.

■ Fruit hairy.

□ Fruit glabrous or with hairs restricted to apex or base.

Fig. 4.5. Distribution of characters in D. kaki and D. roxburghii. For details see key above, and text.

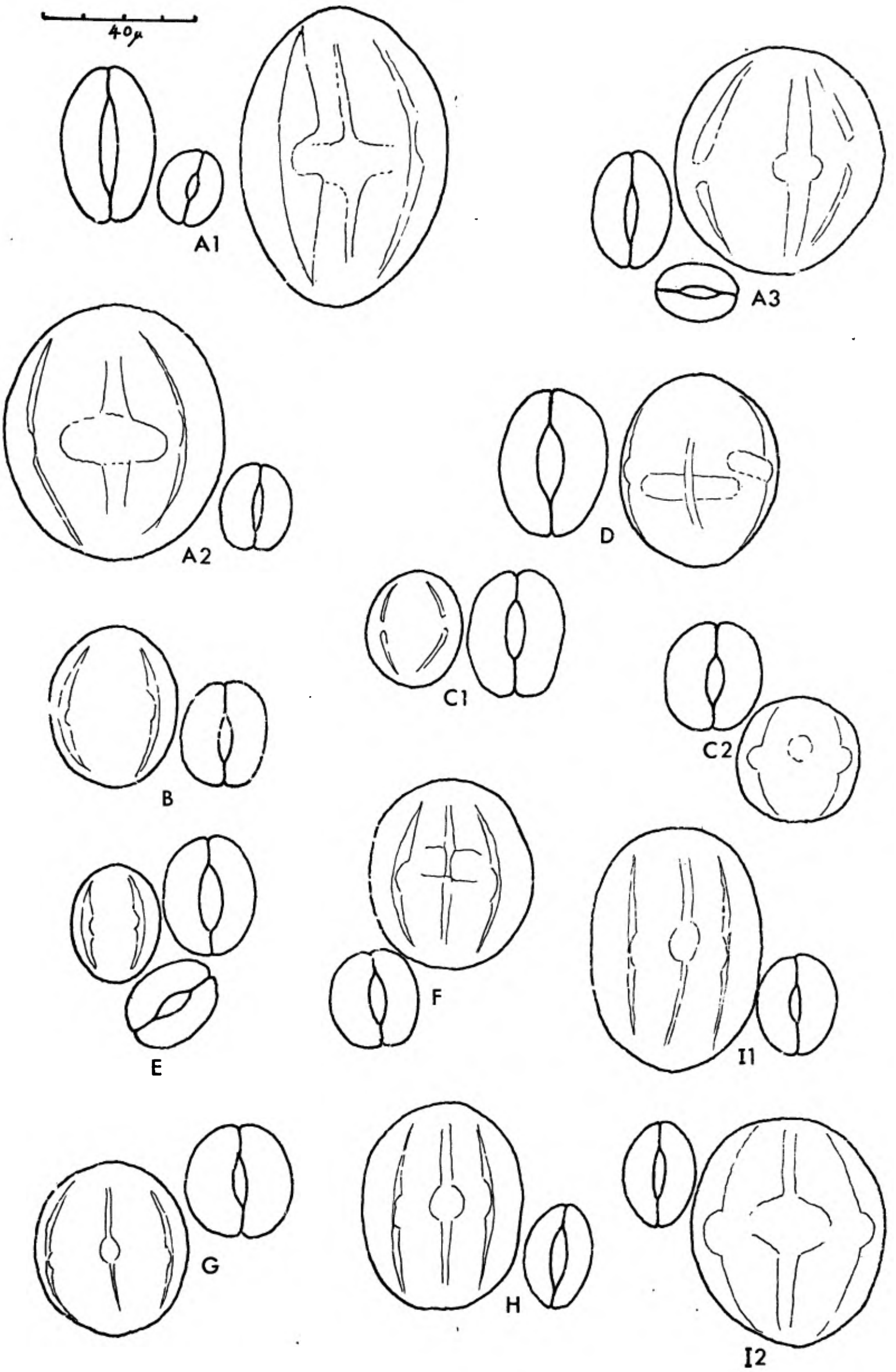


Fig. 4.6. Pollen and stomata sizes: (A) Diospyros kaki 2n = 90 (1: Parker s.n; 2: Savatier 809; 3: Henry 3485). (B) D. ebenum 2n = 90 (CF 105). (C) D. ferrea 2n = c. 48 (1: FRI 5153; 2: Hoogland 6198). (D) D. maingayi 2n = 30 (Pollen: FRI 2724, stomata: FRI 2807). (E) D. confertiflora 2n = 30 (pollen: Mat s.n; stomata: FRI 2809). (F) D. lotus 2n = 30 (Faurie 13303). (G) D. wallichii 2n = 30 (pollen: KEP 98787; stomata: FRI 13049). (H) D. oldhamii 2n = ? (Wilson 10262). (I) D. roxburghii 2n = ? (1: Henry 11618; 2: Kerr 8851).

Diospyros lotus and D. bridelliifolia.

Diospyros lotus, described by Linnaeus in 1753 is the type species of its genus. To Linnaeus, it was a plant of the Mediterranean. But by 1873, specimens had been collected from Turkey to N. Iran, Afganistan and N.W. India, China to Japan. Hiern and subsequent authors considered the species to be naturalised in the Mediterranean region rather than indigenous.

The fruits of D. lotus are sweet and edible, according to Brandis (1874), "much prized by the Afgan tribes, who eat it fresh or dried, plain or with rice, and use it in sherbets." D. lotus fruits are however much smaller than those of D. kaki and therefore less valued for eating where the two species occur together as in China and Japan. In these two countries, D. lotus is often used as a stock on which to graft D. kaki (Rehder & Wilson 1916).

D. bridelliifolia occurs wild on the mountains of the Philippines at about 1400 m., and was considered by Bakhuizen (1941) to be very closely related to D. lotus.

If these two species are plotted on a map (fig. 4.6), it will be seen that the range of D. lotus, though very extensive, is broken up into three parts: China - Japan, Central Asia (comprising Soviet Central Asia, Afganistan, N. Pakistan and N.W. India) and Western Asia between the Black Sea and the S. Caspian. D. bridelliifolia occurs on several islands of the Philippines.

Taxonomically, the situation appears to be quite simple. Although the range of D. lotus is broken up into three widely separated parts, I can find no differences between the three

populations. It is well known however, that although separated by vast distances, the three areas lie on the old silk routes between China and Europe along which men have travelled since prehistoric times, as nomads, traders, plundering warriors and pilgrims. The question arises as to whether human activity is the link between the three populations. We shall examine this in some detail below.

As for D. bridelliifolia, there is no record of its being used by the native population. It appears to be wild and indigenous. It differs from D. lotus only in having the calyx lobes densely hairy instead of glabrous or scantily hairy. I have no hesitation reducing it to the status of a sub-species viz. D. lotus subsp. bridelliifolia.

The origin of D. lotus.

On this subject, a large number of authors have contributed their opinions. Only one point emerges which is beyond dispute, i.e. the species is indigenous and wild in China. Many specimens have been collected by Forrest in the mountains of Yunnan, by Wilson (Rehder & Wilson 1916) in the valleys of W. Szechuan and margins of woods in W. Hupeh where they may grow to 26m. tall, 4m. girth. Lee (1935) records its as being wild and cultivated from Manchuria to Yunnan. Also, wild specimens have been collected in North Vietnam at about 1500m.

From China, D. lotus is believed to have been introduced to Japan (Matsumura 1912, Rehder & Wilson 1916). Wilson did not see any wild trees in his travels in Japan. Ohwi (1965) records it as being "frequently cultivated" only.

The situation in Central Asia is highly controversial. Some authors think that the species was introduced, e.g. Parker

(1924) referring to what was then N.W. India, wrote "Quite wild in Hazara and in parts of the Rawalpindi District, but has the appearance of being naturalised rather than indigenous.... Coppices well and reproduces rather freely from seed in moist places. Often cultivated for its fruits which are eaten fresh or dried." Grubov (1952) in the Flora S.S.S.R. expressed the opinion that D. lotus originated in China, from where it had spread to other parts of its range by cultivation followed by escape and naturalisation. Kitamura in the Flora of Afganistan (1960) thought that the species might have been brought from China as dried fruit along the silk road. He had not come across the plant in the wild, during his travels in Afganistan.

Among those who consider D. lotus to be native in Central Asia are a number of Soviet authors, Korovin, Popov, Zaretskii and others mentioned by Bondarenko (1957) who himself defends this view. Bondarenko's case is based on three claims (i) fossil remains of the species have been found in "ancient deposits" (no further details given) in Central Asia, (ii) the species is today undoubtedly wild and found even in remote mountainous areas and (iii) it is associated with relicts of the tertiary flora such as the walnut, fox-grape and fig.

For Western Asia, Zhukovskii (1950) holds the opinion that D. lotus is indigenous in Talysh in the Caucasus, where it grows in pure stands or in admixture with oak and hornbeam. It is also found wild in W. Georgia but Zhukovskii is uncertain whether it is naturalised or indigenous there.

The facts of present-day distribution allow two contrasting theories to be formulated: (A) An ancestral natural range in E. Asia, extending from China to Vietnam and the Philippines, with man as the agent subsequently responsible for introducing

it to Central Asia and Western Asia. (B) An ancestral trans-eurasian range subsequently broken up by orogenic and climatic changes.

In favour of the first theory are the following facts: (i) D. lotus is well known to have strong weedy tendencies. It reproduces freely from seed. Once established, it maintains itself by coppicing freely (Parker l.c., Bondarenko l.c., Zhukovskii l.c.). It will grow on bare or stony ground (Bondarenko l.c.). It is naturalised in the Mediterranean. (ii) The fruits of D. lotus is often eaten after drying, when it can be carried about easily and eaten along a journey. (iii) Central Asia and the region between the South Caspian and the Black Sea lie on the old silk route by which China traded with India and Europe and along which nomads have moved since prehistoric times. (iv) That D. lotus is wild and indigenous in east Asia (except Japan) has never been disputed by field workers in the Chinese region. Nor have doubts ever been raised by French collectors in Indo-China and American collectors in the Philippines. In contrast, D. lotus in Central and Western Asia strike many observers as being possibly a non-native element, tending to be found around human habitations.

In support of the second theory are the facts already stated by Bondarenko that (a) fossil remains have been found in Central Asia, (b) the species does occur in remote mountainous areas, at least in the Soviet part of Central Asia, (c) it is associated with other tertiary relict species.

I have my doubts about the fossil remains, the identification of which, at species level, must involve a very high degree of uncertainty. Nevertheless, it is difficult to decide between the two theories.

I am, however, inclined to believe that whether or not D. lotus is indigenous in Central and Western Asia, genetic continuity between the three geographically isolated populations has been maintained by humans travelling between the three regions carrying the fruit with them as food and scattering the seeds. This would account for the lack of morphological differentiation between the three populations, although of course, such differentiation need not necessarily occur following geographical isolation.

Key

Calyx lobes of male and female flowers glabrous or scattered-hairy on outer surface. (Mainland Asia and Japan).

... D. lotus subsp. lotus.

Calyx lobes of male and female flowers densely hairy on outer surface. (Philippines). ... D. lotus subsp. bridelliifolia.

Addendum

In view of the fact that D. lotus is sometimes confused with D. kaki, the differences are give here:-

D. kaki & D. roxburghii: basal nerves of leaves ascending steeply to reach half-way up the blade or beyond. Central axis of male cyme (measured from the articulation of the central flower to the base of the peduncle) 3 - 10 mm. long; female flowering peduncle 2 - 12 mm. long. Length of fruiting calyx 16 - 30 mm. Diameter of fruit 23 - 65 mm.

D. lotus: basal nerves of leaves not ascending steeply, rarely reaching half-way up the blade. Central axis of male cyme 1 - 4 mm. long; female flowering peduncle 0.5 - 2 mm. long. Length of fruiting calyx 7 - 14 mm. Diameter of fruit 12 - 26 mm.

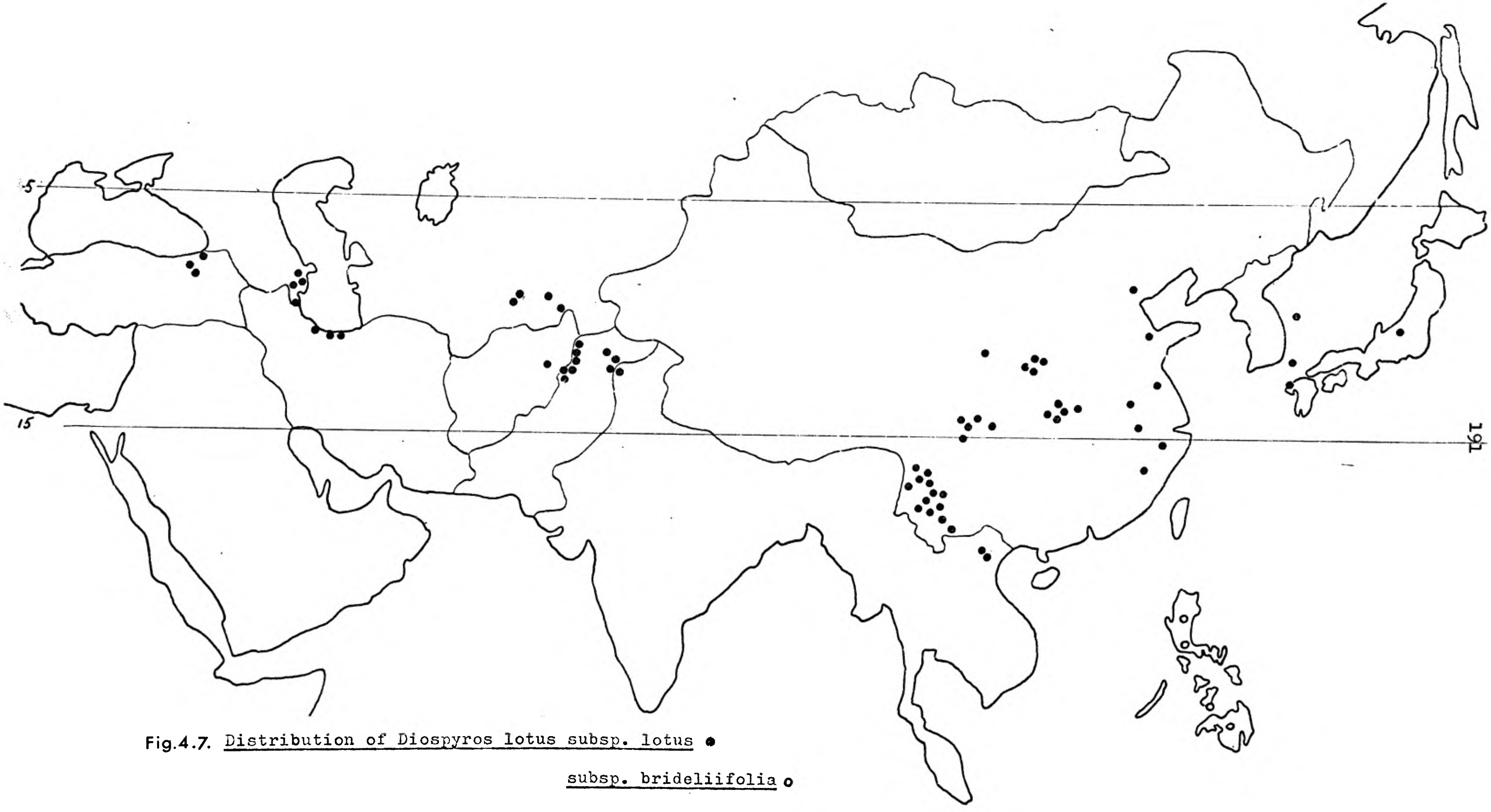


Fig.4.7. Distribution of Diospyros lotus subsp. lotus ●

subsp. brideliifolia ○

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APPENDIX I

List of pollen specimens of Ebenaceae and method of preparation.

1.	Euclea pseudobenus	Peyer 18
2.	E. schimperi	Lawton 1234
3.	E. divinorum	Bainbridge 305/57
4.	Diospyros argentea	SFN 21332
5.	D. borneensis	Kostermans 10675
6.	D. buxifolia	SFN 35164
7.	D. carpinifolia	Alvins 975
8.	D. cauliflora	FRI 8562
9.	D. confertiflora	Mat s.n.
10.	D. curraniopsis	FMS 38922
11.	D. diepenhorstii	Ridley 10847
12.	D. dictyoneura	S 23994
13.	D. discolor	Allen 13
14.	D. ebenum	CF 105
15.	D. ellipsoidea	KL 2037
16.	D. ferrea	Hoogland 6198
		FHI 20234
		SFN 35364
		FRI 5153
		CF 874
17.	D. foxworthyi	SFN 30512
		SFN 30180
18.	D. helferi	FMS 18026
19.	D. hermaphroditica	Ridley 4667
20.	D. heterotricha	Bequaert 1919
21.	D. iturensis	Lebrun 2353
22.	D. kaki	Henry 3485
		Savatier 809
23.	D. lanceifolia	FRI 4727
		Ridley 9212

24.	D. latisepala	FMS 38510
25.	D. lotus	Forrest 7461
		Faurie 13303
26.	D. lolin	Bequin 2212
27.	D. macrophylla	Pennington 7884
28.	D. maingayi	FRI 2724
		SFN 40953
29.	D. mespiliformis	Leteshu 4559
30.	D. nutans	SFN 32304
31.	D. oblonga	SFN 30883
32.	D. oldhamii	Wilson 10262
33.	D. pendula	Scortechini s.n.
34.	D. pentamera	Clemens s.n.
35.	D. rufa	FRI 4742
36.	D. pyrrhocarpa	FMH 78118
37.	D. roxburghii	Henry 11618
		Kerr 8851
38.	D. scortechinii	Ridley s.n.
39.	D. squarrosa	Robson 714
40.	D. styraciformis	FRI 4725
41.	D. sumatrana	King's Coll. 6633
		King's Coll. 6742
42.	D. toposioides	KEP 98410
43.	D. truncata	CF 7851
44.	D. villosa	Edwards 1365
45.	D. wallichii	KEP 98787

Pollen was taken either from herbarium material or from spirit-preserved flowers. Basic treatment involves heating the polliniferous material in an acetolysis mixture (9 : 1 acetic anhydrite : concentrated sulphuric acid) to dissolve away cellulose and other non-resistent substances, to leave a clean pollen-skeleton, but actual details vary from author to author, (Erdtman 1952, 1969, Faegri & Iversen 1964). I found that treatment with 10% sodium hydroxide prior to

acetolysis, gave cleaner grains.

(1) A flower bud is chosen which is just about to open. If from a herbarium sheet, the bud is first boiled to soften. It is then cut open and placed in a small tube containing a little water. The material is gently tapped with a needle. If mature, the anthers should open easily and release clouds of pollen into suspension. The buds are then removed and may be dried and replaced on the herbarium sheet.

This method gives much cleaner preparations than acetolysis of whole anthers or whole flowers, because it starts with a virtually pure suspension of pollen. Furthermore it is a good test for pollen maturity. Pollen which does not easily come out of the anthers nearly always make bad preparations (grains easily torn, wrinkled or crushed) and may be rejected without further waste of time.

(2) Transfer to a centrifuge tube. Centrifuge and tip out water.

(3) Add 10% NaOH, place the centrifuge tube in a water bath, bring bath to boil and simmer for 15 mins. Then centrifuge and tip out NaOH.

(4) Add distilled water to wash, then centrifuge and tip out water.

(5) Add glacial acetic acid, centrifuge and tip out.

(6) Add freshly made acetolysis solution (1 part conc. H_2SO_4 added drop by drop to 9 parts acetic anhydrite with continuous agitation to dissipate heat). Place

tube in water bath, bring bath to boil and simmer till the solution turns dark.

(7) Wash with glacial acetic acid, centrifuge and tip out.

(8) Wash with water, centrifuge and tip out. Repeat once.

The preparation is now ready either for (a) mounting on slides for standard light microscopy or (b) mounting on metal stubs for scanning electron microscopy.

(a) <u>Mounting on slides for light microscopy</u>.

(i) Suck up pollen suspension from the centrifuge tube with a pipette and transfer to a welled slide on an electric warmer (70°C).

(ii) Remove any lumps of extraneous material with a needle.

(iii) Gently stir in a very small piece of glycerine jelly, and keep adding small pieces until the solution is fairly thick. On removal from the warmer the jelly should set. Vigorous stirring or too rapid introduction of jelly will encourage weak grains to collapse. The process can be monitored under a dissecting microscope. Collapsed grains may sometimes be revived by re-introduction of water followed by gradual re-introduction of jelly.

(iv) Allow jelly to cool and harden. Then cut up the jelly into four pieces. Scrape up each piece with a flattened needle and transfer to a clean slide on the electric warmer. As the jelly melts, place a warm cover slip on top, then seal the edges with a drop of paraffin wax (M.P. 60 - 70°C). Remove and cool rapidly, then place upside down to consolidate. This enables the grains to come to rest against the cover slip and reduces

the amount of microscope focussing needed; also it ensures there will be no difficulty with oil-immersion lenses.

(b) Mounting on stubs for S.E.M.

(i) To the pollen suspension in the centrifuge tube, add 50% alcohol, centrifuge and tip out. Repeat with 95% alcohol, then with absolute alcohol.

(ii) Suck up the suspension from the centrifuge tube with a pipette and drop on an S.E.M. stub. The alcohol evaporates, leaving the dry pollen on the stub. It may be necessary to prevent clumping of grains by breaking up clumps with the point of a needle while the alcohol is evaporating. The pollen usually sticks to the stub without difficulty but if not, a small piece of double-side tape may be placed in the centre of the stub and the pollen suspension dropped onto the tape.

(iii) The pollen on the stub is coated with gold-palladium. Ideally, the stubs should be rotated with respect to the source of gold-palladium vapour so that even coating is obtained, even on the sheltered undersides of the grains. Unfortunately, I did not have facilities for even coating, hence my S.E.M. photographs suffer from deflection of the electron beam.

It may also be noted that some grains collapsed while being dried on the stubs and it was immaterial whether they were dried from water or from alcohol. Most Ebenaceae and Styracaceae grains stood up well. Symplocos did not give any problem at all. Grains of Sapotaceae, Sarcosperma and Lissocarpa collapsed badly.

APPENDIX II

List of seed specimens of Ebenaceae and method of preparation.

Seeds were boiled to soften, then free-hand-sectioned, stained in 1 - 5% aqueous safranin, dehydrated by passing through the alcohol series, through xylene, and finally mounted in DPX. Sections of seeds with very dark testas were sometimes bleached in hydrogen peroxide first before staining in safranin.

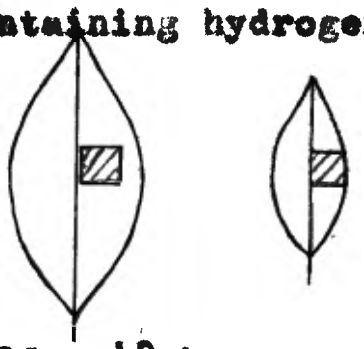
1.	Diospyros borneensis	Pennington 7964
2.	D. carpinifolia	S 19271
3.	D. confertiflora	FRI 2819
4.	D. dictyoneura	Pennington 8007
		S 23852
5.	D. discocalyx	-
6.	D. ehretioides	Put 4262
7.	D. ovena	Ogata 11677
		Pickles 3917
8.	D. ferrea	Pennington 8069
9.	D. foxworthyi	FRI 5440
10.	D. hermaphroditica	S 3771
11.	D. latisepala	FRI 4634
12.	D. maingayi	FRI 2807
13.	D. nutans	FRI 10714
14.	D. pendula	FRI 12843
15.	D. pyrrhocarpa	Pennington 7886
16.	D. rigida	Pennington 7963
17.	D. rufa	FRI 1270
18.	D. sumatrana	FRI 13034
19.	D. sylvatica	Kooney 401
20.	D. toposioides	Pickles 3733
21.	D. wallichii	FRI 15015
22.	D. sp. nov.	FRI 4618

APPENDIX III

Method of preparing leaf epidermal (cuticle) and vascular slides.

(List of Ebenaceae specimens given in table 6)

Leaf-squares about 1 x 1 cm were cut from the middle region of mature leaves, softened by boiling in water, and placed in bottles containing hydrogen peroxide (50% w/v) in



an oven at 60°C for 12 - 48 hours. The length of time needed for maceration varied with the material, but 24 hours was generally found sufficient, at which time the squares that were ready were bleached and seen to contain air bubbles between the upper and lower epidermis. Such squares were soaked in water to remove the peroxide, then placed in water in a petri-dish under a dissecting microscope. With needle and forceps, the two epidermal layers were peeled away from the vascular layer. If necessary, any attached mesophyll was removed from the epidermal and vascular layers by scraping with a needle or gently beating with a soft brush. However, scraping of the epidermal layers may remove the cell walls, leaving only the cuticle. This is not necessarily a disadvantage since the cuticle usually bears a neat imprint of all the epidermal cells and usually the stomatal guard cells and hairs remain intact. However, it may be desirable to leave part of each epidermis uncleaned, for comparison.

The material was stained in an aqueous 1 - 5% solution of safranin, washed in water, dehydrated in alcohol (50%, 95%, absolute in two changes, passed through xylol, two changes) and mounted in D.P.X. on glass slides. For convenience, the two epidermal layers and the vascular plate were mounted side by side on the same slide.

APPENDIX IV

List of chromosome slides and method of preparation.

1.	Diospyros confertiflora	FRI 2819
2.	D. maingayi	FRI 2807
3.	D. wallichii	FRI 13049

Actively-growing root tips were immersed successively in the following solutions :-

(i) 0.05% aequeous solution of colchicine for 4 hours at room temperature, to arrest the mitotic spindle.

(ii) 3 : 1 mixture of absolute alcohol : glacial acetic acid for 2 or more hours at room temperature, to fix the material.

(iii) 1N HCl for 6 - 7 minutes at 60°C to hydrolyse.

(iv) feulgen solution for 1 hour at room temperature to stain.

The root tips were then washed with water, placed in a drop of aceto-carmine on a glass slide and macerated by tapping with a blunt instrument until reduced more or less to a suspension of cells. Any hard lumps were removed.

A cover-slip was smeared with glycerine-albumen on one side, dried slightly on a spirit flame and placed, smeared side downwards on the cell suspension. With the point of a needle, the cover slip was gently tapped to remove air bubbles and to break up the suspension further. The cells were then flattened by pressing down through layers of blotting paper and warmed over a spirit flame.

The slide was inverted in 45% acetic acid for the cover slip to fall off. Then the cover slip, with the cells adhering to it, was dehydrated (80% alcohol 2 minutes, absolute alcohol 2 minutes in two changes) then placed, face downwards, on a drop of DPX on a slide.

APPENDIX V

Microscope Preparations of Sapotaceae, Sarcospermataceae, Lissocarpaceae, Styracaceae, and Symplocaceae.

A. Wood Slides.

Sapotaceae : There are 90 specimens in the collection of the Commonwealth Forestry Institute. Unfortunately, owing to the extreme instability of generic concepts in Sapotaceae, the names on many of the labels of the specimens have become obsolete. I therefore give only a short list rather than a complete one just to convey an idea of the range of material examined.

Achras (Manilkara) zapota	IFI 2233
Achrouteria pomifera	IFI 11422
Aningeria altissima	IFI 12706
Argania spinosa	IFI 11750
Bumelia obtusifolia	IFI 10725
Butyrospermum parkii	FPRL 13532
Chrysophyllum cainito	IFI 3505
C. roxburghii (now lanceolatum)	FMS 1854
Diploknema oliganera	IFI 12028
Ecclinusa psilophylla	IFI 13305
Ganua motleyana	FMS 1001
Lucuma (Planchonella) maingayi	FMS 1002
Lucuma (Pouteria) malaccensis	FMS 1018
Madhuca utilis	FMS 862
Manilkara kauki	IFI 941
Mastichodendron gummeri	IFI 18788
Mimusops elengi	IFI 2696
Palaquium gutta	FMS 1009
Payena dasyphylla	IFI 10167

Sarcospermataceae

Sarcosperma paniculatum	IFI 12034

Lissocarpaceae

Lissocarpa guianensis	IFI 13275

Styracaceae

Bruinsmia styracoides	IFI 12038
Halesia carolina	IFI 4577
H. tetraptera	-
Styrax obassia	IFI 4561
Styrax officinalis	IFI 18140
Styrax polysperma	IFI 6559

Symplocaceae

Symplocos adenophylla	IFI 8094
S. caudata	FRL 14771
S. crataegoides	-
S. fasciculata	IFI 8428
S. henschelii	IFI 10565
S. perakensis	IFI 8095
S. spicata	IFI 2451

B. Pollen Slides

Sapotaceae

Chrysophyllum lanceolatum	FMB 6614
Ganua curtisii	FRI 8154
Ganua motleyana	BNB 2308
Isonandra perakensis	FRI 1914
Madhuca selangorica	KEP 11116
Manilkara sapota	SFN 35520
Mimusops elengi	Nur s.n.
Palaquium maingayi	KEP 16463
Payena lucida	KEP 11045
Planchonella obovata	Curtis 704
Pouteria malaccensis	FA 603

Sarcospermataceae

Sarcosperma paniculatum	FRI 1383

Lissocarpaceae

Lissocarpa guianensis	Sandwith 1590

Styracaceae

Afrostyrax lepidophyllus	Jean Louis 13883
Bruinsmia styracoides	RBNB 131
Halesia diptera	Palmer 7063
Pterostyrax hispidum	Kew 371[n]
Styrax benzoin	FMS 13779

Symplocaceae

Symplocos maingayi	Maingay 961
Symplocos sp	FRI 1559

C. **Microtome Serial Sections of Gynoecia**

Sapotaceae

Chrysophyllum lanceolatum	FRI 1832
Ganua hirtiflora	FRI 6066
Isonandra perakensis	FRI 1914
Madhuca penicillata	FRI 6066
Manilkara zapota	s n (cult. at Kepong)
Mimusops elengi	FRI 1812
Palaquium maingayi	FRI 1813
Payena lucida	FRI 5943
Planchonella maingayi	FRI 1983
Pouteria malaccensis	KEP 99516

Sarcospermataceae

Sarcosperma paniculatum	FRI 1383
Sarcosperma wittienii	FRI 1950

Symplocaceae

Symplocos sp. FRI 16153

Styracaceae

Styrax benzoin FRI 16153

Lissocarpaceae

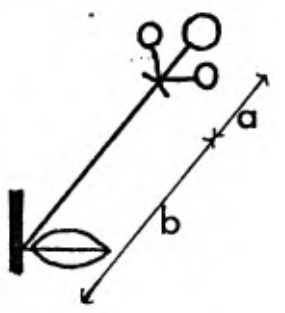
Lissocarpa benthamii Spruce 3504

(from herbarium specimen)

All the gynoecia were from pickled flowers except Lissocarpa for which pickled material was not available. Embedding in wax ("paramat") was carried out by standard methods, and sections were cut at 7.5 - 12.5μ . The sections were fixed to slides, dewaxed, stained in safranin, counterstained in aniline blue, and sealed in DPX following the schedule in Gurr (1965) 306.

APPENDIX VI

Definitions of characters of table 3.2 where not self evident.



6. Inflorescence flagelliform: b > 2a.

   Inflorescence not flagelliform: b ⩽ 2a.

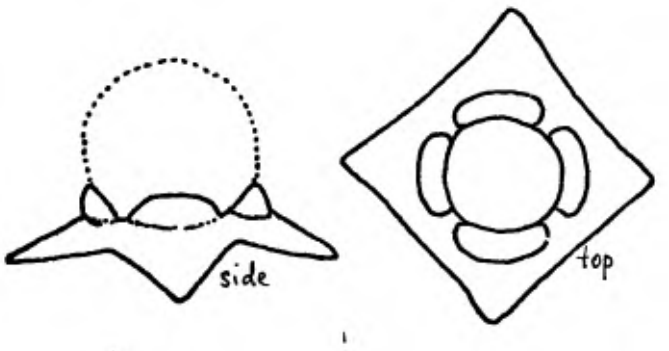
9. Gynoecium reduced: carpel merism ± ½ floral merism (see table 1.3, series 2).

   Gynoecium not reduced: carpel merism = floral merism (see table 1.3, series 1).

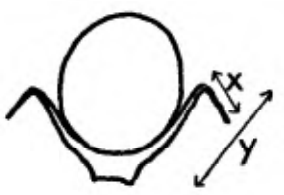
13. Styles free: styles completely free to half-united. 

    Styles united: styles more than half-united to fully united. 

34. Female calyx with internal elevated rim:



37. Fruiting calyx reflexed: x > y.



    Fruiting calyx erect: x < y.

    Fruiting calyx split: calyx tube split during enlargement of the fruit.

    Fruiting calyx spreading: calyx merely pushed outwards by the enlarging fruit, without splitting.

44. Endosperm vascular ruminate: vascular tissue deeply embedded within ingrowths of the testa (fig. 1.8c).

48. Stamens maingayi type: see fig. 1.1e.

    Stamens clavigera type: see fig. 1.1d.

    Stamens "normal": all other types.

APPENDIX VII

List of species of Diospyros used in character analysis.

1. D. adenophora Bakh.
2. D. apiculata Hiern
3. D. areolata King & Gamble
4. D. argentea Griff.
5. D. aurea Teysm. & Binnend.
6. D. australis (R. Br.) Hiern
7. "B" (SAN 29378, FRI 2670, KEP 94624, FMS 56851)
8. D. bibracteata Bakh.
9. D. borneensis Hiern
10. D. bridelliifolia Klm.
11. D. buxifolia (Bl.) Hiern
12. D. carpinifolia (Ridl.) Bakh.
13. D. castanea (Craib) Fletcher
14. D. cauliflora Bl.
15. D. clavigera Clarke
16. D. confertiflora (Hiern) Bakh.
17. D. confusa Bakh.
18. "D" (FRI 4618, SFN 11661, FRI 11751)
19. D. daemona Bakh.
20. D. dictyoneura Hiern
21. D. diepenhorstii Miq.
22. D. discocalyx Merr.
23. D. discolor Willd.
24. "E" (S 5051, S 2127, S 9032)
25. D. ebenum Koen.
26. D. ehretioides Wall. ex G. Don
27. D. elegantissima Bakh.
28. D. ellipsoidea King & Gamble
29. D. elliptifolia Merr.
30. D. eriantha Champ. ex Benth.

31. D. evena Bakh.

32. D. ferrea (Willd.) Bakh.

33. D. ferruginescens Bakh.

34. D. foxworthyi Bakh.

35. D. frutescens Bl.

36. D. gambleana Bakh.

37. D. glandulosa Lace

38. D. hallieri Bakh.

39. D. brachiata King & Gamble

40. D. hasseltii Zoll.

41. D. hebecarpa A. Cunn. ex Benth.

42. D. hermaphroditica (Zoll.) Bakh.

43. D. kajangensis Bakh.

44. D. kaki L. f.

45. D. kingii Bakh.

46. D. kurzii Hiern

47. D. consanguinea Merr.

48. D. lanceifolia Roxb.

49. D. maritima Bl.

50. D. multiflora Blanco

51. D. undulata Wall. ex G. Don

52. D. latisepala Ridl.

53. D. levigata Bakh.

54. D. lolin Bakh.

55. D. lotus L.

56. D. mabacea (F. Muell.) F. Muell.

57. D. macrophylla (Vieill.) Hiern

58. D. maingayi (Hiern) Bakh.

59. D. malabarica (Desr.) Kostel.

60. D. mollis Griff.

61. D. montana Roxb.

62. D. nana Bakh.

63. D. novoguineensis Bakh.

64. D. nutans King & Gamble

65. D. packmanni Clarke

66. D. papuana Val. ex Bakh.

67. D. pauciflora King & Gamble

68. D. penangiana King & Gamble

69. D. pendula Hasselt ex Hasak.

70. D. pentamera F. Muell.

71. D. perfida Bakh.

72. D. elmeri Merr.

73. D. helferi Clarke

74. D. oblonga Wall. ex G. Don

75. D. polyalthicides Korth. ex Hiern

76. D. pilosanthera Blanco

77. D. piscicarpa Ridl.

78. D. poncei Merr.

79. D. pubicalix Bakh.

80. D. puncticulosa Bakh.

81. D. pyrrhocarpa Miq.

82. D. retrofracta Bakh.

83. D. rhodocalyx Kurz

84. D. ridleyi Bakh.

85. D. rigida Hiern

86. D. rufa King & Gamble

87. D. saxosa Fletcher

88. D. scortechinii King & Gamble

89. D. selangorensis Bakh.

90. D. siamang Bakh.

91. D. siamensis Hochr.

92. D. styraciformis King & Gamble

93. D. subtruncata Scheff. ex Hochr.

94. D. suluensis Merr.

95. D. sumatrana Miq.

96. D. toposia Ham.

97. D. transitoria Bakh.

98. D. truncata Zoll. & Mor.

99. D. ulo Merr.

100. D. variegata Kurz

101. D. wallichii King & Gamble

102. D. yoobi Bakh.

APPENDIX VIII

Main input data for CHARANAL.

"Objects" in first column refer to species identified by number (see Appendix VII). The first row identifies the characters by number (see table 3.1). The states of each character are numbered 1, 2.....n consecutively. If a character is not observed, the figure 0 is entered.

MAIN INPUT DATA

OBJECT CHARACTER STATES

	1 2 3 4 5 6	9 10 11 13 14 15	19 20 22 26	31 33 34 36	37 44 48 51 52 53 54	55
1	000121	201000	0000	0212	4202020	2
2	221221	131122	1020	3211	4212221	1
3	241211	231222	1113	2212	1212222	2
4	251211	231122	2233	2211	2212221	1
5	000321	211222	1020	1112	2212222	2
6	251211	232122	1133	1212	2212222	2
7	241211	100000	0022	1112	4202221	1
8	000151	231100	0000	0210	0002020	2
9	331330	231022	2120	2212	3212222	2
10	241211	231122	2020	2210	0212222	2
11	221211	131122	1022	1112	4212221	1
12	251351	211223	1122	1112	4211112	2
13	151121	201022	1020	1112	4211112	2
14	151151	131323	2233	1212	1212221	1
15	151151	000022	1011	1112	4230221	1
16	251221	231122	2322	3212	1211112	3
17	251321	131122	1022	1111	4232221	1
18	221111	231022	2020	2212	3212222	2
19	351111	000022	2020	1112	4210221	0
20	251213	121122	2040	2212	2212222	2
21	151331	241223	1122	1212	4212221	1
22	251210	231022	2030	2212	2212222	2
23	251211	231022	1030	1111	4212221	1
24	241211	231000	0000	0212	1202020	2
25	241221	241321	2112	2222	1212222	2
26	251221	131122	1022	1212	1212222	2
27	000211	131200	0102	0112	4202020	1
28	151351	000022	1010	1112	4230221	1
29	351321	231222	1111	2212	2012222	2
30	211221	131222	1020	3212	2212222	2
31	211211	132200	1111	1112	4101221	1
32	241221	232222	1022	3212	2211112	2
33	351311	131022	1020	2212	4211222	2
34	151151	231022	1120	1212	4212222	2
35	351351	131122	2322	1112	4212222	2
36	000000	000000	0000	0112	4200020	1
37	251000	000022	2020	3211	2212222	2
38	251251	231022	2030	1112	1212222	2
39	351151	231222	2122	2212	2012222	2
40	351151	231222	2222	2212	2212222	2
41	000051	231000	0000	0222	1202020	2
42	351351	331123	3322	3112	1211112	2
43	211211	131322	1022	1112	4232221	1

MAIN INPUT DATA

OBJECT	CHARACTER STATES 1 2 3 4 5 6	9 10 11	13 14 15	19 20	22 26	31 33 34 36	37 44 48	51 52 53 54	55
44	241211	201	021	20	2 0	1212	4 2 1	2222	2
45	341221	000	022	10	1 0	1112	4 0 3	0221	1
46	251231	141	323	33	2 2	1212	1 2 1	2222	2
47	251021	231	022	20	2 0	2211	2 0 1	2222	2
48	351331	231	122	21	2 2	2212	2 2 1	2222	2
49	351331	231	122	21	2 2	2212	2 2 1	2222	2
50	351121	000	022	20	2 0	2212	2 2 1	2222	2
51	241211	231	022	21	2 2	2212	2 2 1	2222	2
52	251212	131	110	11	4 4	2212	2 2 1	2222	2
53	351151	000	022	10	3 0	1002	4 2 1	2222	2
54	221211	201	022	10	3 0	1212	4 2 1	2221	0
55	000211	231	100	02	0 1	0210	4 2 1	2222	2
56	241211	232	122	11	2 2	1110	0 0 1	2222	2
57	251000	000	022	10	2 0	2212	1 0 1	0222	2
58	331331	312	210	11	3 3	1112	4 1 2	1221	1
59	251211	221	122	22	2 2	2212	2 2 1	2222	2
60	251211	201	023	30	1 0	1002	1 2 1	2222	0
61	251211	241	123	33	1 2	3312	1 2 1	2223	1
62	000311	000	000	00	0 0	0112	4 2 0	0020	1
63	000211	231	200	01	0 2	0222	1 2 0	2020	2
64	252252	131	210	11	2 2	1111	4 2 1	2221	1
65	241221	131	222	21	3 3	2210	0 0 1	1222	2
66	251221	231	222	22	3 3	1112	4 2 1	2222	2
67	000311	231	000	00	0 0	0212	3 2 0	2020	2
68	000151	131	100	01	0 2	0111	4 2 0	2020	1
69	341210	231	022	20	3 0	2212	4 2 1	2222	2
70	241211	132	122	20	2 0	1222	2 2 1	1222	2
71	341131	231	122	32	1 1	2212	2 2 1	2221	1
72	251241	231	122	11	3 3	2211	2 0 1	2222	2
73	251221	231	122	23	3 3	2212	2 2 1	2222	2
74	251241	231	122	21	3 3	2212	2 2 1	2222	2
75	251251	231	122	11	2 2	2212	2 2 1	2222	2
76	351341	231	022	20	3 0	2212	1 2 1	2222	2
77	251251	231	010	20	2 0	2210	2 0 1	2222	2
78	000211	131	000	00	0 0	0110	0 0 0	2020	1
79	201000	000	022	20	2 0	2000	0 0 1	0202	0
80	000211	132	200	01	0 3	0110	0 0 0	1020	1
81	241211	201	022	10	2 0	2212	1 2 1	2222	2
82	221211	331	010	10	3 3	1212	4 2 1	2222	2
83	251211	131	322	22	3 3	2212	4 2 1	2221	3
84	221211	231	000	00	2 0	2212	4 2 0	2222	2
85	000200	221	000	00	0 0	0012	2 2 0	2022	2
86	351151	231	022	10	3 0	2212	4 2 1	0222	2
87	351311	131	022	20	3 0	2212	1 2 1	2222	2
88	221211	000	022	10	1 0	1212	4 2 3	0221	1
89	000211	030	000	00	0 0	0212	4 2 0	0020	2
90	151131	231	022	20	2 0	2001	2 2 1	2222	0
91	251211	221	021	22	3 3	2212	4 2 1	2222	2
92	351031	231	022	20	2 0	2211	2 2 1	2222	2
93	251210	231	022	20	2 0	1111	4 2 1	2222	2
94	251231	131	222	21	2 2	1212	4 2 1	2222	2
95	231221	141	223	11	3 3	3312	2 2 1	2222	2
96	241211	231	110	30	3 0	3212	1 2 1	2222	2
97	000221	231	200	01	0 3	0212	4 2 0	2020	2
98	331231	211	221	10	1 1	1112	2 2 1	2222	2
99	000320	231	000	00	0 0	0111	4 2 0	2020	2
100	351341	231	122	11	1 1	2210	0 0 1	2221	1
101	151131	231	122	22	2 2	2211	2 2 1	2222	2
102	351051	201	022	20	3 0	2002	4 2 1	0222	0

APPENDIX IX

Species to be excluded from Ebenaceae

BLUMEA 18 (1970) 412

NOTES ON THE EBENACEAE [1])
VI. FOUR SPECIES TO BE EXCLUDED FROM THE FAMILY [2])

F. S. P. NG
Commonwealth Forestry Institute, University of Oxford.

In the course of a study on Indo-Malesian *Ebenaceae* currently being carried out in the Oxford Forest Herbarium, it has been discovered that four species previously accepted as *Diospyros* do not belong to that genus and must be excluded from the family. They are as follows.

1. *Diospyros addita* Fletcher, Kew Bull. (1937) 386. — Type: *Put 3109* (K, ABD). Is reduced to **Vatica philastreana** Pierre *(Dipterocarpaceae)*.

The fruit is shallowly three-lobed and has a persistent five-lobed calyx. It contains a single large seed the bulk of which consists of four massive cotyledonary lobes. Fletcher mistook the cotyledonary lobes for four separate seeds.

2. *Diospyros hierniana* (King & Gamble) Bakh., Gard. Bull. S.S. 7 (1933) 173. — *Maba hierniana* King & Gamble, J. As. Soc. Beng. 74 (1905) 203. — Type: *King's Collector 7920* (K, SING). Is reduced to **Salacia grandiflora** Kurz *(Celastraceae)*.

King & Gamble described the flowers of this species but both the Kew and Singapore isotypes have lost their flowers. Hence I am unable to re-examine the floral morphology. However, the peculiar position of the 'floriferous knobs' which are opposite and extra-axillary, together with the opposite insertion of the leaves, made this species highly suspect.

At my request, Mr. K. M. Kochummen at Kepong examined the Singapore specimen while Mr. P. S. Green and Dr. D. Cutler of the Herbarium and Jodrell Laboratory at Kew respectively, examined the Kew specimen. They independently arrived at the same conclusion. Mr. Kochummen recognized it immediately to be a *Salacia*. In the meantime Dr. Cutler examined the twig anatomy and suggested *Celastraceae*. Mr. Green took up this suggestion and matched the specimen to *Salacia*.

King & Gamble mistook the stamens for staminodes, and misinterpreted the pistil. Nevertheless, their description of the flower is compatible with *Salacia*.

3. *Diospyros micromera* Bakh., Gard. Bull. S.S. 7 (1933) 176. — Type: *Curtis 3463* (SING). Is reduced to **Cleistanthus nitidus** Hook. *f.* var. **curtisii** (Jabl.) Ridl. *(Euphorbiaceae)*.

Bakhuizen based his description on a sterile specimen. There are small appressed stipules at the twig apices which leave inconspicuous scars. *Ebenaceae* is always without stipules!

For the correct identification of the species, I am indebted to Mr. H. K. Airy Shaw.

4. *Diospyros sororia* Bakh., Revisio Ebenacearum Malayensium in Bull. Jard. Bot. Btzg III, 15 (1937) 125—126; (1955) t. 16. — Type: *Sitam 46* (K, KEP). Is reduced to **Ilex borneensis** Loes. *(Aquifoliaceae)*.

The fruits, with persistent flat stigmas and bony endocarp, are wrong for *Ebenaceae* and also, contrary to the published illustration, the leaf margins are not entire, but rather very faintly serrulate. The thick 'testa' described and illustrated is actually endocarp.

For the correct identification of the species, I am indebted to Mr. L. L. Forman.

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[1]) This series is edited by F. White, University of Oxford.
[2]) Continued from Bull. Jard. Bot. Etat, Bruxelles, 33 (1963) 345.

Diospyros beteogensis Fletcher, Kew Bull. (1937) 382. - Type: Kerr 7673 (K), is reduced to Drypetes pendula Ridley (Euphorbiaceae).

The presence of stipule-scars excludes this species from Ebenaceae. The deciduous calyx and internal structure of the fruit are also wrong. Mr H.K. Airy Shaw provided the correct identification.

APPENDIX X

List of specimens examined in the species-analyses of Part 4.

Diospyros ehretioides Wall. ex G. Don

BURMA: Forest School s.n. (March 1930); Kurz 3011; Lace 2852; Wallich 4137a, 4137b.

THAILAND: Boonchuang 104; Kerr 577, 1147, 5249, 5262, 5811, 10608, 20186, 20193, 20663; Kostermans 728; Phengklai 107, 2139; Put 2834, 4262; Umnat 133; Vanpruk 445; Winit 227b.

CAMBODIA: Bejaud s.n; Fleury 30052; Pierre 5039; Poilane 14601, 14811.

VIETNAM: Pierre 5036; Poilane 836; Squires 928; Thorel 2115.

CHINA Hainan: How 70685.

Diospyros kaki L.f.

VIETNAM North: Balansa 4348, Bon s.n.

CHINA Yunnan: Cavalarie 3249; Forrest 13815; Maire 482. Kwangtung: McClure 57, 263; Tsang 20197, 20767, 21282, 21418; Vampon & Hance 13753. Fukien: Chung 1666, 2210, 2747, 2898; Price 1145, 1155. Szechuan: Fang 6443; Schneider 651. Hupeh: Chun 3593; Henry 1560, 1962, 3441, 3485, 3567, 3861, 6235a; Maries s.n; Wilson 399, 472, 511, 790, 2914. Anhwei: Ching 2747, 3185; Fan & Li 156; Kiangsu: Meyer 1424; Ren 12563; Tso 1336, 1828. Shangtung: Chiao 2513, 2875; Taiwan: Oldham 299.

KOREA: Taquet 2978; Wilford 756.

JAPAN: Maximowitz s.n; Ohashi 660266; Oldham 528; Savatier 809; Wilson 6959.

Diospyros lotus L. subsp. lotus.

WESTERN ASIA Turkey: Bornmuller 351; Davis 47506, 47714, Davis & Hedge 32042. Azerbaijan: Balansa 1464; Balls & Goulay 1935; Kohenacher s.n; Raddle 306. Iran: Cowan & Darlington s.n; Furse & Lynge 280; Rechinger 2349, 5567.

CENTRAL ASIA Afganistan: Aitchinson 150; Griffith 1289; Harsukh 14860, 15399. Chitral: Deane s.n; Duthie 62; Harris 16357; Toppin 680. Punjab: Drummond 21957; Rodin 5379; Sprague 103, 124. Kashmir: Clarke 28214; Keshavanand 217.

CHINA Yunnan: Cavalerie 7883; Ducloux 33; Maire 440, 481, 1753, 2415, 3090; Forrest 7461, 7599, 7708, 13861, 14922, 23471, 27732; Henry 9898d, 9898e; Schneider 1650, 2788. Szechuan: Fang 3753; Pratt 150; Henry 7044; Wilson 2915. Kansu; Meyer 1950. Shensi: Licent 2980; Purdom 903; Wilson 1273. Hupeh: Henry 2871, 3014, 5820; Wilson 429, 621, 1399. Hopei: Potanin s.n. Shangtung: Chiao 2681. Kiangsu: Tso 1120. Anhwei: Lei 2988; Ching 3310. Chekiang: Law 1146. Fukien: Ching 2506.

KOREA: Wilford 583; Wilson 8521.

JAPAN: Faurie 13302, 13303; Ohwi s.n; Oldham 529; Wilson 751; Wright 189.

VIETNAM North: Petelot 4451; Poilane 12586.

Diospyros lotus subsp. bridelliifolia (Klm.) Ng

PHILIPPINES: Conklin & Buwaya PNH 80459; Elmer 9722, 14203; Ocampo BS 27969, Santos BS 31801.

Diospyros roxburghii Carr.

INDIA Assam & Manipur: Ber 2720; Clarke 41150; Hooker & Thompson 41150; Watt 6264.

BURMA: Kurz 1008; Lace 3119, 3198; Saw Maung Mya 5381, 5400; U Tha Hla 1999.

THAILAND: Kerr 3461, 3584, 3586, 4675, 6265, 8705, 8851, 20236; Larsen et al. 2000; Phengklai & Sangkhachand 956; Pinnin et al. 106; Smitinand 13867; Winit 1324.

LAOS: Harmand 1304, 1389; Poilane 2011, 13489, 15884.

VIETNAM North: Bon 353; Eberhardt 4732.

CHINA Yunnan: Forrest 5536, 5537, 7667, 9936, 11519, 11868, 15662, 24175, 24476, 25178; Henry 9341, 9898c, 11618, 11618c, 11618d; Maire 1041; McLaren 82a, 87a; Schneider 3208. W. Hupeh: Wilson 840, 2913. Kwangtung: McClure 13394. Chekiang: Meyer 1493.

FRANCE Cult. Thuret s.n.

Diospyros sylvatica Roxb. subsp. sylvatica.

INDIA: Gamble 9242, 13769, 16025; Haines 2368, 2458, 4853; Hastell 4853; Law s.n; Lushington s.n; Mooney 401, 792, 998; Roxburgh s.n; Talbot 3592.

CEYLON: Thwaites C.P. 2729.

Diospyros sylvatica subsp. hermaphroditica (Zoll.) Ng

BURMA: Helfer 3618; Parker 2561.

THAILAND: Annandah s.n; Collins 590, 1796; Kerr 16255, 16551, 16613, 17476, 18518; Marcan 1246; Phengklai 12287; Smith 311; Smitinand 2150; Vanpruk 701; Vesterdal s.n.

CAMBODIA: Harmand 391.

VIETNAM: Pierre 11, 29; Thorel 788.

MALAYA: Abdullah FMS 47386; Ali FMS 34147; Burkill SF 3242, SF 3385; Curtis 705, 2577, 2579, 2586, 3418; Delman FMS 21481; Gadoh KL 1008, KL 2104; Haniff 15536; Henderson SF 23050; Holttum SF 15081, SF 15122; Jaamat & Sou KEP 57006; King's Collector 7877; Koehummen KEP 94912; Meijer & Yong KEP 94861; Ngadiman SF 36926; Nur SF 32596; Osman FMS 29251; Ridley 4667, 4961, 12190, 14922, 15535; Whitmore FRI 3752; Wray 1269.

BORNEO: Abu Bakar FMS 38604; Anderson S 4146, S 14657, S 15294, S 16050; Ashton S 18377; Beccari 1670, 1822; Brian S 15912; Chew 518; Clemens 50222; Cundra A 273; Galau S 15649; Haviland 776; Kostermans 4900, 4949; Lajangah SAN 44586; van Steenis 1365.

JAVA: Kostermans UNESCO 152, 19321; Soepadmo 307; Wirawan 144; Teysmann s.n.

SUMATRA: Achmad 600, 1345; Kostermans & Anta 323.

Diospyros sylvatica subsp. fasciculosa (v. Muell.) Ng.
JAVA: FRI Ja 4904; Koorders 29593b, 30141b.

AUSTRALIA: Brass 19969; Dallarky s.n; Hill 100; Mueller s.n; O'Shanesy s.n.

NEW CALEDONIA: Balansa 467; Deplanche 206, 311; McKee 3264, 4598; Pennington 8141; Schlechter 15057; Vieillard 899.

FIJI: Kuruveli & Qoro s.n.