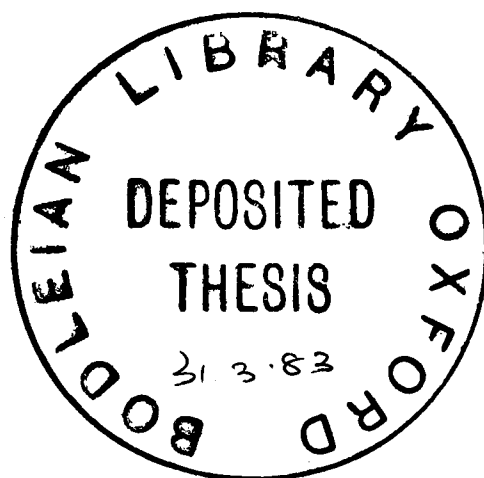


STUDIES IN THE GENUS DIALIUM (CASSIEAE-CAESALPINIOIDEAE)

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Doctor of Philosophy
at the
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PREFACE

When I applied for a scholarship in England for advanced study in plant taxonomy, I did not have any particular group of plants already in my mind to investigate. However, I was certain that I would study a genus the species of which are composed of trees. This is because I am a forester by training and besides, I already had experience in revising a genus with member species being all trees (Rojo, 1972).

In 1978, a year before I started this study, I met in Manila Dr. T.C. Whitmore, a University Research Officer (at the Commonwealth Forestry Institute) of the University of Oxford, who was designated supervisor of my study. We had preliminary talk about what group of plants I have to work on. That year the International Legume Conference was held at the Royal Botanic Gardens in Kew to assess among others, the advances in legume systematics for the last century or so. We thought it timely to work in considerable detail a genus in the Leguminosae. Also the spoken papers on systematics in that legume conference had not as yet been published then, and we thought it would be of interest to compare later the result of my work with that of the published data (Polhill and Raven, 1981). Dr. Whitmore and I decided that I study a genus, the size of which is neither so big nor so small to finish within a 3-year period of my scholarship. The genus Dialium was chosen.

TO EMELDA, MILDRED AND JANUS

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As with any revisionary work of this kind, this study could not have been successfully carried out without the generous cooperation of the Directors of herbaria from which I have borrowed specimens to make this revision as complete as possible. Of the herbaria listed below, I have not been able to visit Bogor (BO) and Berlin (B). Apart from the Forestry Herbarium of the University of Oxford (FHO), herbarium materials have been made available from: Botanischer Garten und Botanisches Museum (B), Berlin-Dahlem; British Museum (Nat. Hist.) Botany Department (BM), London; Herbarium Bogoriense (BO), Bogor; Jardin Botanique National de Belgique (BR), Meise; Royal Botanic Gardens (K), Kew; Forest Research Institute Herbarium (KEP), Kepong; Rijksherbarium (L), Leiden; Laboratoire de Phanérogamie (P), Paris; Forestry Department Herbarium (SAN), Sandakan; Forestry Department Herbarium (SAR), Sarawak and Botanic Garden (SING), Singapore. Wood and wood section slides were made available from: Centre Technique Forestier Tropical (CTFT), Nogent-sur-Marne; Commonwealth Forestry Institute (CFI), Oxford and Forest Products Research Laboratory (FPRL), Princes Risborough.

A number of individuals helped me in many ways, particularly in the Commonwealth Forestry Institute, Department of Agricultural and Forest Sciences, University of Oxford: to them I give my sincere appreciation.

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Lastly, I owe very much the success of this study to my wife, Emelda who opted to stay behind in the Philippines to take care of our daughter, Mildred and son, Janus for her pushing and continuous encouragement and moral support, without which my sojourn abroad would have been unbearable indeed. To her and to our children, this work is lovingly dedicated.

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by

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ABSTRACT

The present study is the first detailed worldwide revision of the whole genus Dialium. The genus has previously been revised and subdivided into infrageneric taxa (with enumeration of species of Africa and the Neotropics only) but their delimitations have been based solely on gross morphology. Therefore, in order to define the taxa, the present study reviewed the gross morphological characters and augmented them with data from anatomy, palynology, cytology and phytochemistry. This made possible a new classification which better reflects the relationships of the infrageneric taxa.

The various characters are reviewed, covering gross morphology, indumentum and other epidermal characters of the leaflets, anatomy of the pulvinus, testa and wood, palynology, cytology and phytochemistry.

The important taxonomic characters in Dialium are pointed out and used to define the genus and infrageneric taxa, as well as in recognising species and varieties. Some taxonomic characters are discussed in relation to geographical distribution in order to explain the present-day occurrence of infrageneric taxa east of, and one species west of, continental Africa. Evolutionary trends are explained based on these taxonomic characters.

The genera in the subtribe Dialiinae are found to be closely inter-related. However, the majority of them are more closely related to each other than they are to Dialium itself. The genera Baudouinia, Eligmocarpus and Mendoravia are taxonomically rather remote from the rest of the Dialiinae and their position needs further evaluation. The subgenus Uittienia is found not to belong to Dialium and has to be reinstated as a monotypic genus but within the same subtribe.

The thesis concludes with a formal taxonomic treatment of Dialium. The arrangement of the infrageneric taxa is such that it reflects their supposed taxonomic relationships. There are no new species described. Previously reduced species and infraspecific taxa are reviewed and further reductions are made. As a result, only 27 species (4 with varieties) are now recognised out of the previously estimated 40 species.

SYNOPSIS OF THE TAXA RECOGNISED

I. Subgen. AROUNA (Aublet) Stey.

A. Sect. AROUNA (Aublet) Taubert, ampl. Rojo

a. Subsect. PIRULA Stey.

1. Dialium schlechteri Harms
2. Dialium pobeguinii Pellegrin
3. Dialium bipindense Harms
4. Dialium guianense (Aublet) Sandw.
5. Dialium dinklagei Harms
6. Dialium orientale Baker f.
7. Dialium holtzii Harms
8. Dialium reygaertii De Wild.
9. Dialium excelsum Louis ex Stey.

b. Subsect. INDUMENTOSA Stey.

10. Dialium pentandrum Louis ex Stey.
11. Dialium polyanthum Harms
12. Dialium tessmannii Harms
13. Dialium angolense Welw. ex Oliver
 - 13a. var. angolense
 - 13b. var. kasaiense (Louis ex Stey.) Rojo, stat. & var. nov.
14. Dialium pachyphyllum Harms

B. Sect. CODARIUM (Sol. ex Vahl) Benth., ampl. Rojo

15. Dialium englerianum Henriq.
16. Dialium guineense Willd.
17. Dialium zenkeri Harms

II. Subgen. DIALIUM

18. Dialium hydnocarpoides de Wit
19. Dialium platysepalum Baker
20. Dialium ovoideum Thwaites

21. Dialium cochinchinense Pierre

22. Dialium indum L.

22a. var. indum

22b. var. bursa (de Wit) Rojo, comb. nov.

III. Subgen. DANSERA (Steenis) Stey.

C. Sect. HOVA (Irwin & Barneby) Rojo, stat. & sect. nov.

23. Dialium occidentale (Capuron) Rojo, stat. nov.

23a. var. occidentale

23b. var. septentrionale (Capuron) Rojo, stat. & var. nov.

24. Dialium madagascariense Baillon

25. Dialium unifoliolatum Capuron

D. Sect. DANSERA

26. Dialium kunstleri Prain

26a. var. kunstleri

26b. var. trifoliolatum (de Wit) Rojo, stat. & var. nov.

27. Dialium procerum (Steenis) Stey.

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PART I. INTRODUCTION

1. INTRODUCTION

1.1. Purpose of the Study

This study is the first detailed worldwide revision of the whole genus Dialium. There have been accounts of species in local and/or regional Floras, especially in tropical African countries where the greatest concentration of Dialium species are found. Examples of these accounts, to mention only the more recent ones, are those of Aubréville (1968, 1970) in Cameroon and Gabon, Steyaert (1952) in the Belgian Congo (Zaire), Brenan (1967) in tropical E Africa, Torre and Hillcoat (1956) in Angola and White (1962) in N Rhodesia (Zambia). Also, in other parts of the tropics, species of Dialium have been delimited, e.g. in Madagascar by Capuron (1968) and in W Malesia by Whitmore (1972) in Peninsular Malaysia and Cockburn (1976) in Sabah. These accounts, however, are mostly of local value and interest. Some of them have only fair evaluation of the relationships of species within the country vis-a-vis species in adjacent countries. The revision of the whole genus by Steyaert (1951), which treats mainly the African species but also makes some reference to Madagascan and Indo-Malesian species, is the only critical study on a wider regional basis before this present one. In addition, there are studies of the relatives of Dialium which will be considered in the following historical review.

The selection of Dialium as the subject of this study, as previously hinted in the preface, came about as an offshoot of the International Legume Conference of 1978. Leguminosae is such a vast family that only a few genera, even within a tribe, have been critically revised on a worldwide basis. This systematic study, therefore, supplements the results arrived at, in particular, in the systematics of the Cassieae (Irwin and Barneby, 1981).

A second but nonetheless important purpose of this study is to set the nomenclature right for all species, especially as basis for enumeration and descriptive study in local Floras. Dialium is composed of trees, most of which have long been commercially exploited. Their correct names are of vital importance to research and utilization in forestry. We know, for example, that in the tropics many species have been previously proposed as new to science based on single collections only. This state of affairs was not only prevalent in Malesia but also in other botanical regions of the tropics (e.g. tropical Africa and the Neotropics). Even at the present time, much of the flora of the tropics falls under the so-called 'pioneer (or exploratory) phase' (Davis and Heywood, 1973: p. 3) -- the phase where much of the activities of botanists are primarily concerned with collection and identification of botanical materials. In many cases, previously published species become so-called 'paper species' or 'dust-bin species' after revisionary work (van Steenis, 1950; Rojo, 1973; Davis and Heywood, 1973; Whitmore, 1976) because variability can now be adequately assessed with abundant materials not available before. For proper utilization, proliferation of names of a single species is confusing not only to one who produces or harvests the trees but also to users of its products. Revision or monographic work, therefore, is necessary not only as an academic exercise but also for economic reasons.

The third important purpose of this study is to reassess the characters in Dialium and find out whether or not previous infrageneric and species delimitations are taxonomically sound in the light of evidences (not only from gross morphology but also from other disciplines, e.g. anatomy and palynology) derived from observations of much more material coming from a wider area than previously available. An attempt is made to explain the characters in evolutionary or phylogenetic terms in order to convey the overall picture of their relationships.

1.2. Materials and Methods

1.2.1. Materials

Herbarium materials used in this study were made available to me through loan from and visits to the herbaria listed in the acknowledgement. A separate identification list is prepared and can be obtained from me on request. Materials used in the study of pollen, pulvinus vascular pattern, anatomy of mature wood and twigs, and stomata types are listed under separate headings in the Appendix.

1.2.2. Methods

1.2.2.1. Wood and twigs

Wood blocks of approximately 1 x 1 centimetre were prepared in such a way that at least one true face each of radial and tangential directions showed on the block. Twigs were cut in convenient lengths of at least a centimetre long. The prepared blocks and twigs were boiled for an hour or more or until determined soft enough to be cut with a microtome knife. The twigs were ready for sectioning as soon as they were fully saturated with water and settled at the bottom of the beaker. The samples were sectioned through a Reichert sliding microtome, at least 20 microns thick. Thinner than 20 microns did not give satisfactory result. The sections were stained with safranin and dehydrated by passing them through alcohol series of 50, 70, 80, 90 and 95 % and absolute, then through xylol and xylene before being mounted. The dehydrated sections were shaped or trimmed to the desired size and mounted on glass slides using Canada balsam and covered with glass slips.

The prepared slides (i.e. dried, cleaned and labelled) were observed using a Wild microscope. The standard procedure of measurement and description summarized in Hafford, Dickison, Massey and Bell (1974;

pp. 167-179) was followed. At least an average of 25 measurements were taken per slide on features measured for diameter, number, height, thickness, etc..

Maceration of wood was done using Jeffrey's solution (equal volume of 10% aqueous nitric acid and 10% aqueous chromic acid). The vials with stoppers were placed in an oven at a temperature of 60°C for at least 24 hours. The washed macerated materials were stained with safranin and temporarily mounted on slides for measurement. An average of 25 measurements of the length of vessels and fibres were taken per slide.

Photomicrographs were taken using a Leitz Orthoplan microscope. For observation of silica inclusions in wood by Scanning Electron Microscope (SEM), the samples were split from blocks and directly mounted (without prior treatment) on SEM stubs using colloidal graphite or quick drying silver paint.

1.2.2.2. Stomata

The leaflets taken from herbarium materials were first boiled for 10 to 20 minutes. Sectioning was done freehand using stainless steel razor blades. A few trials were first made until adeptness was acquired in getting suitable thin sections for observation. The sections were temporarily mounted on glass slides using 50-50 distilled water and glycerine as medium.

1.2.2.3. Pulvinus

Samples were obtained from herbarium sheets. These were taken mostly from fertile specimens, i.e. in fruit or in flower. As expected the petioles (i.e. with pulvini) are generally shorter and smaller in diameter than those that can be obtained from mature sterile materials. The number of samples per species depended upon available herbarium sheets and their suitability for sampling. Some sheets are not suitable

for sampling, either because of historical reasons (e.g. type specimens) or because they are difficult to remove (most glued specimens) without destroying the sheets. Therefore, the samples were carefully taken from loose materials inside pockets, then from those that were particularly hidden under the twigs or the leaves and finally from specimens with a good number of duplicates. The procedure was undertaken as carefully as possible to appear as if nothing had been taken away from the herbarium sheets.

It is assumed that the base of the pulvinus or the whole length of the petiole is the abscission layer -- the part where the petiole separates from the twig. The abscission layer or the base could not be easily determined for some petioles which do not detach with ease from the twigs. In order to get comparable data, sections were observed from the base, the middle and the top points of the pulvinus. The top point is where the usually darker-coloured and wrinkled (in herbarium materials) surface disappears. The middle point is halfway between the base and the top of the pulvinus (see Figs.2.22 and 2.23) and this was first determined and marked with a nick girdled around it before sectioning.

After boiling, the samples were sectioned freehand using stainless steel razor blades. Since the petioles are small and difficult to hold, they were first placed in-between splits of cork for easy handling and to avoid cutting the finger with the razor blade. Sections were placed on observation glass discs and stained with phloroglucinol, then followed by 75% hydrochloric acid to enhance dark colour (red) to vascular tissues. Staining with phloroglucinol is useful especially for quick examination of vascular tissues on samples not requiring permanent mounting on slides (Stern, Brizicky and Eyde, 1969; Rojo, 1978).

The stained sections were temporarily mounted on slides and observed using a Wild microscope. Later on, as familiarity with vascular tissues was acquired, it was no longer necessary to stain and mount the sections on slides but instead place them directly into a petri dish with enough water and observe them under a binocular stereoscope.

1.2.2.4. Pollen

Pollen grains were obtained from anthers of dried herbarium specimens. The flowers were first boiled until soft and placed in a petri dish with enough water for dissection by removing the stamens (anthers) from the sepals and petals. The anthers were then teased with a dissecting needle until the desired pollen grains were separated at the bottom of the dish. The pollen grains were removed by a pipette and transferred to a pointed-bottom test tube and allowed to settle down. Then using again a pipette the water was carefully (i.e. without disturbing the settled pollen grains) removed from the test tube until very little amount of it was left with the pollen grains. Ten samples (clean except for unavoidable bits of anther tissues) at a time were prepared for acetolysis.

The acetolysis method described by Erdtman (1966; pp.6-8) was used. Briefly, it involved boiling the pollen samples in a solution of 9 parts acetic anhydride and 1 part concentrated sulphuric acid to remove extraneous materials that may be coating the exine wall. Boiling was stopped when the solution in the test tube turned blackish brown. The test tubes were then centrifuged and the solution decanted. The samples were washed three times with distilled water, centrifuged and decanted between each washing. After the third washing, the test tubes were placed in an inverted position on a sheet of blotting paper.

The pollen grains were either mounted on slides using glycerine jelly and sealed with paraffin wax (for microscope observation) or mounted on SEM stubs.

For mounting on SEM stubs, alcohol was first poured into the test tubes, then the pollen grains were removed by a pipette and transferred to the surface of a double-sided cello tape adhered to the top surface of a SEM mounting stub. The alcohol was allowed to evaporate and the stubs were made ready for coating with gold before SEM observation.

Unacetolyzed pollen were mounted directly from the anthers to the SEM mounting stubs, i.e. also with double-sided cello tape. To achieve this, the boiled anthers were placed on slides (the excess water being removed by blotting paper) and dissected under the stereoscope. The pollen grains (adhering together and sticking at the end of the needle) were transferred to the stubs. The pollen on the stubs dried soon after they stuck onto the double-sided cello tape.

The prepared stubs were diode-sputter-coated with gold to approximately 0.03 microns thick. These were observed under a Cambridge Stereoscan 150 Scanning Electron Microscope (SEM) at either 10 or 20 KV and the desired pollen were photographed either at polar or equatorial view.

Measurements were made from 2 views: equatorial, to determine the length (P) and width (E_1), and polar, to determine the thickness (E_2). On the average of 15 pollen grains were measured for each specimen examined.

The description mostly followed that of Erdtman (1966). Emphasis was focused on light and scanning electron microscopy of surface features (size, shape, apertures, sculpture patterns). Surface features have been considered to be most likely to provide data readily available to the problem of tribal classification in the Caesalpinioideae (Graham and Barker, 1981). Stratification of the exine wall could

be able to provide useful data but only very few transmission electron microscopy (TEM) sections have been published, i.e. only in Parkinsonia (Larson and Lewis, 1961) and further information is needed before its value to classification in Caesalpinioideae can be assessed (Graham and Barker, 1981). Therefore, no attempt was made by me to study the structural features of the exine wall.

The light photomicrographs were taken using the Leitz Orthoplan microscope. The Wild light microscope was used especially to get measurements of width, length and thickness of pollen grains. Measurement could also be taken from SEM photomicrographs by obtaining the ratio of the length (say diameter of lumina or thickness of the muri) over the length of the bar scale located at the bottom left of the SEM photomicrographs taken with the Cambridge machine. Bar scale, however, is sometimes not provided for in other SEM models.

1.3. Historical Background and Previous Generic Concept

1.3.1. Historical background

The genus Dialium was created by Linnaeus in 1767 to accommodate his D. indum which he described at the same time. At the end of the 18th century only 2 species were added, i.e. D. guianense (Aublet) Sandw.-- originally Arouna guianensis Aublet from tropical America, and D. guineense Willd. from W Africa. Most species later added were discovered during the last and early part of the present century. From 1970s onward, no new species were discovered and D. unifoliolatum Capuron (a Madagascan species) was in 1968 the last species to be published.

The modern classification of Dialium started with De Candolle (1825) in his Prodrumus. He classified Dialium under Leguminosae in the tribe Cassieae. The genus remained in Cassieae until Bentham

(1840) reorganized the Caesalpinioideae into eight tribes. Here, Bentham made changes in Cassieae and placed Dialium in another tribe (i.e. Cynometreae). Nearly three decades later, however, Bentham (1865) in *Genera Plantarum* modified his views and placed Dialium under Cassieae, i.e. in agreement with De Candolle's classification. Oliver (1871) followed Bentham.

In 1964, Schulze-Menz (1964) essentially agreed with De Candolle's and Bentham's concept of the tribe Cassieae. At the same time, however, Hutchinson (1964) found Bentham's classification of the Caesalpinioideae (Cassieae) no longer workable because of new genera added to it through the years whose characters could no longer be fitted in Bentham's various tribes. Hutchinson offered a new and rather radical classification by dividing the Caesalpinioideae into groups without nomenclatural status. The genera under each group are separated by means of keys. In the keys, Dialium showed up in groups 1 and 4, respectively.

In the current classification of the Leguminosae (Polhill and Raven, 1981), Hutchinson's view of grouping of genera is more or less followed within tribal ranks when convenient. In the Cassieae, however, no informal grouping is effected; instead, the tribe is split into subtribal ranks making Dialium the type of one of the five new subtribes (Irwin and Barneby, 1981). Once again, Dialium goes back to Cassieae as de Candolle originally intended.

While the genus is itself well-placed supragenerically, there had been certain disagreements on its infrageneric division. As materials accumulated, variations among subsequently discovered species occur and as early as 1865, Bentham (1865) already recognised one section, i.e. Codarium Sol. ex Vahl (Vahl, 1804). In 1892, Taubert (1892) established two sections: section Arouna Aublet (1775),

for species without petals and section Codarium (which Bentham had previously established as a section), for species with 1 or 2 petals and with a stipitate ovary inserted on the side of the disc. Steyaert (1951) attributed Bentham (1865) to be the first to recognise Arouna as a section but Bentham merely had it as a synonym of Dialium (Polhill, pers. comm.). Over two decades later, Harms (1915) reassessed the two sections above and found the criteria based on the presence and absence of petals artificial. In lieu of these two sections, Harms established three entirely different new sections based on the number of stamens, i.e. Eudialium, for species with 2 stamens, Mesodialium, for species with 5 stamens and Neodialium, for species with 10 stamens. Baker (1930) followed Harms and the sections stood almost four decades until Steyaert (1951) revised Dialium on a wider regional basis, i.e. for all species in Africa and including one species in tropical America. Steyaert also made some reference to Madagascan and Indo-Malesian species in his revision. By about that time, the herbarium materials of Dialium had tremendously increased and for Africa, Steyaert had these materials accessible to him not only from his homebase Brussels (BR) but also in the neighbouring great herbaria of Europe, notably Kew (K), Leiden (L) and Paris (P).

In his revision, Steyaert (1951) found that previous sectional classifications were unsatisfactory. He then established two subgenera based on the type of receptacle, i.e. presence (subgenus Arouna) and absence (subgenus Dialium) of a disc and proceeded to revise the species belonging to the former subgenus only. This subgenus (i.e. Arouna) was subdivided into two sections based on the shape of the filaments, i.e. whether straight (section Recta) or geniculate (section Geniculata) and split these sections into smaller taxonomic groups

down to subsections and subseries by using combination of characters in the flowers and the fruits.

In 1909, the genus Andradia Sim was published (Sim, 1909). Steyaert (1951) failed to notice this genus but Hutchinson (1964) had rightly reduced it to Dialium.

During the course of Steyaert's revision, two new genera, i.e. Dansera and Uittienia were published by van Steenis (1948). These two genera were eventually studied by Steyaert (1953) who reduced them to subgenera under Dialium. Recently, in revising Cassieae, Irwin and Barneby (1981) not only recognised Steyaert's (1953) 4 subgenera but also added yet another subgenus, i.e. Hova, for species in Madagascar which Steyaert (1951) previously included in his subgenus Dialium. At the start of this present study, therefore, Dialium has 5 subgenera, to wit: Arouna, Dansera, Dialium, Hova and Uittienia. As to whether or not the above subgenera hold good, is one of the objectives of this present investigation.

1.3.2. Previous generic concept

Up till the recent study of Irwin and Barneby (1981) and the present one, the concept of the genus had been largely based on the characters of the flower (see Chapter 5, section 5.1). All the taxa (see historical review above) which were at one time considered distinct genera had been reduced to Dialium on the basis of flower characters. We consider them below.

The genus Arouna Aublet (1775), which was described eight years after the publication of Dialium in 1767, is essentially similar to Dialium, i.e. they both have 5 imbricate sepals and 2 stamens but without petals. They only differ one from the other because Arouna has a receptacle with a disc while Dialium has no disc. In 1804,

another genus, i.e. Codarium Sol. ex Vahl (1804) was published. Codarium is similar to Arouna in that they both have a receptacle with a disc. The only difference between the two is the presence of a petal in the former and the absence of it in the latter. On the other hand, Codarium differs from Dialium in two characters, i.e. by having a receptacle with a disc and a petal as well. Towards the turn of the 19th century the distinction of these genera still seemed clear but subsequent discoveries of new species especially from Africa from the beginning of the 20th century onwards changed that. For example, some of the new species added to Arouna like D. angolense Welw. ex Oliver and D. pachyphyllum Harms have flowers with one petal. Dialium englerianum Henriq., added to Codarium, has flowers with 5 petals and 5 stamens. This addition of species largely obscured the distinction of Arouna and Codarium such that even as early as 1865 and 1892, Bentham (1865) and Taubert (1892) reduced the two genera into sections of Dialium.

The genus Andradia Sim (1909: p. 46) with its only species A. arborea Sim exactly matches (i.e. having a disc and 8 to 10 stamens) D. schlechteri Harms (1899) described ten years earlier. Dialium schlechteri (now under section Arouna) and D. englerianum (now under section Codarium) deviate from the general pattern of the majority of Dialium species which possess only two stamens.

The relatively recently-created genus Dansera van Steenis (1948) differs from Dialium by having 3 sepals instead of 5. Probably, van Steenis was not aware at that time that a Madagascan species, i.e. D. madagascariense Baillon (1888) based solely on a plate has 3 sepals just like Dansera. It is also possible that van Steenis assumed Baillon's species to have 5 sepals because the description provided later by Drake del Castillo (1902: p. 95) did not mention the number of sepals at all.

From the above discussion, it can be seen that the various 'genera' were only founded on the characters of the flower. However, there is so much variation in the flower that here I find that its characters, particularly of the perianth and androecium, cannot be used as basic determinants of Dialium. The genus must be founded on conservative characters, especially of the fruits (see discussion in Chapter 5) which bind the 'genera' together into one coherent group. I agree with Irwin and Barneby (1981) who had originally reached the same conclusion.

1.3.3. The meanings of the word Dialium

We now discuss the different meanings of the word 'Dialium' of which one meaning pertains to a part of the flower.

Why Linnaeus used Dialium as a generic name for his only plant which supposedly originated from India is not certain. A number of meanings or interpretations of the word 'Dialium' are shown below.

- A Latin form of a Greek plant name 'Dialion' used by Linnaeus indiscriminately for this genus (Voorhoeve, 1979: p. 179).

- Dialium, derived from a Greek word for 'destroyed' which refers to petals that soon fall off (Keay, Onochie and Stanfield, 1964: p. 24).

- Dialium, Greek 'to destroy' from the ancient use of the plant against bed bugs (Nielsen, 1965: p. 112).

- A name attributed to 'Dialis', a priest of Jupiter, to signify high rank (Gunawardena, 1968).

- A Greek plant name for a kind of heliotrope (Corner, 1940: p. 393; Whitmore, 1972: p. 255).

There could be other meanings of the word 'Dialium' but what is certain is that it is a Greek word. Taxonomically, the interpretation

by Keay, et al., seems the most logical one because petals in Dialium flowers (if they happen to have petals at all) do easily fall off when the buds open. It is possible Linnaeus could have thought D. indum has petals but found none when he examined them. The facts now reveal that the majority of Dialium species are apetalous (about 63%) and the rest with 1 (22%), 3 (11%) or 5 (4%) petals, respectively. As to Dialium being a heliotrope or used against bed bugs, these are not supported by facts.

PART II. GENERAL OBSERVATIONS

2. THE GENUS DIALIUM

This chapter deals with the general observations on morphology, anatomy and palynology. Data on cytology and phytochemistry are compiled from literature. Important taxonomic characters are summarised in Table 2.1, of which the features of the flower, pollen, pulvinus and wood are especially discussed in Chapter 5 for their taxonomic significance and/or relationships at the infrageneric level.

2.1. Morphology

2.1.1. Habit (Fig. 2.1)

All species of Dialium are trees, small to large-sized or rarely attaining a stature of shrub (D. orientale Baker f.), not climbing, unarmed. One herbarium specimen (Prance, et al. 10662) of D. guianense from the Brazilian Amazonia was collected from a 'liana'. This is highly doubtful, but it has to be reconfirmed by subsequent collection particularly from the same area.

The crown is usually roundish, or when the upper bole is forked, rather dome-like or spreading. It is usually dense or congested (Fig. 2.1 A). The branching is sympodial, the branches usually at sharp angle with the axis. The bole is straight or sometimes crooked, more or less cylindrical with a rather gradual taper but usually fluted just above the buttresses.

The majority of the species have buttresses which are thin and spreading near the ground (Fig. 2.1 B); others are narrow with more or less rounded edges. On the trees I have observed in the Singapore Botanic Garden and in the arboretum of the Forest Research Institute at Kepong, Peninsular Malaysia (both places on dry land), buttresses are about a metre high from the ground. They are much higher and

Fig. 2.1. Habit of D. platysepalum Baker. A, crown of the tree where herbarium material (FRI 11458) and fruits were taken; B, buttresses of a tree in a non-inundated area. All trees were observed in Kepong, Peninsular Malaysia.



planklike in trees growing in other habitats (Snythies, 1965: p. 78, plate 26; Corner, 1940: p. 394; 1978: p. 26). Some African species (D. dinklagei Harms, D. reygaertii De Wild., D. pachyphyllum and D. zenkeri Harms) do not have buttresses or only slightly marked (Steyaert, 1952).

The outside bark is rather smooth, generally pale-coloured, greyish to creamy or yellowish-brown and usually with whitish irregularly outlined lichen patches (Fig. 2.1 B) and in old trees sometimes scaling off. When slashed the bark is more or less a centimetre thick, the inner part pinkish to brownish or pinkish fawn, smells of bean and exudes reddish-brown sap which soon clots to a thick reddish-black resin. The reddish-brown exudate had been noted by Steyaert (1952) and Aubréville (1968; 1970) in African species, Capuron (1968) in Madagascan species, Corner (1940) and Whitmore (1972) in Peninsular Malaysian species, Cockburn (1976) in species of Sabah and van Steenis (1948) in D. procerum (Steenis) Stey. I have observed this in D. indum and D. platysepalum Baker in Peninsular Malaysia. Some field notes also indicated occurrence of reddish-brown exudate from the inner bark of the trees from which herbarium materials were collected.

The architectural model of Dialium has not as yet been reported. The photograph of the tree (Fig. 2.1 A) offers only some hints. The obviously older branch which plagiotropically extends to the right is being superposed at its base by the younger branch which assumes a more or less vertical position. The older branch becomes a lateral branch while the younger one acts as the erect axis. This growth pattern, i.e. the axis contributes part trunk, part branch and the proximal part becoming erected, falls under the Troll model (Hallé and Oldeman, 1970; Hallé, Oldeman and Tomlinson, 1978: p. 242) of tree architecture. A majority among all trees belong to this model

Table 2.1 Legend

AP - Sect. Arouna subsect. Pirula

AI - Sect. Arouna subsect. Indumentosa

CO - Sect. Codarium; HO - Sect. Hova; DA - Sect. Dansera

AF - Africa; AM - America; WM - West Malesia (including Lower Burma, Thailand, Laos, Cambodia and S Vietnam)

MA - Madagascar; SL - Sri Lanka (including Kerala, India)

na - not available

- + - 1 leaves imparipinnate, 2 inflorescence terminal, 3 receptacle with disc, 4 sepals five, 5 petals present, 6 stamens two, 7 anther apex on the adaxial side acute, 8 anther abaxial side humped, 9 filaments straight to slightly curved, 10 pollen striate, 11 fruit more or less ellipsoid or globose, 12 exocarp thin and brittle, 13 and 14 axial parenchyma cell inclusion of wood and twig silica only, 15 mid pulvinus ridge bundle generally one
- - 1 leaves unifoliolate, 2 inflorescence axillary, 3 receptacle with disc absent, 4 sepals three, 5 petals absent, 6 stamens more than two, 7 anther apex on the adaxial side retuse, 8 anther abaxial side flattish, 9 filaments geniculate, 10 pollen reticulate, 11 fruit compressed, 12 exocarp thick, 13 and 14 axial parenchyma cell inclusion of wood and twig oxalate crystal only, 15 mid pulvinus ridge bundle generally two
- / - 1 leaves imparipinnate and partly unifoliolate, 5 one petal sometimes or aberrantly present, 7 anther apex deeply cleft, 8 anther abaxial side slightly humped, 13 and 14 axial parenchyma cell inclusion of wood and twig predominantly silica and partly together with oxalate crystals
- o - 7 anther on the adaxial side not acute, nor retuse, nor deeply cleft

Table 2.1. Summary of important taxonomic characters in Dialium.

Subgen./Sect. Species	Region	Leaves	Inflo- rescence		F	l	o	w	e	r	s	Pollen	Fruit	Wood	Twig	Petiole
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
AROUNA/AP																
schlechteri	AF	+	+	+	+	-	-	+	+	+	+	+	+	/	/	-
pobeguiniif	AF	+	+	+	+	/	-	+	+	+	+	+	+	na	/	+
bipindense	AF	+	+	+	+	-	+	+	-	+	+	+	+	/	/	+
guianense	AM	+	+	+	+	/	+	+	+	+	+	+	+	/	/	+
dinklagei	AF	+	+	+	+	-	+	+	+	+	+	+	+	/	/	+
orientale	AF	+	+	+	+	-	+	+	+	+	+	+	+	+	/	-
holtzii	AF	+	+	+	+	-	+	+	+	+	+	+	+	na	/	+
reygaertii	AF	+	+	+	+	-	+	+	+	+	+	+	+	na	+	+
excelsum	AF	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+
AROUNA/ AI																
pentandrum	AF	+	+	+	+	+	-	+	+	-	+	-	+	na	/	+
polyanthum	AF	+	+	+	+	+	+	+	+	-	+	-	+	/	+	+
tessmannii	AF	+	+	+	+	+	+	+	+	-	+	-	+	na	/	+
angolense	AF	+	+	+	+	+	+	+	+	-	+	-	+	na	/	+
pachyphyllum	AF	+	+	+	+	+	+	+	+	-	+	-	+	/	/	+
AROUNA/ CO																
englerianum	AF	+	+	+	+	+	-	-	-	+	-	+	+	+	/	-
guineense	AF	+	+	+	+	+	-	-	-	+	-	+	+	/	+	+
zenkeri	AF	+	+	+	+	+	-	-	-	+	-	+	+	+	+	+
DIALIUM																
hydnocarpoides	WM	+	+	-	+	-	+	o	-	+	-	+	+	na	-	-
platysepalum	WM	+	+	-	+	-	+	o	/	+	-	+	+	-	-	-
ovoideum	SL	+	+	-	+	-	+	o	/	+	-	+	+	-	-	-
cochinchinense	WM	+	+	-	+	-	+	o	/	+	-	+	+	-	-	-
indum	WM	+	+	-	+	-	+	o	/	+	-	+	+	-	-	-
bursa	WM	+	+	-	+	-	+	o	/	+	-	+	+	-	-	-
DANSERA/HO																
occidentale	MA	+	-	-	-	+	-	/	+	+	-	+	+	/	+	-
septentrionale	MA	-	-	-	-	+	-	/	+	+	-	+	+	na	+	-
madagascariense	MA	+	-	-	-	+	-	/	-	+	-	+	+	+	+	-
unifoliolatum	MA	-	-	-	-	+	-	/	-	+	-	+	-	+	+	-
DANSERA/DA																
kunstleri	WM	+	-	-	-	-	-	o	-	+	-	+	-	+	+	-
trifoliolatum	WM	/	-	-	-	-	-	o	-	-	-	+	-	+	+	-
procerum	WM	-	-	-	-	-	-	o	-	+	-	+	-	+	+	-

and in Malesia, it is represented by many leguminous taxa (Hallé, et al., 1978). The tree described above must have had the same growth pattern while still young. The architectural model of a tree, however, can only be judged accurately when the trees are still young and undisturbed.

2.1.2. Leaves (Figs. 2.2 - 2.4)

Dialium leaves are generally compound and imparipinnate. It is only in subgenus Dansera where species (i.e. D. occidentale var. septentrionale (Capuron) Rojo, D. procerum and D. unifoliolatum) with unifoliolate leaves occur. The petioles are terete except at the pulvinus where they are broader and more or less flattish at the adaxial side. Lengths of rachis (including the petiole) are generally from 5 to 8 cm long or sometimes to 16 cm long. Two species (D. hydnocarpoides de Wit and D. platysepalum) sometimes have rachises reaching 20 to 24 cm long. Species with trifoliolate leaves like D. angolense or D. kunstleri Prain var. trifoliolatum (de Wit) Rojo have short (to 3.5 cm) rachises.

In imparipinnate leaves, the number of leaflets varies from 1 (D. angolense) to 9 pairs (D. dinklagei and D. hydnocarpoides) but the majority of the species have from 2 to 5 pairs of leaflets. Leaflets are usually alternate, sometimes subopposite or rarely opposite but generally not more than 1 or 2 pairs are opposite in any given leaf. The petiolules are generally from 2 to 4 mm long and are usually wrinkled when dry.

The blades are generally subcoriaceous, sometimes stiffly coriaceous (D. indum var. bursa (de Wit) Rojo, D. madagascariense) or more or less chartaceous (D. bipindense Harms, D. cochinchinense Pierre, D. ovoideum Thwaites). The colour of the blades when dry is generally

Fig. 2.2. Outlines of leaflets of some Dialium species in section Arouna subsection Pirula. a, D. dinklagei (Vigne 134, Ghana); b, D. excelsum (Louis 1159, Zaire); c, D. guianense (Lindeman 8463a, Surinam); d, D. schlechteri (Barbosa and Lemos 7962, Moçambique). Illustrations from left to right represent terminal, middle and base leaflets (taken from a rachis), respectively. All X1.

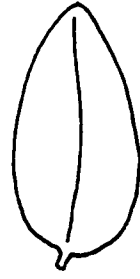
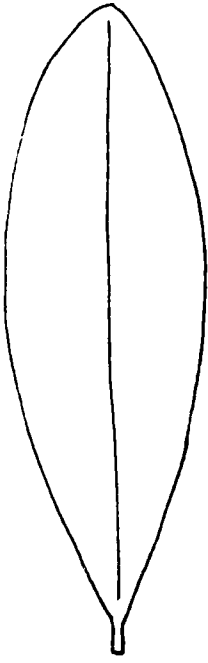
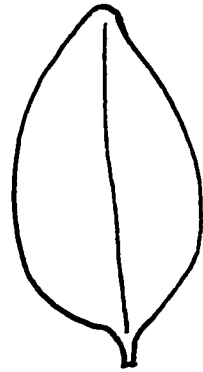
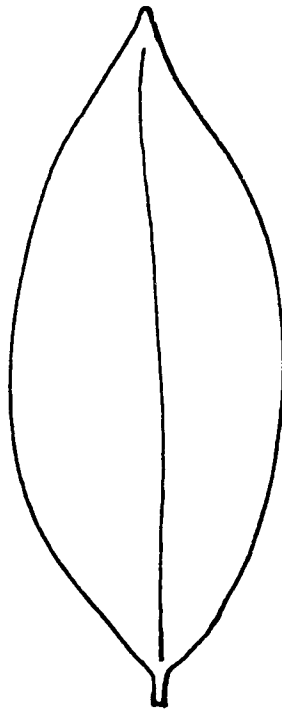
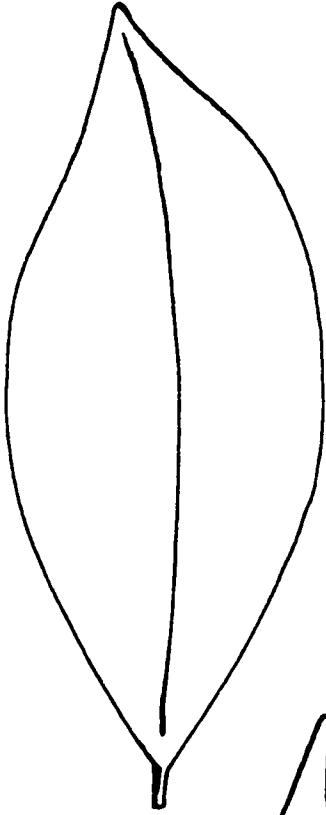
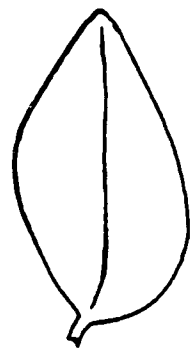
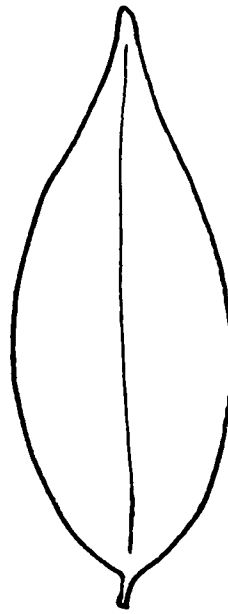
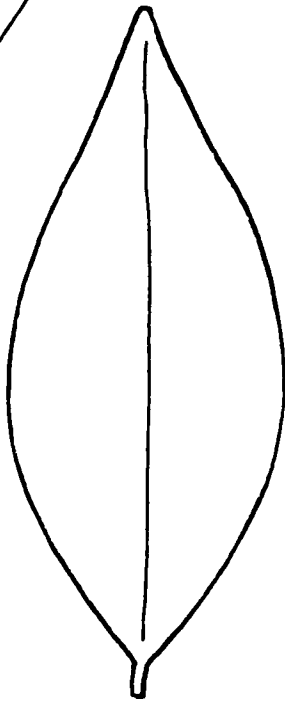
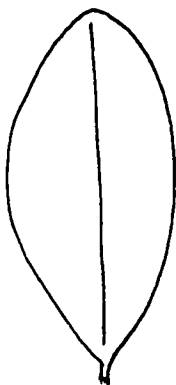
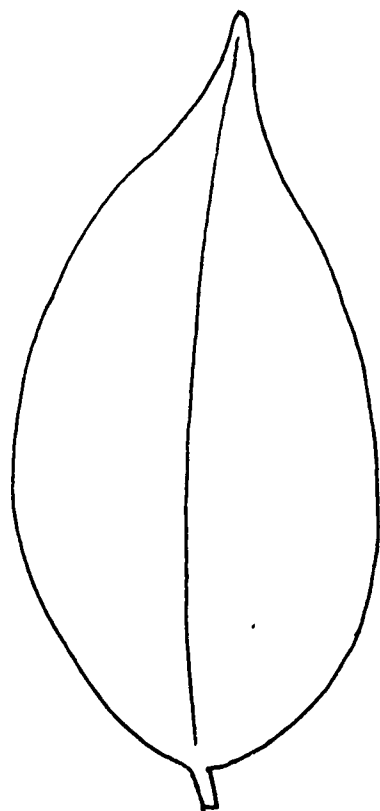
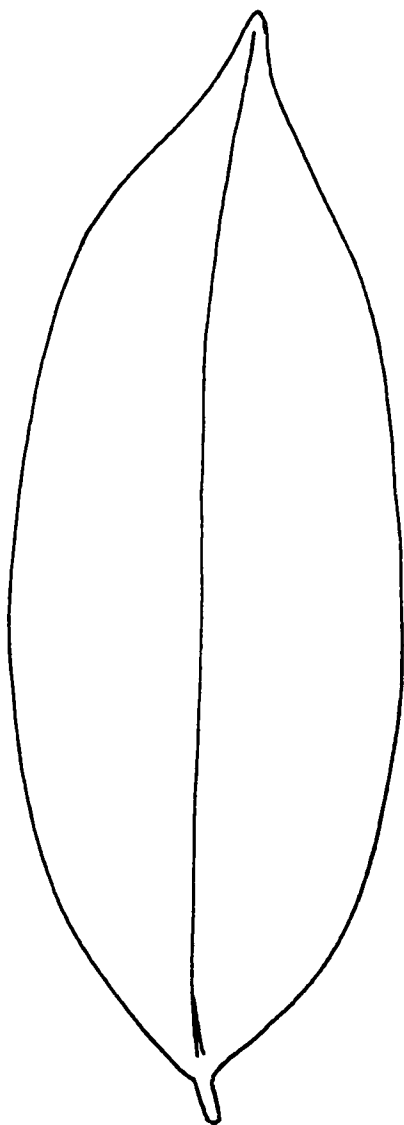
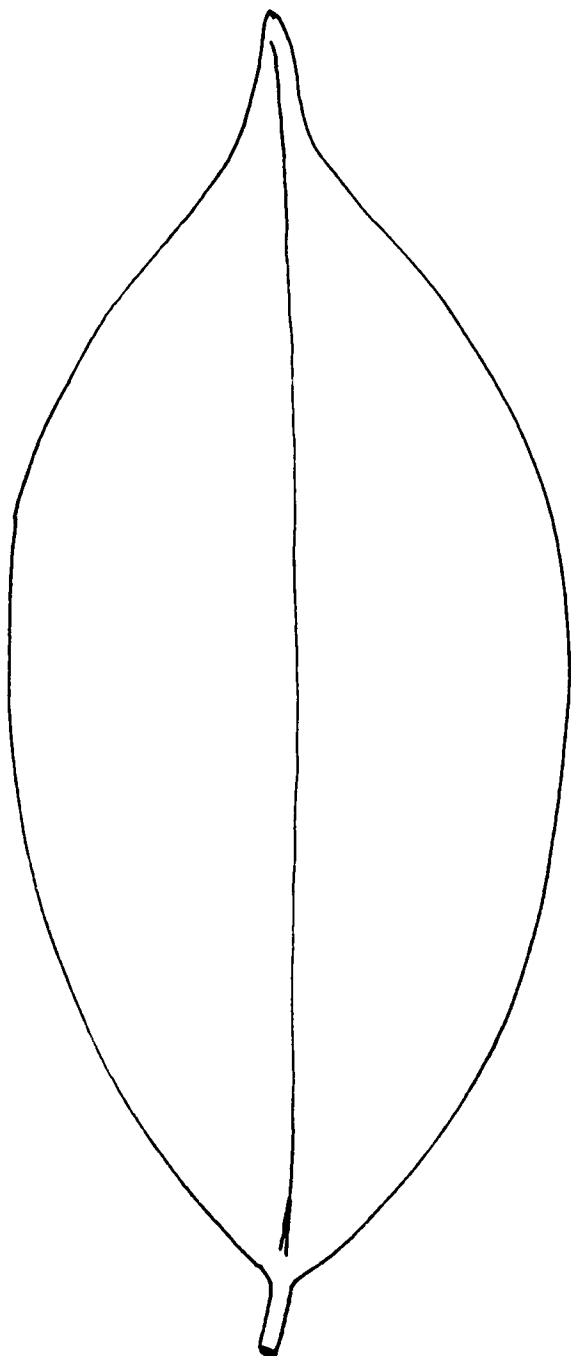
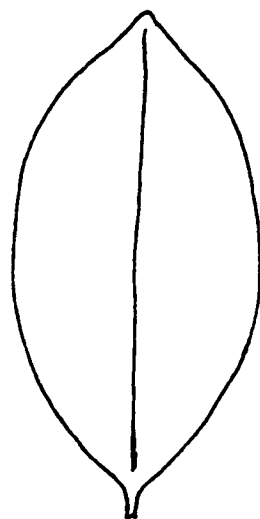
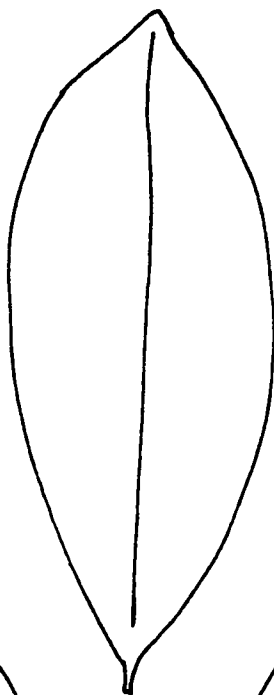
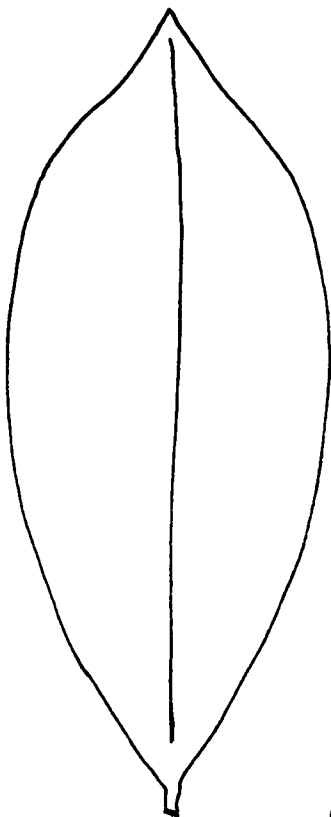
a**b****c****d**

Fig. 2.3. Outlines of leaflets of some Dialium species in section Arouna subsection Indumentosa (a) and section Codarium (b and c). a, D. pachyphyllum (Louis 2268, Zaire); b, D. guineense (FHI 16756, Nigeria); c, D. englerianum (White 3476, Zambia). Illustrations from left to right represent terminal, middle and base leaflets (taken from a rachis), respectively. All X1.

a



b



c

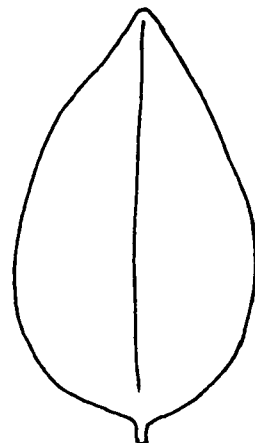
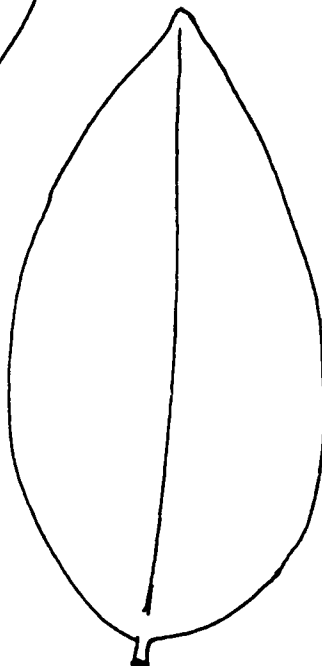
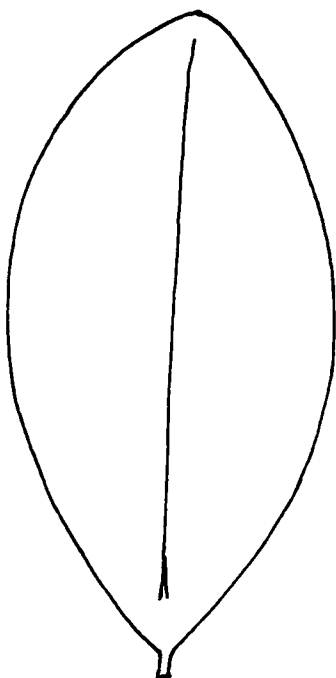
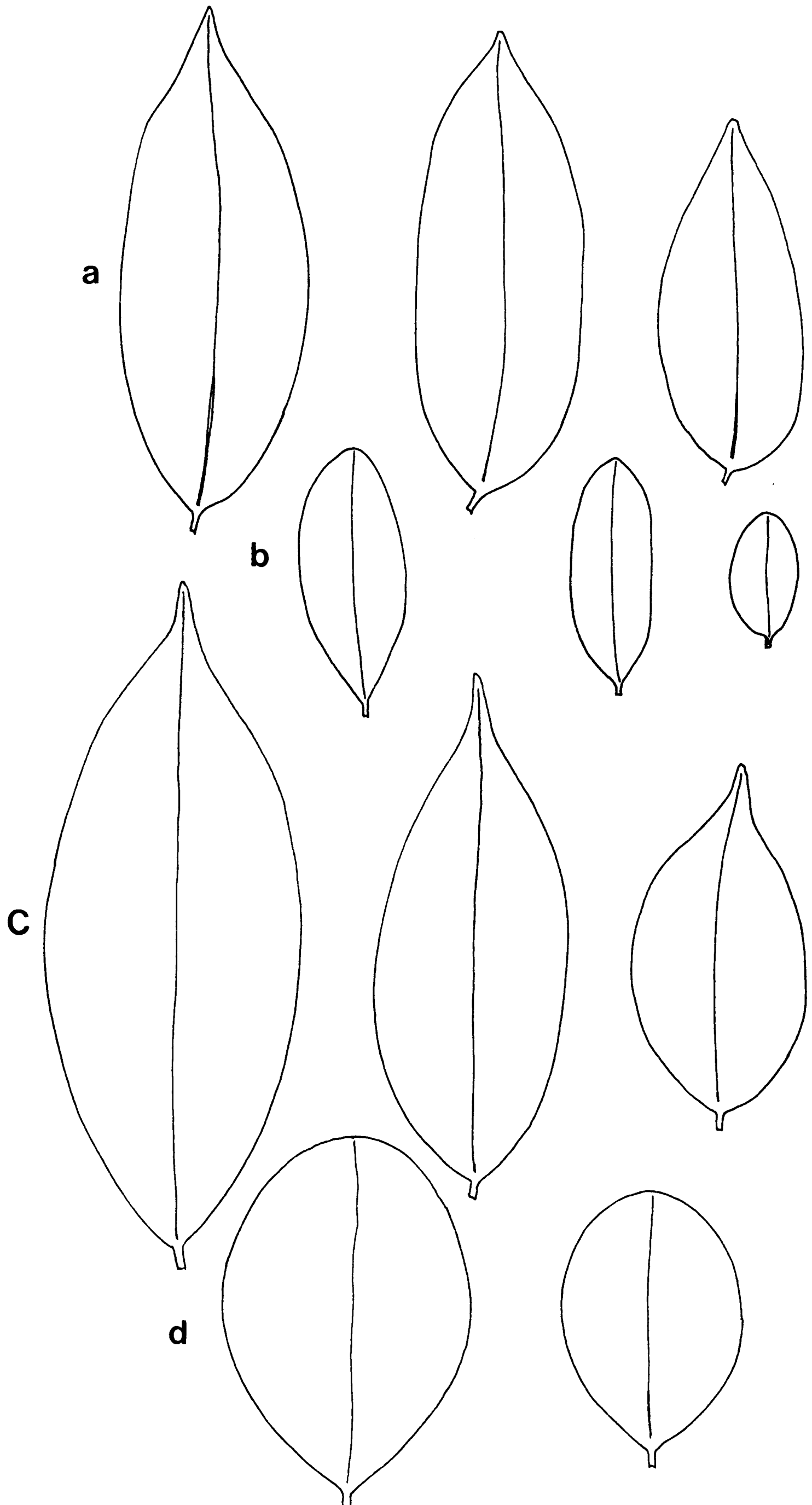


Fig. 2.4. Outlines of leaflets of some Dialium species in subgenera Dialium (a and b) and Dansera (c and d). a, D. platysepalum (SAN 30163, Sabah); b, D. hydnocarpoides (T. 540. 29/4, Sumatra); c, D. kunstleri (SAN 53516, Sabah); d, D. madagascariense (8625 SF, E Madagascar). Illustrations from left to right represent terminal, middle, and base leaflets (taken from a rachis), respectively. All X1.



greyish brown with a greenish tinge and the upper surface is usually darker-coloured than beneath. A Zairean species (D. reygaertii) has usually greenish leaflets when dry.

The blades are entire. The shapes of the blades are generally elliptic to ovate-lanceolate (see Figs. 2.2 - 2.4) with the terminal leaflet differing from the others in being widest above the middle. Variations in shape are few and leaflets may be oblong as in D. dinklagei (Fig. 2.2 a, the middle leaflet) and D. hydnocarpoides (Fig. 2.4 b, the middle leaflet) or obovate as in some specimens of D. madagascariense (Fig. 2.4 d). There is always some variation between the leaflets of a single leaf. In terminal leaflets, the blades are usually broadly elliptic, the middle leaflets usually ovate-lanceolate and sometimes oblong and the lower ones usually ovate. The majority of the blades are symmetrical but a few are asymmetrical. The blades of D. schlechteri (see Fig. 2.2 d, the middle and lower leaflets) are mostly asymmetrical. The base of the blades is generally obtuse to more or less rounded, sometimes acute to slightly cuneate; the apex is usually long acuminate, sometimes acute or rarely rounded.

The venation pattern is eucamptodromous (Hickey and Wolfe, 1975; Hickey, 1979), i.e. the secondary veins are upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondary veins by a series of cross veins without forming prominent loops (see Figs. 7.4 and 7.7). They are usually distinct on both sides of the leaflets but in D. platysepalum group 'platysepalum', they are faint on the undersurface of the blade due to thick covering of hairs. In D. procerum (subgenus Dansera) sometimes the last two to three pairs of secondary veins arc sharply towards the top and merge at the apex (see Fig. 7.7 A). Reticulations are distinctive in some African (subsection Indumentosa) and Madagascan (D. madagascariense) species where they are distinctly areolate. Most species, however, have

laxly set tertiary veins which are clearly visible but not prominently raised.

2.1.3. Stomata (Fig. 2.5)

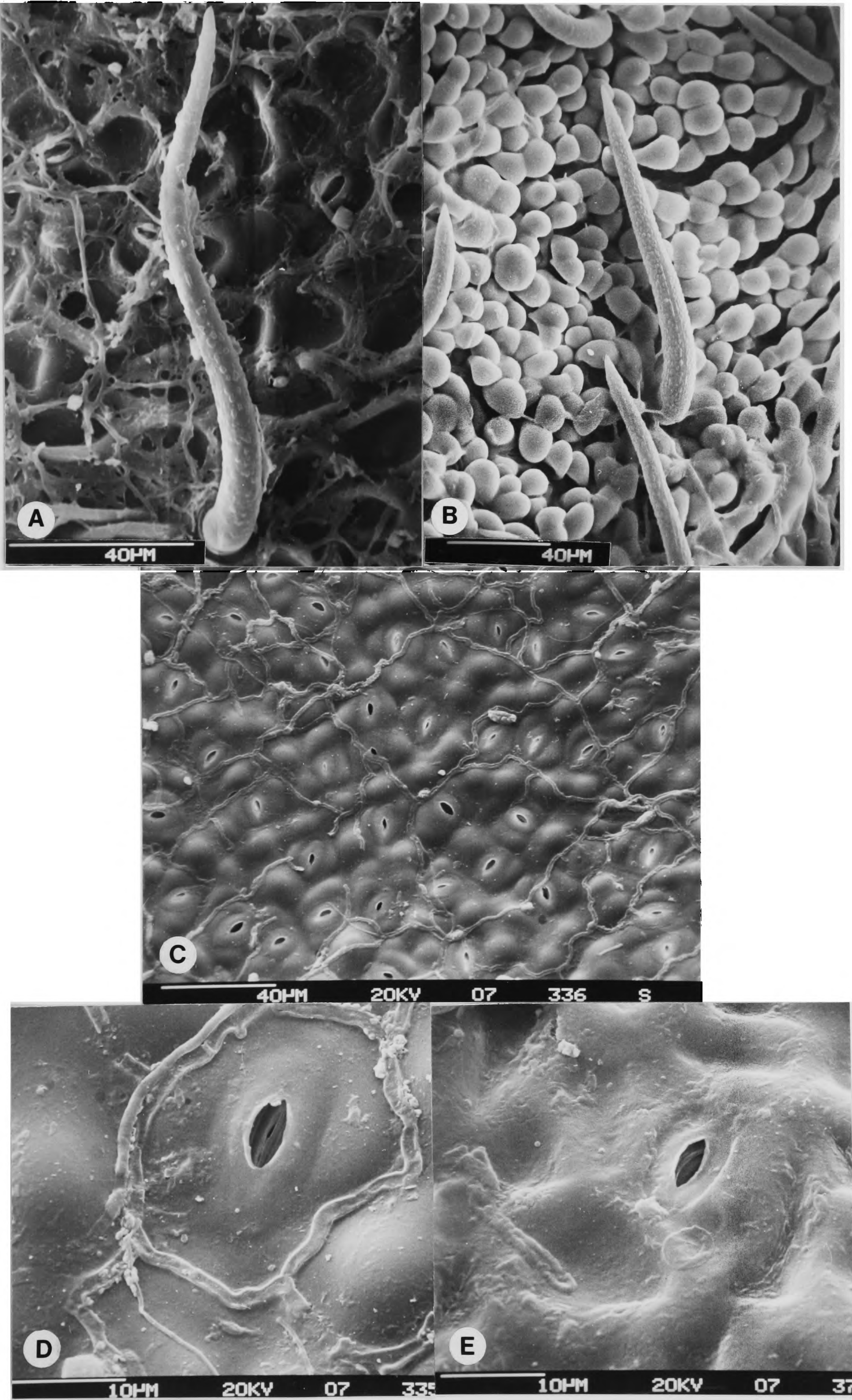
Watson (1981) stated that the stomata in Caesalpinioideae are mainly abaxial, the adaxial ones being scarce and confined to zones closely adjoining the veins. In this study, observations of stomata were focused on the abaxial side of the leaflets.

The general pattern of the stomata in Dialium is paracytic -- a type where the subsidiary cells are parallel to the long axis of the pore and the guard cells. Slight variations of the paracytic type were observed even within a single microscope field which confirms the findings of Metcalfe and Chalk (1950) in the stomata of the Caesalpinioideae. The stomata in SEM view are shown in Fig. 2.5 C, D & F. The pores are always narrowly elliptic. The outer stomatal ledge (rim) is slightly sunken (Fig. 2.5 E) in relation to the surrounding epidermal surface. The guard cells are faintly outlined by the depression between the outer stomatal rim and the inner margin of the guard cell itself (Fig. 2.5 D, at left of the pore). Although it is rather difficult to distinguish the guard cells at high magnification in the SEM photomicrographs, they can be seen at lower magnification (Fig. 2.5 C) as raised cells between depressions. The guard cells can be clearly seen in an epidermal preparation under a light microscope. The subsidiary cells can also be seen very distinctly in the low power photomicrographs of the leaflet surface (Fig. 2.5 C) as raised cells parallel to the guard cells.

In the review of the stomata of the Caesalpinioideae, Watson (1981) indicated that numerous species and genera show a preponderance of paracytic stomata, while others have them mostly anomocytic, actino- or cyclocytic, or mixtures. As far back as 1908, Solereder (1908) noted that the stomata in Dialium (as well as Apuleia and Dicorynia of the Dielliinae, see Chapter 3) are of the paracytic type. Metcalfe and Chalk (1950) and this study confirmed Solereder's findings.

Fig. 2.5. Hairs and stomata (SEM photomicrographs).

A, D. guianense (Irwin et al, 55368, Surinam); B, D. englerianum (White 2987, Zambia); C-D, D. madagascariense (2945 SF, Madagascar); E, D. guianense (Krukoff 6262, Brazil).



2.1.4. Stipules

Stipules are small, usually less than a centimetre long, slightly falcate and soon caducous. They are normally absent in herbarium materials and therefore not of particular taxonomic use.

2.1.5. Indumentum and other leaf surface features (Fig. 2.5 A and B)

Hairs are found on young parts of twigs, inflorescences, leaves especially when young, parts of the flowers and surfaces of exocarps. They are uniformly simple and unicellular. The only exception is D. tessmannii Harms in which the hairs on the ovary are interspersed with some different whitish glandular ones which have not been studied in detail.

Hairs on the undersurface of the leaflets are shown in Fig. 2.5, A and B. Under the SEM at c. X115 - X130 the surface of these hairs is sparsely set with dot-like whitish protruberances which are reminiscent of lenticels on twigs. But under ordinary light microscope at c. X100 these 'protruberances' could not be observed.

In D. platysepalum, Solereder (1908) and Metcalfe and Chalk (1950) noted spear-shaped hairs provided with one or two tooth-like prongs towards the apex. I have examined a number of specimens of this species but I was not able to observe such hairs.

On the undersurface of leaflets the hairs of the majority of species are more or less sparsely set and ordinarily not distinctive except in some specimens of D. platysepalum where they are densely set which often obscure the veinlets.

The epidermal abaxial surfaces of representative specimens of some species from each section and/or subgenus presently recognised were examined under the SEM. The majority of them show plain patterns (Fig. 2.5, A and C). However, in one species (D. englerianum, Fig.

2.5, 3) the abaxial surface shows distinct wart-like blobs which can be referred to as globular papillae (Theobald, Krahulik and Rollins, 1979; Wilkinson, 1979).

Depending on the taxa under investigation, indumentum and other leaf surface features provide useful information to delimit taxa. Solereder (1908), Metcalfe and Chalk (1950), Theobald, et al. (1979) and Wilkinson (1979) recognised the value of hairs, trichomes and scales to distinguish one group of plants from another. Trichome characters, for example, are now commonly used in routine determination of members of the Brassicaceae and the genera Combretum, Rhododendron and Epilobium (Stace, 1980). In the series of studies by Stace (1965, 1969, 1973), he found that trichome anatomy in the Combretaceae is of immense significance in classification at all levels, from family down to separation of species and even varieties and has led to the improvement of tribal classification within the family and an improved subgeneric and sectional classification within the largest genus, i.e. Combretum. The epidermal abaxial leaf surfaces of species in the Anacardiaceae have been studied and photographed under SEM which revealed important taxonomic features to separate generic taxa or sometimes even as diagnostic characters for separating species (Ding Hou, 1978). In a more recent study, Pannell (1980) found that the structure and distribution of the indumentum on the leaves is frequently diagnostic of a species in the genus Aglaia (Meliaceae). It has therefore been possible for her to write a key using the leaf characters alone of species of Aglaia in Peninsular Malaysia. The use of indumentum and other characteristic features of leaf surface has been reviewed by Davis and Heywood (1973), Theobald, et al. (1979) and Wilkinson (1979).

On the other hand, hairs and other leaf surface features seem not taxonomically useful in the Leguminosae. In general terms, the hairs in Leguminosae are simple and unicellular (Solereider, 1908; Metcalfe and Chalk, 1950). For example, a thorough investigation of epidermal surfaces of the leaflets in Erythrina (Ayensu, 1977) failed to establish any pattern which could separate taxa either at the higher or at the species level. In Caesalpinioideae, other types of hairs or features such as papillae occur but they are displayed in few and unrelated groups (Watson, 1981). Observations of indumentum and other surface features of leaflets in this study agree with the above observations in Leguminosae. In Dialium, types of hairs or trichomes cannot be used to separate infrageneric taxa nor species. The globular papillae in D. englerianum is rather an exception.

2.1.6. Inflorescences (Figs. 2.6 - 2.8)

Inflorescences are paniculate. The panicles are either terminal or axillary or both. Terminal panicles are usually many-branched and long with one or two lower primary branches subtended by leaves (Fig. 2.6). Axillary panicles are short and those arising from the axils of old nodes are usually in fascicles.

Species do not strictly possess terminal or axillary inflorescence. Both inflorescence types occur in all species although one type predominates over the other and vice-versa. For example, in D. indum (a species which is primarily with terminal inflorescence) axillary panicles occur (Fig. 2.7, see arrow). This is not uncommon in subgenera Arouna and Dialium. On the other hand, in subgenus Dansera (ordinarily with axillary panicles) terminal panicles also occur (Fig. 2.8, see arrow).

As can be deduced from herbarium materials, all species have erect inflorescences. There is no information from field notes to indicate whether inflorescences are pendulous.



Fig. 2.6. A terminal panicle with lower primary side branches supported by leaves. D. dinklagei (Vigne 194, Ghana), x $\frac{1}{2}$.

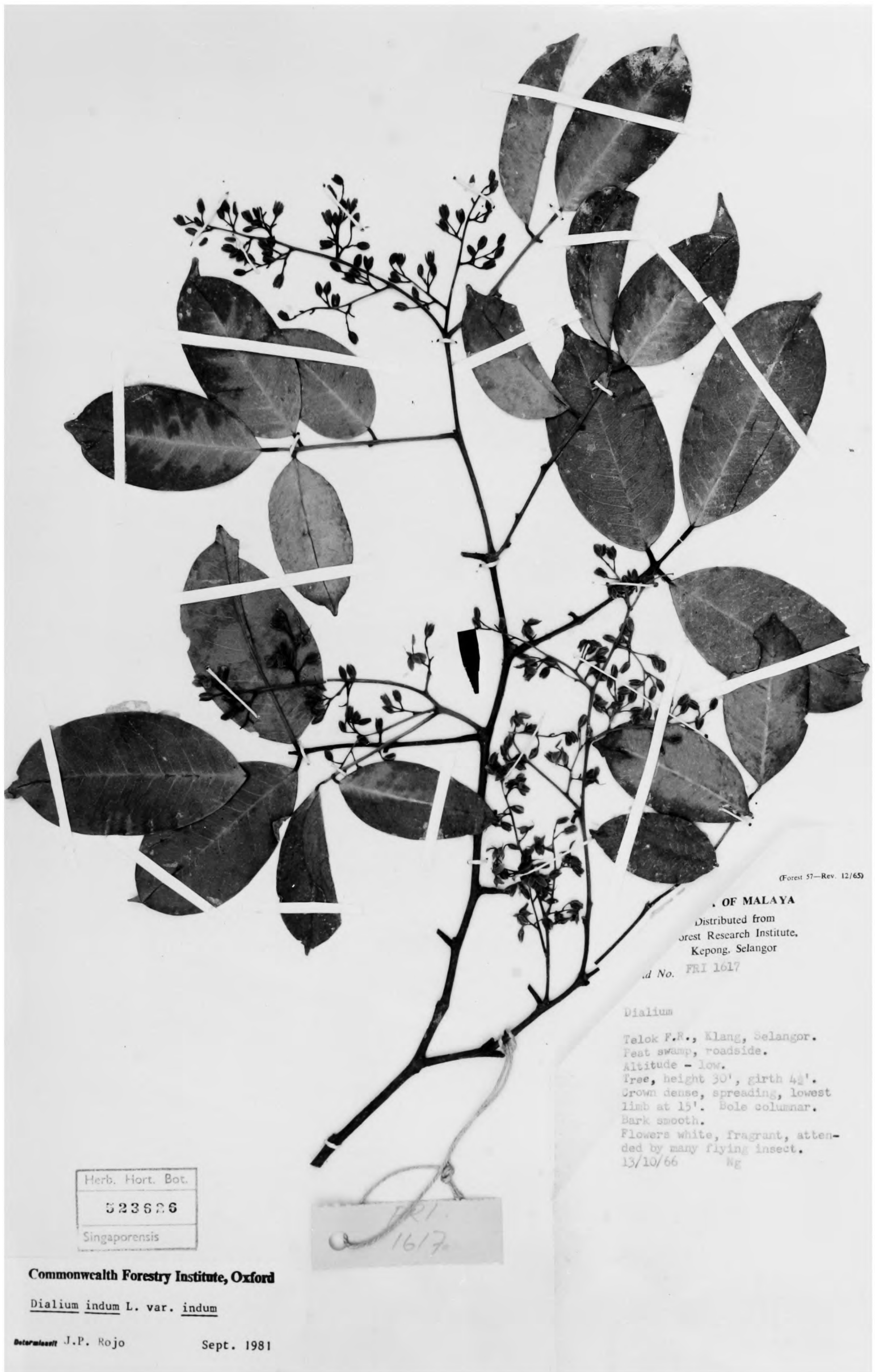


Fig. 2.7. A mixed terminal and axillary (see arrow) panicles.

D. indum var. *indum* (FRI 1617, Peninsular Malaysia), x $\frac{1}{2}$.



Commonwealth Forestry Institute, Oxford

Dialium procerum (Steenis) Stey.

Determined J.P. Rojo

Sept. 1981



TYPE
 Dansera procera
 v. Steenis

Revised for Flora Malesiana

Dansera procera v. Steenis
 Type

det. H. C. D. de Wit 195 2

No.

Communic. ex. Herb. Hort. Bot. Bog.

Dialium

Archipel. Ind. Sumatra Res Palembang
 Rematang Mir act. 46

Leg. Beschtaepstation no. 1753900 18/5
 det.

201280

Fig. 2.8. A terminal inflorescence (see arrow) in a species with axillary panicles. *Dialium procerum* (117P.3P.390, Sumatra), x $\frac{1}{2}$.

The general appearance of inflorescences in the herbarium is ferrugineous to dark brown. This is partly enhanced by the brown colour of the hairs when dry.

2.1.7. Bracteoles

Bracteoles are soon caducous. In the herbarium, bracteoles can only be seen subtending young flower buds. These are rather deeply concave at the base, acute at the apex and hairy on the outside. The shape (more or less triangular) and size (generally 4-5 mm long by 2-3 mm wide) are uniform in all species.

2.1.8. Flowers (Figs. 2.9 - 2.13)

2.1.8.1. General

Flowers are hermaphrodite, weakly zygomorphic or very rarely semi-regular? (in subgenus Dansera). The flower buds are pedicellate, the pedicels inarticulate. The sizes (in bud) are more or less uniform except in D. occidentale (Capuron) Rojo (Fig. 2.13 A), D. bipindense and D. unifoliolatum which are small (c. 2.5-3.5 mm long by 1.5-2.5 mm wide) and in D. platysepalum (Fig. 2.12 B) and D. tessmannii which are big (c. 5-6.5 mm long by 4-5.5 mm wide). The majority of the flower buds fall within the size-range from 3.5-5.5 mm long by 2-3 mm wide (Figs. 2.9 - 2.11). The shapes of the flower buds are generally trulloid* (see Figs. 2.9 A and 2.10 A) in African species and ovoid-ellipsoid in Madagascan (Fig. 2.13 A and B) and Indo-Malesian (Fig. 2.12 A and B) species. All buds are hairy outside but in Madagascan (section Hova) species (Fig. 2.13 A and B), the hairs are rather sparsely set and glabrescent. In the rest of the species the hairs are densely set and persistent.

* A solid with widest axis below middle and with straight margins; ovoid but margins straight and angled below middle (Radford, et al. 1974: p. 129).

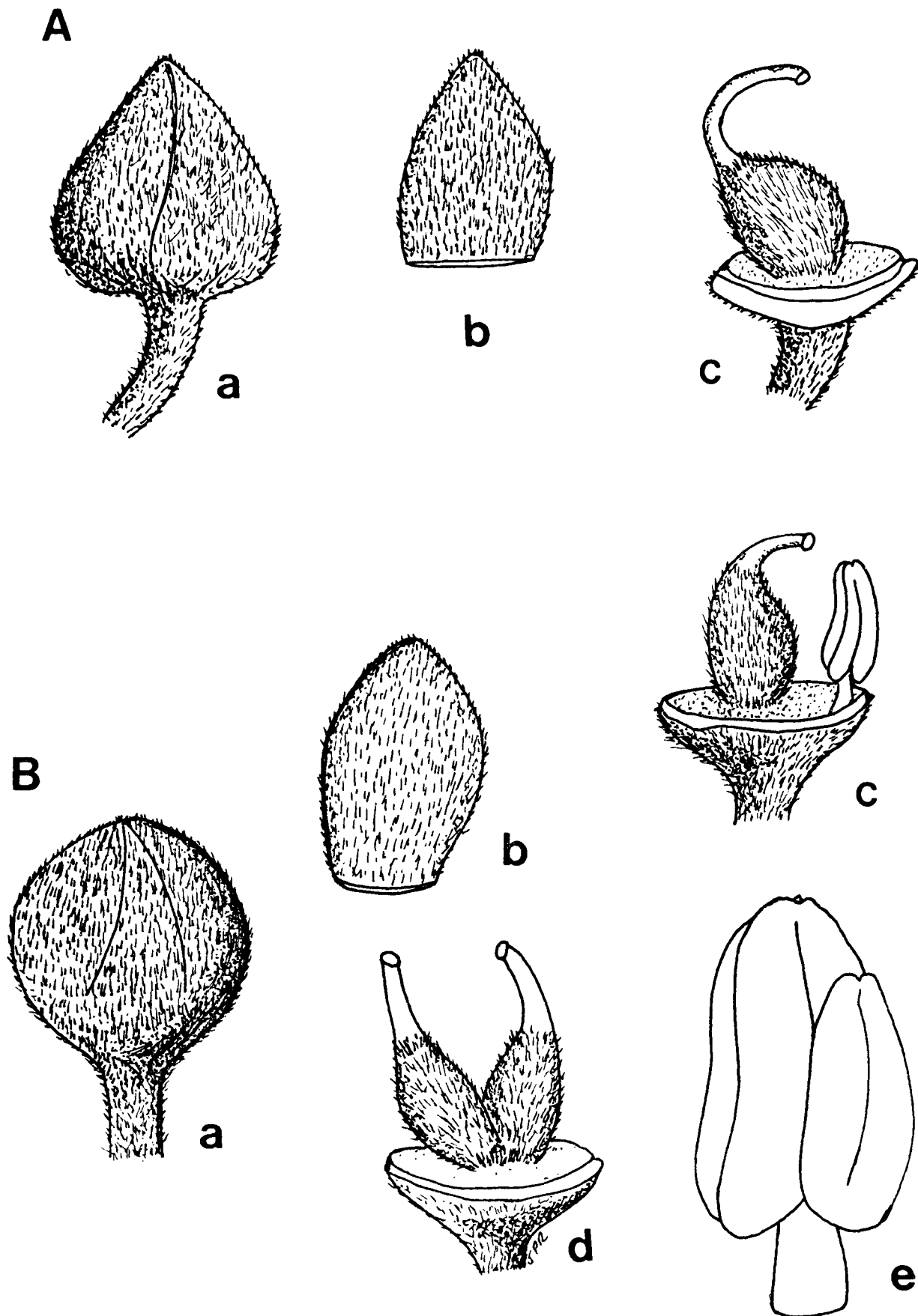


Fig. 2.9. Flowers (unopened bud, sepal, ovary and stamen) of representative species of section Arouna subsection Pirula.

A. D. dinklagei (Klaine 417, Gabon). a, trulloid bud; b, more or less triangular sepal and c, obliquely set ovary. B. D. schlechteri (Barbosa and Lemos 7962, Logambique). a, roundish bud; b, more or less elliptic sepal; c, ovary, more or less at the centre of the disc and one of ten stamens at the edge of the disc; d, branched or double ovary; e, branched or double anthers. X10 except Bc which is X30.

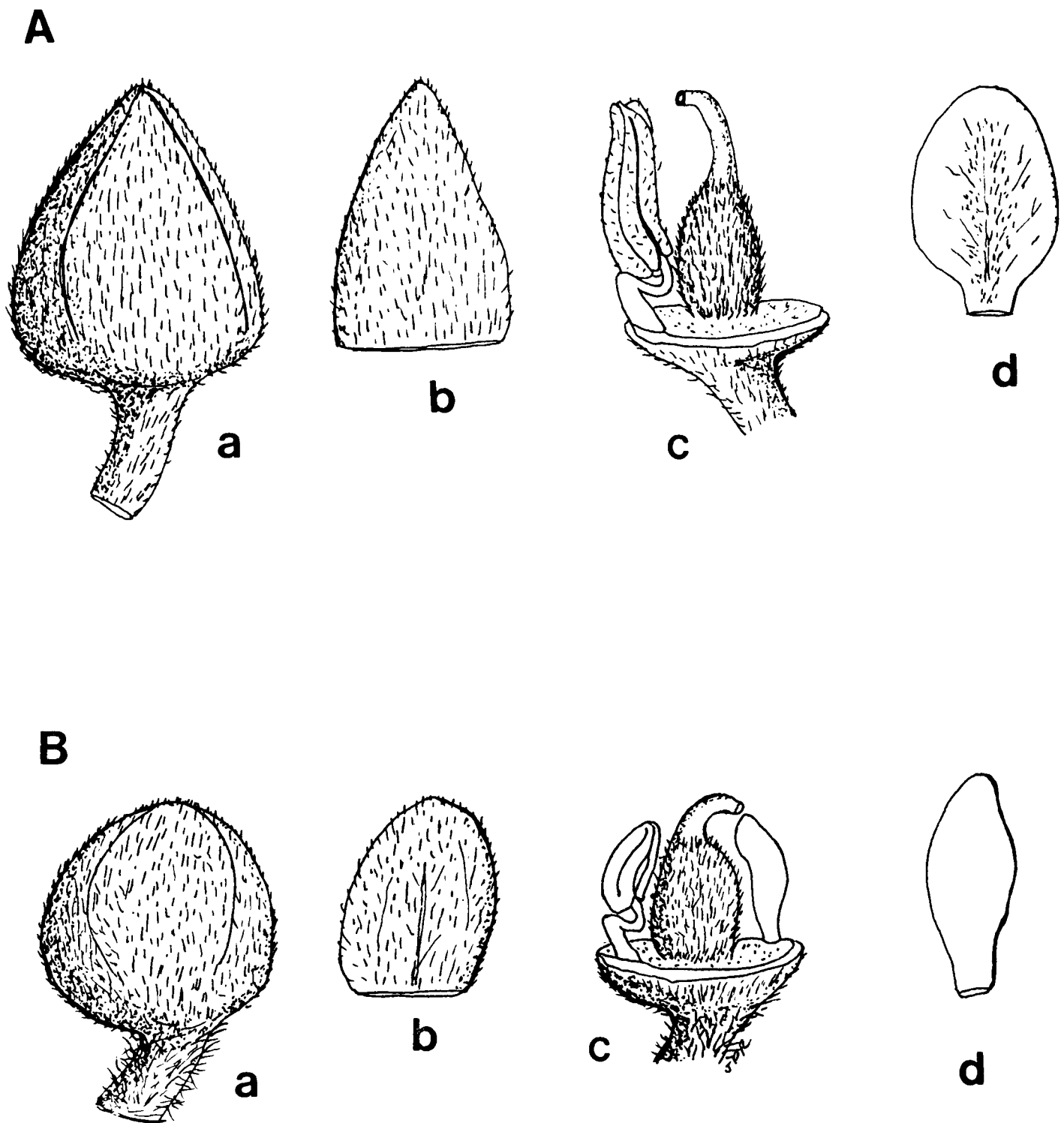


Fig. 2.10. Flowers (unopened bud, sepal, ovary and petal) of representative species of section Arouna subsection Indumentosa.

A. D. pachyphyllum (Zenker 2360, type, Cameroon). a, trulloid bud; b, triangular sepal; c, ovary and position of one of two stamens; d, petal which is hairy on the abaxial side. B. D. pentandrum (Louis 4017, type, Zaire). a, roundish bud; b, sepal; c, ovary together with one of five stamens and petal; d, petal. X10 except Bd which is X20.

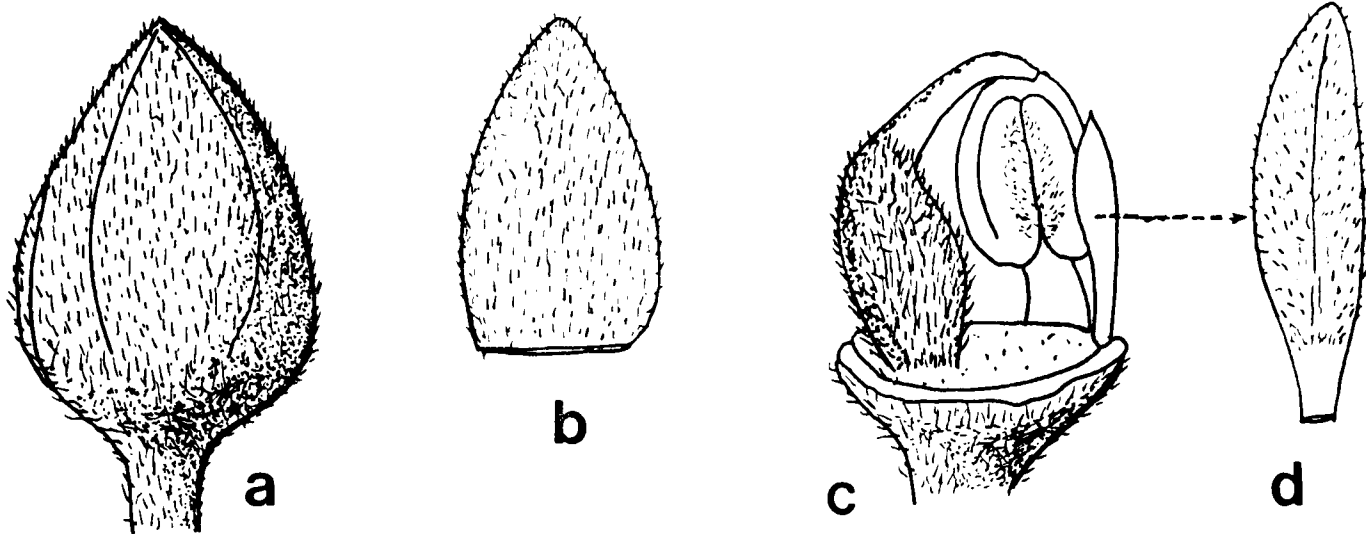
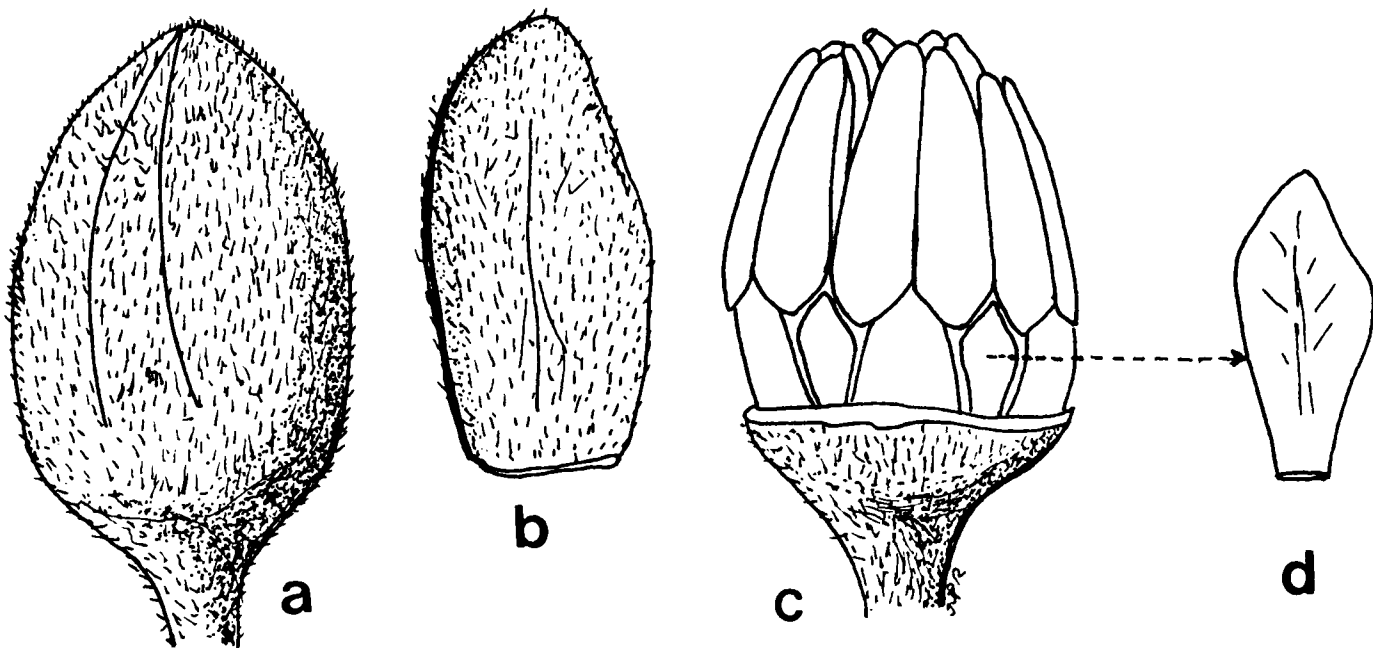
A**B**

Fig. 2.11. Flowers (unopened bud, sepal, ovary and petal) of representative species of section Codarium. A. D. guinnense (Hepper 1465, N Cameroon). a, ovoid-trulloid bud; b, $\pm$ triangular sepal; c, obliquely set ovary; d, petal. B. D. englerianum (Gossweiler 13911, Angola). a, ellipsoid-oblongish bud; b, elliptic-oblong sepal; c, bud with sepals removed to show position of three of five stamens and two petals; d, petal enlarged. X10 except Ad and Bd which are X20 and X30, respectively.

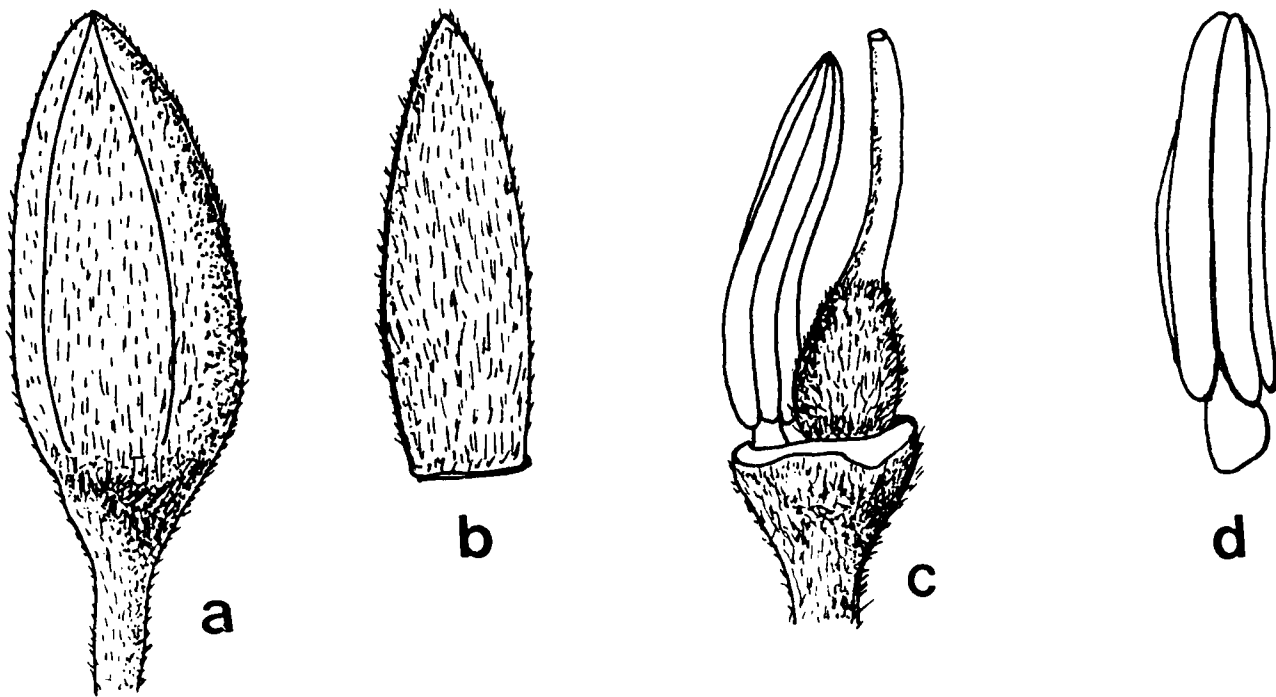
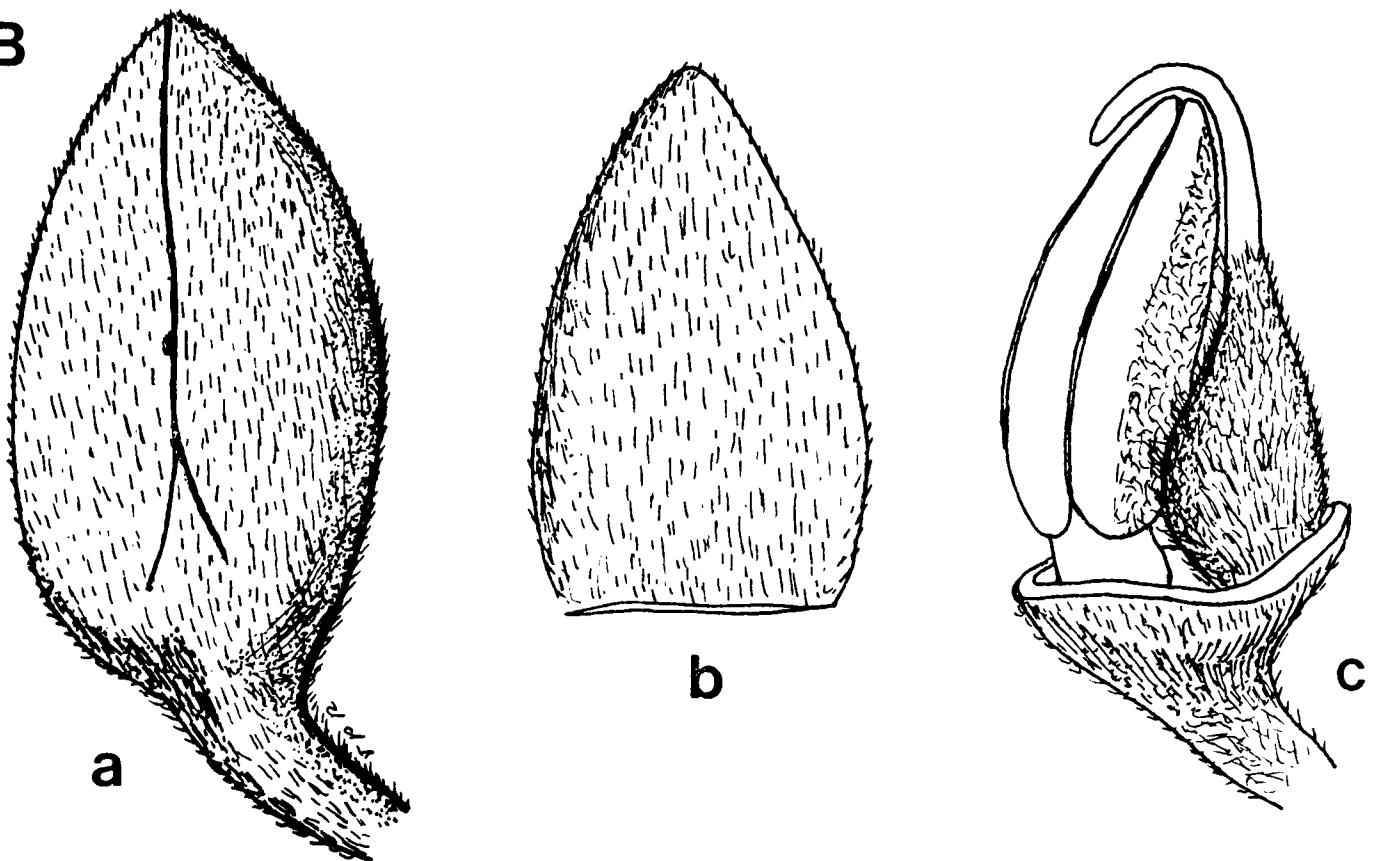
A**B**

Fig. 2.12. Flowers (unopened bud, sepal, ovary and stamen) of representative species of subgenus Dialium. A. D. ovoideum (Thwaites C.I. 3142, Sri Lanka). a, $\pm$ ellipsoid bud; b, $\pm$ elliptic sepal; c, ovary and position of one of two stamens; d, stamen, abaxial side. B. D. platysenalum (Kunstler 8187, W Malaysia). a, $\pm$ ellipsoid to ovoid bud; b, broadly elliptic sepal; c, ovary, obliquely set and the position of stamens. X10.

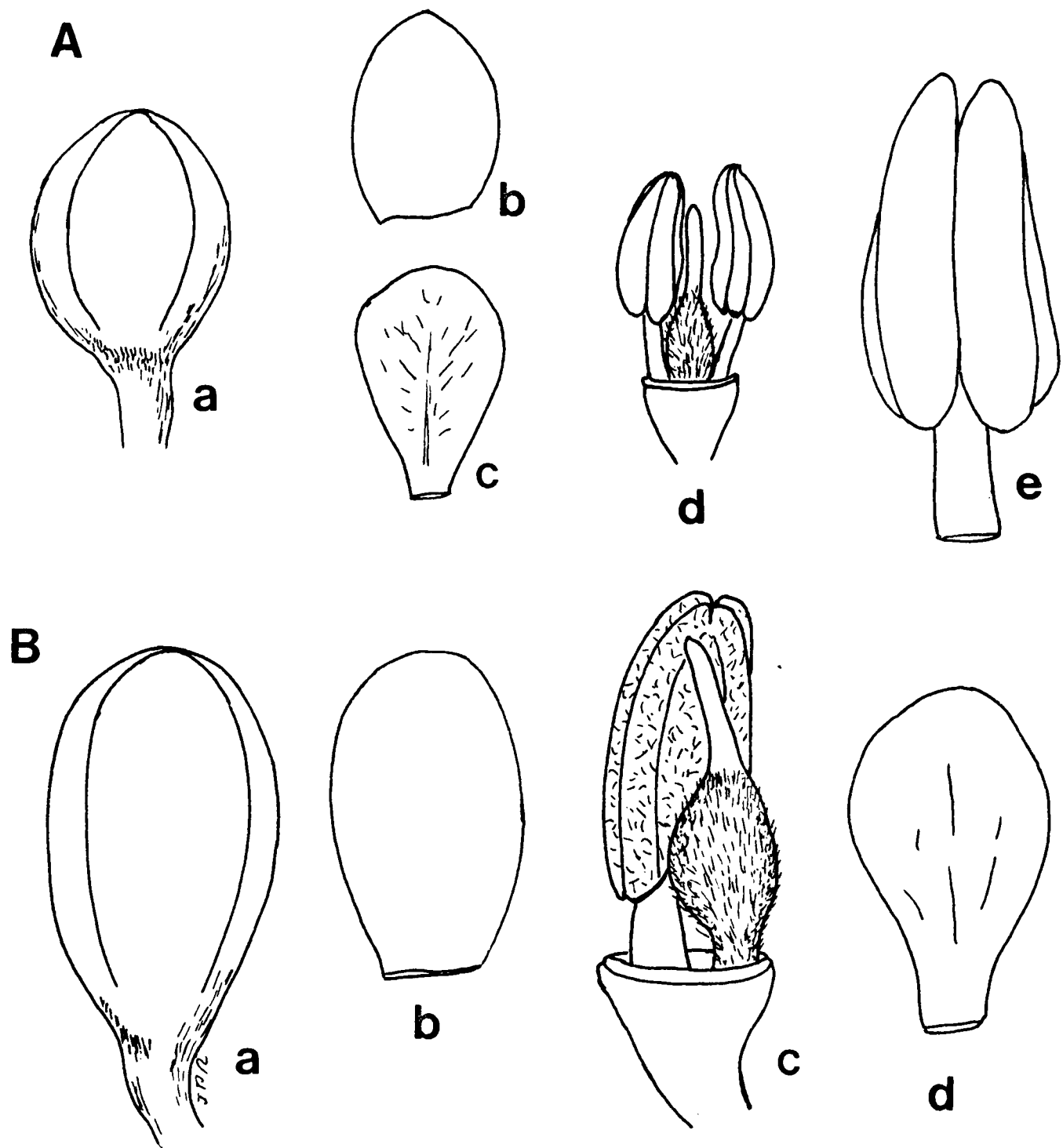


Fig. 2.13. Flowers (unopened bud, sepal, ovary, stamen and petal) of representative species of subgenus Dansera section Hova. A. D. occidentale (8664 SF, W Madagascar). a, obovoid to roundish bud; b, ovate to rounded sepal; c, $\pm$ obovate petal; d, ovary and position of two stamens with the three petals removed; e, stamen, abaxial side. B. D. madagascariense (8625 SF, E Madagascar). a, $\pm$ obovoid to ellipsoid bud; b, $\pm$ obovate sepal; c, ovary, obliquely set and position of one stamen with the three petals removed; d, $\pm$ obovate petal. All X10 except Ae which is X20.

2.1.8.2. Sepals (Fig. 2.14)

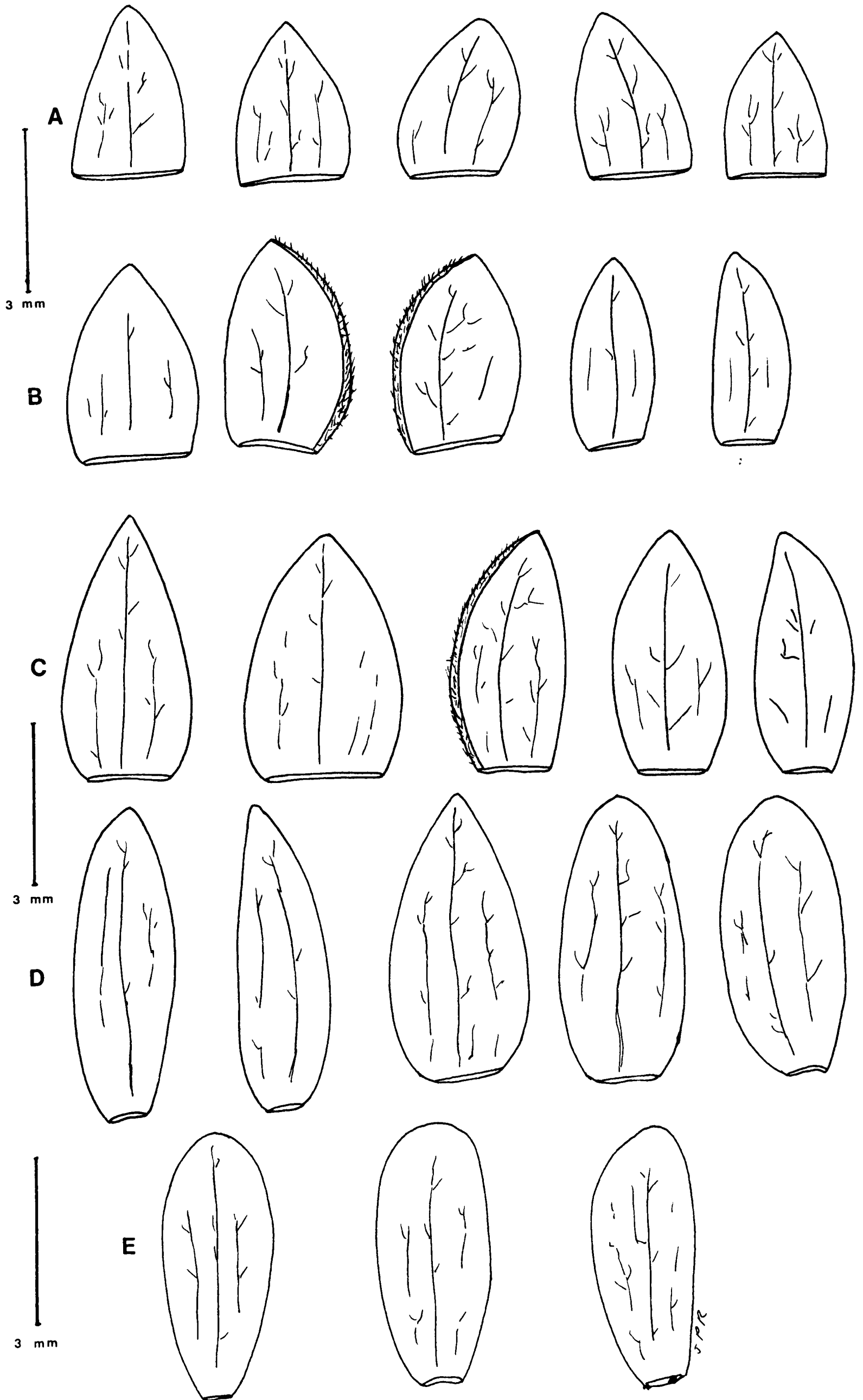
The sepals (calyces) are imbricate in bud. They are completely enclosing the other floral parts or rather strongly overlapping each other before anthesis except in Madagascan species where sometimes the upper part of the sepals do not completely enclose the petals. This condition indicates that the sepals are imbricate only near the receptacle but rather somewhat valvate or at least do not overlap at the upper part of the bud. The number of sepals or calyx lobes are 3 in subgenus Dansera and 5 in subgenera Dialium and Arouna.

Sepals are generally subequal. In flowers with 5 sepals, one of the two outer and one of the three inner sepals (i.e. third sepals in Fig. 2.14 A-D) tend to be bigger than the rest of the five sepals. The last inner sepal is usually the smallest (Fig. 2.14 A-D, fifth sepals). In 3-sepaled flowers, the three sepals are more or less of the same size (Fig. 2.14 E).

The shape of the sepals varies. In flowers with disc (subgenus Arouna), especially those with trulloid buds, the smaller outer petal is more or less triangular and more flattish (Fig. 2.14 A-C, first sepals). The other outer sepal and the bigger inner sepal may also be triangular in shape or may vary to some extent but they are rather deeply concave (Fig. 2.14 B). In flowers without disc (subgenera Dialium and Dansera) and with ovoid-ellipsoid buds, the outer sepals are generally elliptic to ovate (Fig. 2.14 D-E). The inner sepals may also have the same shape as the outer ones or may vary to some extent as shown in Fig. 2.14 D.

The abaxial side of the sepals is generally adpressed hairy (see Figs. 2.9 - 2.12, all b) while the adaxial side is glabrous or sometimes sparsely minutely hairy. Sepals are more or less distinctly veined (Fig. 2.14 A-E).

Fig. 2.14. Sepals of some Dialium species representing subgenus Arouna (A-C), subgenus Dialium (D) and subgenus Dansera (E). A, D. dinklagei (Klaine 417, Ghana); B, D. pachyphyllum (Gossweiler 6260, Mayumbe, Angola); C, D. englerianum (Lebrun 6475, Zaire); D, D. indum (Beccari 3381, Sarawak); E, D. procerum (FRI 117T. 3P.579, Sumatra). Illustrations from left to right represent 2 outer and 3 inner sepals, respectively or 1 outer and 2 inner sepals in E. All viewed on the adaxial side.



2.1.8.3. Petals (Figs. 2.10, 2.11 and 2.13)

Generally, petals are absent. As found in this study, 63% of the species do not have petals, and 22% with 1, 11% with 3 and 4% with 5 petals. With the exception of the Madagascan species (Fig. 2.13 A & B), petals are generally smaller than the sepals (see Fig. 2.10 A, b & d and B, b & d; Fig. 2.11 A, b & d). In D. englerianum, the petals are much more reduced and suppressed in-between the much bigger stamens (see Fig. 2.11 B, c & d).

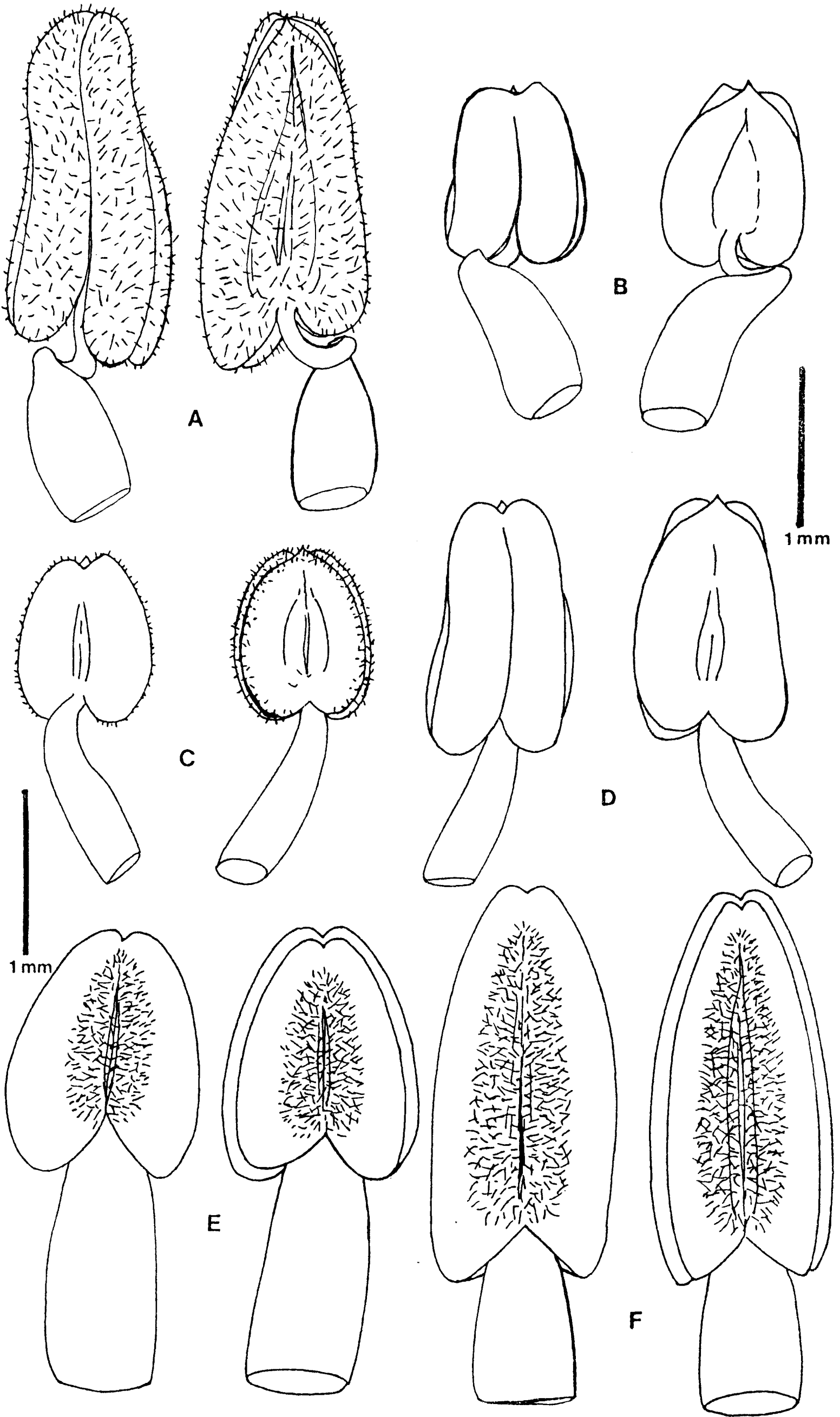
The petals are clawed and the claws are rather thick. The limbs are more or less ovate (D. pachyphyllum, Fig. 2.10 Ad), elliptic (D. guineense, Fig. 2.11 Ad) or obovate (D. madagascariense and D. occidentale, Fig. 2.13 Ac and Bd). They are more or less deltoid in D. englerianum (Fig. 2.11 B, c & d). Petals are either hairy (especially along the middle part of the limb) or glabrous on both the abaxial and adaxial sides. In D. pachyphyllum and D. guineense (Figs. 2.10 Ad and 2.11 Ad) the limbs are hairy while in D. pentandrum Louis ex Stey. (Fig. 2.10 Bd) and the Madagascan species (Fig. 2.13 Ac and Bd), they are glabrous.

2.1.8.4. Stamens (Figs. 2.15 - 2.16)

Stamens are variable in number as well as size. The majority of the species have 2 stamens which represent 78% of the total number of species recognised in this study. The remaining species are with 5 (11%), 6 (7%) and 8-10 (4%) stamens.

The sizes (anthers and filaments together) are usually 3-4 mm long by 1.5 mm wide, i.e. especially in African (mostly in section Arouna subsection Pirula, see Fig. 2.15 B, C & D) and Madagascan species (except D. madagascariense) of section Hova (see Fig. 2.16 F). The bigger-size stamens, i.e. 4-6 (-7) mm long by 2.25 mm wide, are

Fig. 2.15. Stamens of Dialium, subgenus Arouna
subsection Indumentosa (A-B), subsection Pirula (C-D)
and section Codarium (E-F). A, D. pachyphyllum (Bates
1832, Cameroon); B, D. polyanthum (Adames 427, Liberia);
C, D. bipindense (Zenker 2695, Cameroon); D, D. schlechteri
(Gomes et Sousa 1650, Mocambique); E, D. guineense
(Hepper 1465, Cameroon); F, D. englerianum (Gossweiler
13911, Angola). The left and the right of each pair of
illustrations represent abaxial and adaxial sides of a
stamen (anther), respectively.



represented by species belonging to section Arouna subsection Indumentosa (D. pachyphyllum, Fig. 2.15 A; D. tessmannii), section Codarium (D. englerianum, Fig. 2.15 F) and subgenus Dialium (D. platysepalum, Fig. 2.16 C).

2.1.8.4.1. Anthers

Characteristic features are found in the apex of the anthers. The apex shows distinct shapes. Section Arouna (subgenus Arouna) characteristically have acute apex at the adaxial side (Fig. 2.15 A-D) while section Codarium (subgenus Arouna) have retuse apex at both abaxial and adaxial sides (Fig. 2.15, E-F). Section Hova (subgenus Dansera) have deeply-cleft apex (Fig. 2.16, E and F). In subgenus Dialium and section Dansera, the anther apices are slightly notched to roundish (Fig. 2.16 A-D). Also, the abaxial side of the anther shows distinct shapes. They are humped in subgenus Arouna (excepting section Codarium) (see Fig. 2.15, A-D) and in D. occidentale (Fig. 2.16, F) from W Madagascar. They are more or less flattish in subgenus Dialium, section Codarium, E Madagascan species of section Hova and section Dansera.

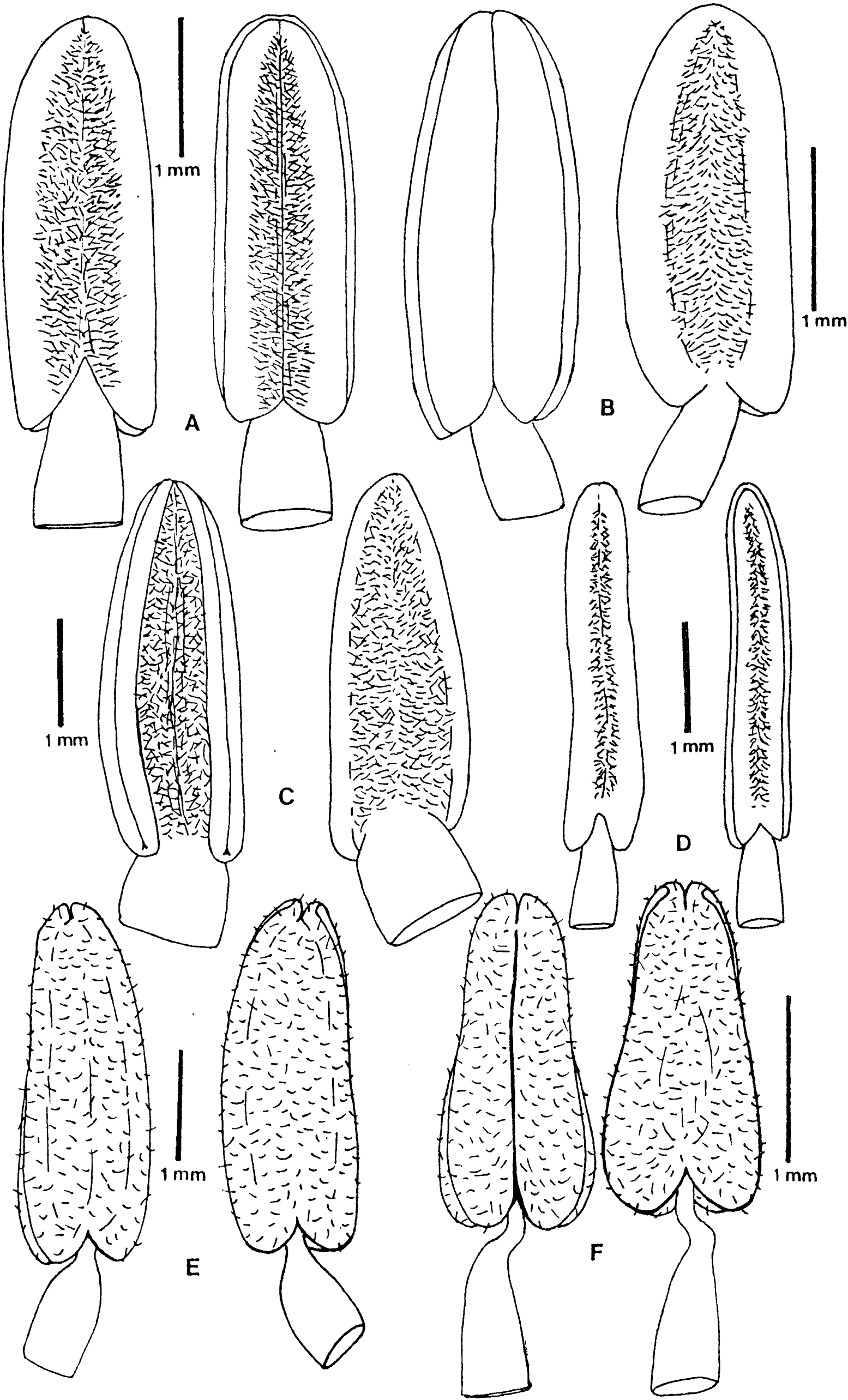
There are two types of anther dehiscence, namely: dehiscing basipetally and dehiscing evenly along the slits. Basipetally dehiscing anthers are those species belonging to section Arouna (except species in section Codarium). The rest of the species have anthers that more or less dehisce evenly along the slits.

An unusual branched or double anthers was observed in D. schlechteri (see Fig. 2.9, Be).

2.1.8.4.2. Filaments

There are two types of filaments, i.e. straight to very slightly recurved and geniculate (Fig. 2.15, A-B). Geniculate filaments are

Fig. 2.16. Stamens of Dialium, subgenus Dialium (A-C) and subgenus Dansera (D-F). A, D. hydnocarpoides (SAN 65854, Sabah); B, D. cochinchinense (Pierre 123, S Vietnam); C, D. platysepalum (SING 36908, Peninsular Malaysia); D, D. kunstleri var. kunstleri (SAN 65841, Sabah); E, D. mada-gascariense (8625 SF, Madagascar); F, D. occidentale var. occidentale (26554 SF, Madagascar). The left and the right of each pair of illustrations represent abaxial and adaxial sides of a stamen (anther), respectively.



characteristics of species belonging to subsection Indumentosa (D. angolense, D. pentandrum and D. polyanthum Harms) while the rest have straight to slightly recurved filaments (e.g. subsection Pirula and section Codarium). All filaments are more or less narrowly elliptic in cross section (except in D. platysepalum which is rather flattish, Fig. 2.16 C) and gradually taper towards the top (anther base).

2.1.8.5. Pistil (ovary and style, Figs. 2.9 - 2.13)

The pistil is uniform in all species observed, i.e. it is sessile to very shortly stipitate with the ovary covered densely with more or less straight and adpressed brown hairs (see Figs. 2.9 - 2.13, all c except 2.13 Ad). The style is glabrous or sometimes only sparsely hairy at the base, slightly bent at the top or sharply recurved over the ovary as in D. platysepalum (see Fig. 2.12, Bc) and in some species in subsection Codarium (see Fig. 2.11, Ac). Double ovaries were observed by Chakravorthy (1969) in D. guineense. I have seen this phenomenon in D. schlechteri (Fig. 2.9, Bd) and D. turbinatum de Wit (now D. indum).

The ovules are usually two, rarely one or three. They are marginally attached to the adaxial side of the ovary wall and slightly bent towards the funicle (see Figs. 7.1, 7.4 and 7.7, all D).

2.1.8.6. Disc

The receptacle has either a disc or ^{is} without a disc. All African species (plus one Neotropical) have more or less prominent discs (see Figs. 2.9 - 2.11, all C) which are more or less fleshy in life while species from Madagascar and Indo-Malesia (see Fig. 2.12 - 2.13, all C except 2.13 Ad) are without a disc. Discs are rather thick in D. dinklagei (see Fig. 2.9 Ac). All discs are minutely hairy.

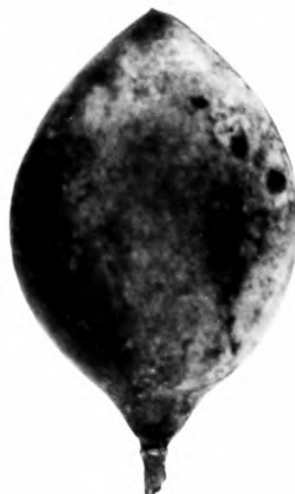
D. hydnocarpoides of W. Malesia is intermediate. It has a receptacle with a flattish top which is more or less as wide as the ovary and appears like a narrow but indistinct disc. The presence and/or absence of disc is the main basis for the original division of Dialium into two subgenera, i.e. Arouna and Dialium (Steyaert, 1951).

2.1.9. Fruits (Figs. 2.17 - 2.18)

The fruit of Dialium is what Irwin and Barneby (1981) call the signature of the genus. The characters of the fruit are common to all species regardless of what subgenera the species belongs to. The pod is indehiscent and has a pericarp with a thin crustaceous exocarp of half a millimetre or less thick (see Fig. 2.18, a and b). The exocarp is supported by the mesocarp which varies in thickness from about one to two millimetres thick. The thickness of the mesocarp determines the hardness or brittleness of the pod when crushed by the fingers. For example, the thick (c. 1.5 - 2.0 mm) mesocarps of D. platysepalum, D. unifoliolatum, D. kunstleri Prain and D. procerum (Fig. 2.17 L-P) make their fruits rather difficult to crush between the thumb and the forefinger. The next layer of tissue of the pod is the endocarp which completely envelops the seed. This layer of tissue easily separates from the mesocarp as well as from the testa. It is pulpy, reddish brown when ripe and edible in all species.

Anatomical studies of legume pods have recently been conducted by Pate and Kuo (1981). According to Pate and Kuo, the cross section of a pod usually shows an exocarp which consists of only an epidermis but may also include a hypodermis of one or more layers of thick-walled cells. The mesocarp comprises layers of thin-walled, large vacuolated cells - the outer layer with well-developed chloroplast and containing a bulk of the chlorophyll of the pod, the inner layer often with abundant reserves of starch.

Fig. 2.17. Fruits of Dialium, subgenus Arouna (A-I), subgenus Dialium (J-L) and subgenus Dansera (M-P). A, D. dinklagei (de Wilde 3122, Ivory Coast); B, D. excelsum (Louis 3820, Zaire); C, D. orientale (Graham 790, Kenya); D, D. polyanthum (Leeuwenberg 2411, Ivory Coast); E, D. tessmannii (Donis 1914, Zaire); F, D. pachyphyllum (Louis 359, Zaire); G, D. englerianum (Robyns 3731, Zaire); H, D. zenkeri (Leonard 30, Zaire); I, D. guineense (Chapman 5415, Nigeria); J, D. indum (SAR 29688, Sarawak); K, D. indum (BRUN 5212, Brunei); L, D. platysepalum (For. Dept. 17111 (left), Peninsular Malaysia; SAN 8186 (right), Sabah); M, D. unifoliolatum (9033 SF, Madagascar); N, Dialium kunstleri var. kunstleri (SAR 25286, Sarawak); O, Dialium kunstleri var. trifoliolatum (SAN 40490; Sabah); P, Dialium procerum (BRUN 856, Brunei).

**A****B****C****D****E****F****G****H****I****J****K****L****M****N****O****P**

5 cm

Fruits are more or less globose in most species in subsection Pirula (section Arouna, Fig. 2.17 A-C) or slightly to much compressed in subsection Indumentosa (section Arouna, Fig. 2.17 D-F) and section Codarium (subgenus Arouna, Fig. 2.17 H-I), respectively. In globose or slightly compressed pods, a suture is visible round the narrow part of the pod either faintly or distinctly. In the much compressed ones, two-seeded fruits can be easily detected by a shallow constriction between the seeds.

Exocarps are variously hairy. The thickly-set hairs in D. platysepalum (subgenus Dialium) and in D. guineense and D. zenkeri (section Codarium) make them more distinct from the rest of the species in the genus. In some species hairs are caducous (at least with age) which is characteristic of subgenus Dansera (Fig. 2.17, M-P) and some species in section Arouna (Fig. 2.17, A-F).

2.1.10. Seed and testa (Fig. 2.18 - 2.20)

2.1.10.1 Seed

In each fruit usually only one seed develops or sometimes two. In two-seeded fruits the seeds are smaller and appear as if they are split from one seed. This is because their adjacent ends or sides are pressed to each other which then become flattish at maturity. The solitary seed, however, is usually more or less reniform.

The cross section of the seed (see Fig. 2.18 c) shows a thin testa, endosperm and cotyledons. The endosperm in Dialium seeds is as thick as or slightly thicker than the cotyledons.

2.1.10.2. Testa

In the herbarium, the testa is always brown to dark brown and more or less shiny. To the naked eye the outside surface of the testa is

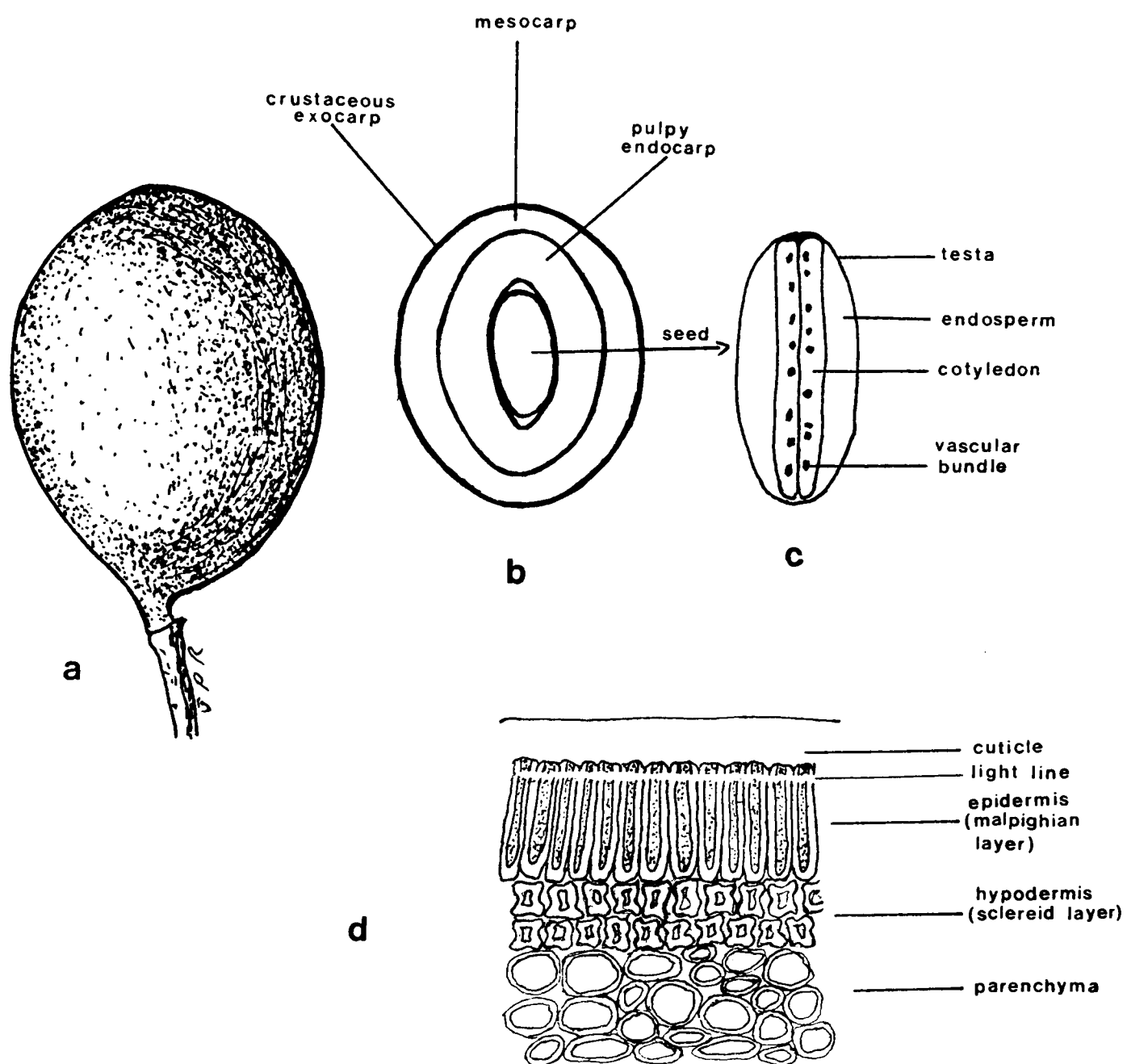


Fig. 2.18. Fruit, seed and testa of Dialium platysepalum Baker
(FMS 1711, Peninsular Malaysia). a, fruit viewed on the compressed
side; b, transverse section of the fruit; c, transverse section
of the seed; d, anatomical features of cross section of the testa.
a and b = X2; c = X4; d = c. X260

smooth but at higher magnification the appearance "recalls the crackling often seen in a glaze on old pottery" (Brenan, 1967). This is well demonstrated in SEM photomicrographs (Fig. 2.19) at C.60 and 300 times magnification.

The cross sections of the testa of 3 species, i.e. D. pachyphyllum (subgenus Arouna), D. platysepalum (subgenus Dialium) and D. procerum (subgenus Dansera) were anatomically examined in this study. In Dialium seed the testa is thin (i.e. more or less 0.25 mm thick) and hard when dry. It was first tried to boil the seed in water to soften the testa for sectioning but it swelled and became gelatinous. Since there were no fresh unripened seeds (recommended by Corner (1951) for the study of the leguminous testa), dry seeds were used. A safety thin razor blade was first used to cut the testa freehand but this did not give a satisfactory result because the cutting edge of the blade could not withstand the hardness of the testa. A sharp thick-bladed knife was used instead to cut sections freehand. The seed was first cut into two halves across its width (see Fig. 2.18, c), Then one half of the seed was held by the forefinger and thumb and pressed down against a wood block. Thin sections were obtained by cutting the testa, i.e. sliding the sharp knife down the wood block. Sections cut this way were not of uniform thickness but thin ones suitable for anatomical observations were obtained. The suitable sections were then temporarily mounted on slides with cover slips using 50-50 distilled water and glycerine as mounting medium. The prepared slides were stored overnight to enable the thin sections to absorb the mounting medium. Some curled sections were then straightened out with dissecting needles before observation under the light microscope at c.X100.

The cross section of the testa, which is diagrammatically illustrated in Fig. 2.18, d from a light photomicrograph shown in Fig. 2.20,

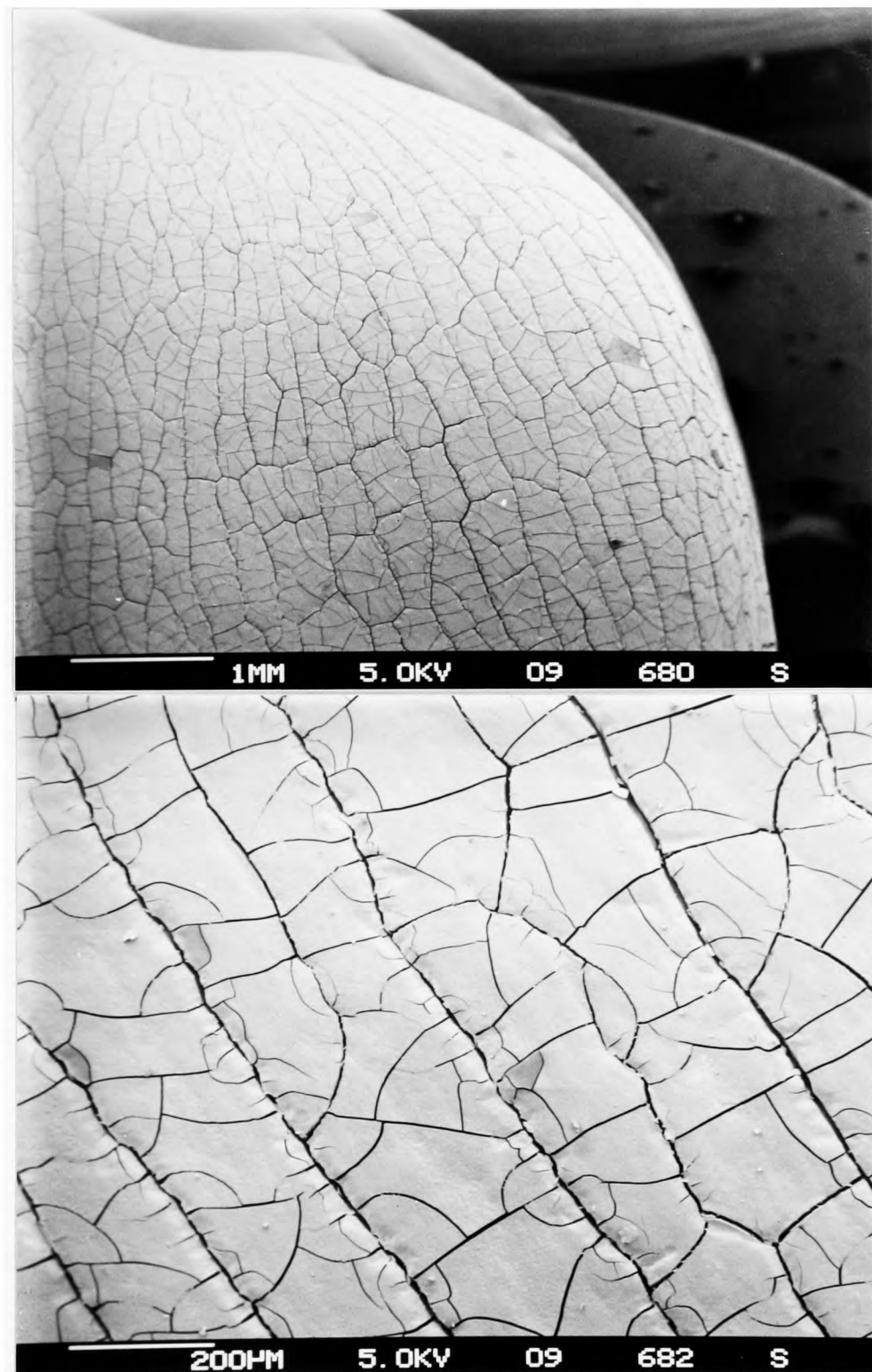


Fig. 2.19. Testa of a *Dialium* seed. *D. pachyphyllum* (Donis 3879, Zaire).

reveals at least four distinct layers of tissue. The first layer is the cuticle. Gunn (1981) states that it is composed of waxy, fatty hemicellulose or pectinaceous substance. It is more or less half as thick as the next layer which is the epidermal or malpighian layer. The malpighian layer is composed of radially elongated cells, palisade-like and devoid of intercellular spaces. It has a light or optical line, also called linea lucida (Corner, 1951) at near its top, i.e. close to the cuticle (see Fig. 2.18, d and Fig. 2.20). Next to the malpighian layer is the hypodermis or sclereid layer. It is usually composed of thick-walled cells with rather large intercellular spaces between them and is also called the hypodermal hour-glass layer (Corner, 1951). The last visible layer is the mesophyll or parenchyma layer. Typically, this layer of tissue is composed of stellate-like parenchyma cells but in Dialium, they appear roundish or oval-shaped. Corner (1951) stated that in some cases it is very difficult to make out the shape of the cells in this layer without reference to unripened seed. In the caesalpinoid testa, there is said to be another layer between the mesophyll and the embryo called the remnant layer (Gunn, 1981) which is usually a very thin layer of parenchyma tissues. I could not distinguish this layer from the mesophyll in the sections I prepared. Probably my sections were too thick.

The result of the above observation clearly confirms the studies of Corner (1951, 1976) and Gunn (1981) on the testa of some Caesalpinioideae. As noted, the testa of Dialium is not only thin but also hard when dry. Moreover, the size of the seed (normally 6-10 mm long by 4-8 mm wide) is small. These make the testa difficult enough to handle by the fingers when making freehand sections for anatomical observations. Because of this, only one testa from each subgenus was observed in this study. As the anatomical features of Dialium testa are similar to the ones in other genera of the Caesalpinioideae already

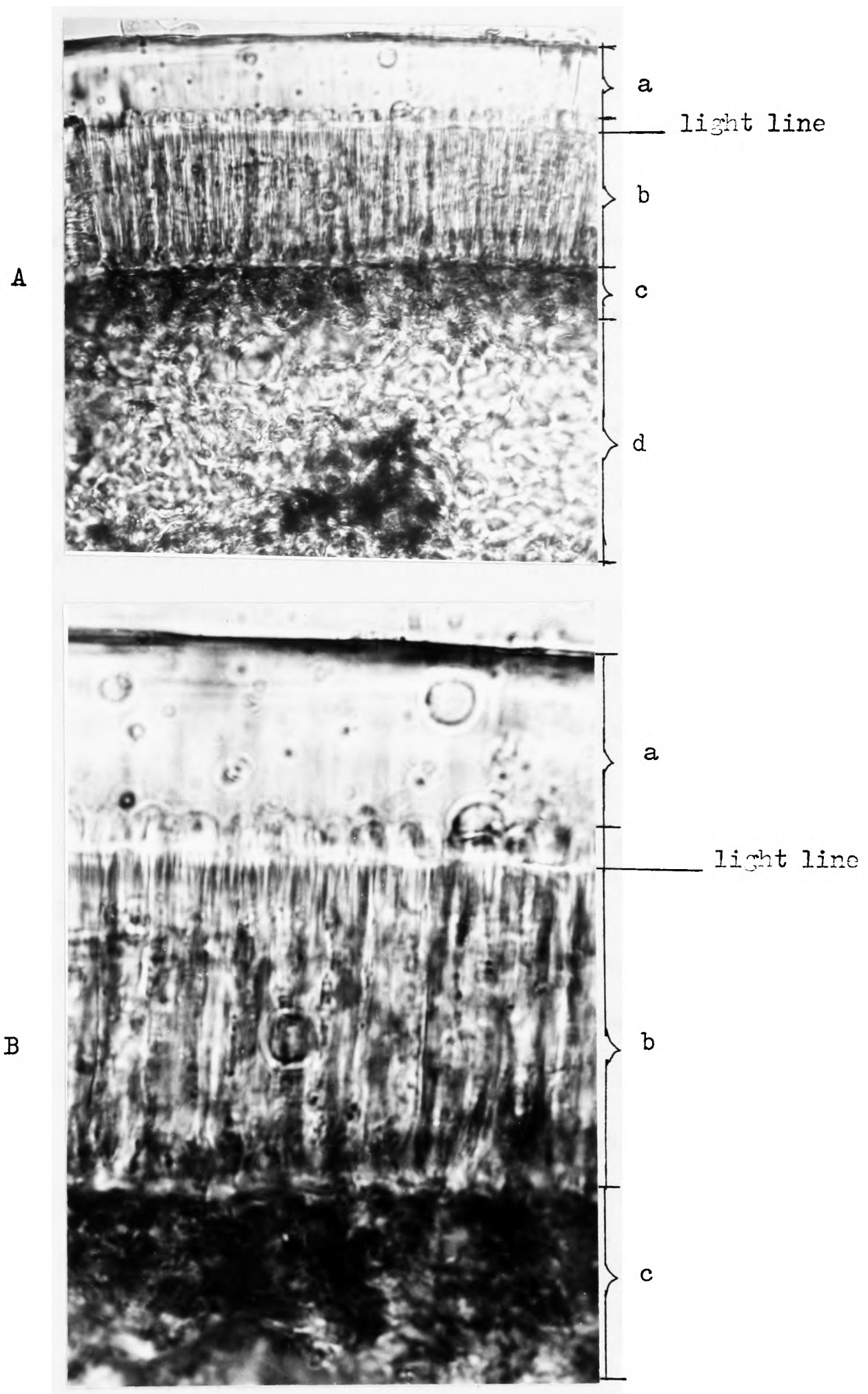


Fig. 2.20. Light photomicrographs of cross section of a *Dialium* testa. *D. platysepalum* (FMS 17111, Peninsular Malaysia). a, cuticle; b, malpighian layer; c, sclereid layer; d, parenchyma layer. A = X340; B = X850.

studied (Corner, 1951; 1976), I do not think that further anatomical observations of the testa from other Dialium species would yield anatomical data different from the above result.

2.1.11. Seedling morphology and development (Fig. 2.21)

Seeds of D. platysepalum were sown in the glasshouse of the Forestry Department, University of Oxford. At first, the testa breaks at the soil level exposing the creamy-white more or less succulent cotyledons. As the seedling grows the hypocotyl lifts the cotyledons above the soil level leaving the testa behind on or sometimes partly in the soil. The clasping cotyledons spread and do not change colour immediately but remain creamy-white for sometime until the first leaves, i.e. the eophylls, are developed. The cotyledons turn green only after the first leaves fully opened, and remain attached to the hypocotyl until the leaves become fully mature (see Fig. 2.21, A).

The hypocotyl is about 4 to 6 centimetres long. The epicotyl (the part between the cotyledons and the first eophylls) is about the same length as the hypocotyl (see Fig. 2.21, B). The seedlings (wild) from the previous fruiting season which were collected from the tree (see Fig. 2.1 A) have the same dimensions as those grown in the glasshouse. The first leaves are either 2-opposite or 4-verticillate (see Fig. 2.21, B). A similar seedling development described above were observed by Taylor (1960) on D. aubrevillei Pellegrin (now D. polyanthum Harms) and D. dinklagei and Voorhoeve (1979), also on D. aubrevillei.

The seedling belongs to the epigeal type (Ng, 1978) or to "Sloanea subtype A" (de Vogel, 1980: p.61 & 84) of seedling development. The two types are synonymous except that the "Sloanea subtype A" indicates the cotyledons to have a haustorial (storage) function. But they all



Fig. 2.21. Seedlings. D. maingayi (FRI 11458, Peninsular Malaysia).

have cotyledons exposed (without the seedcoat) and borne above the soil on a long hypocotyl. A more appropriate term which combines the above terminology is "phanero-epigeal", with storage cotyledons (Duke and Polhill, 1981). It indicates an epigeal condition with cotyledons above the soil and with the testa shed off.

An anatomical study of the legume cotyledons with emphasis on the vascular tissues has recently been conducted by Smith (1981).
 that
 Smith states the Neotropical D. guianense belongs to type 4A, i.e. where the vascular system is more or less confined to one plane. This is confirmed in D. platysepalum cotyledon (see Fig. 2.18, c). Cotyledons of this type are storage organs lacking any differentiation into palisade and spongy mesophyll. The superficial tissues turn green but contribution of cotyledon photosynthesis to seedling development is minimal (Smith, 1981).

2.2. Anatomy

2.2.1. Pulvinus vascular bundle (Figs. 2.22 - 2.23)

The vascular bundle pattern of the petiole at the three points (i.e. the base, the middle and the top) is uniform. The base (abscission layer) has either ^{an}invaginated or cylindrical vascular bundle while the sections at the middle and the top points have each 1 main cylindrical bundle at the abaxial side and 2 ridge bundles at the adaxial side. The vascularization of the pulvinus, however, shows a different pattern. Serial sections through the pulvinus reveal that the middle point has either 1 or 2 ridge bundles at the adaxial side.

An example of a type with 1 ridge bundle at the mid point of the pulvinus is shown in Fig. 2.22, a-h and 1-4. Here, the base of the pulvinus starts with an invaginated vascular bundle at section a.

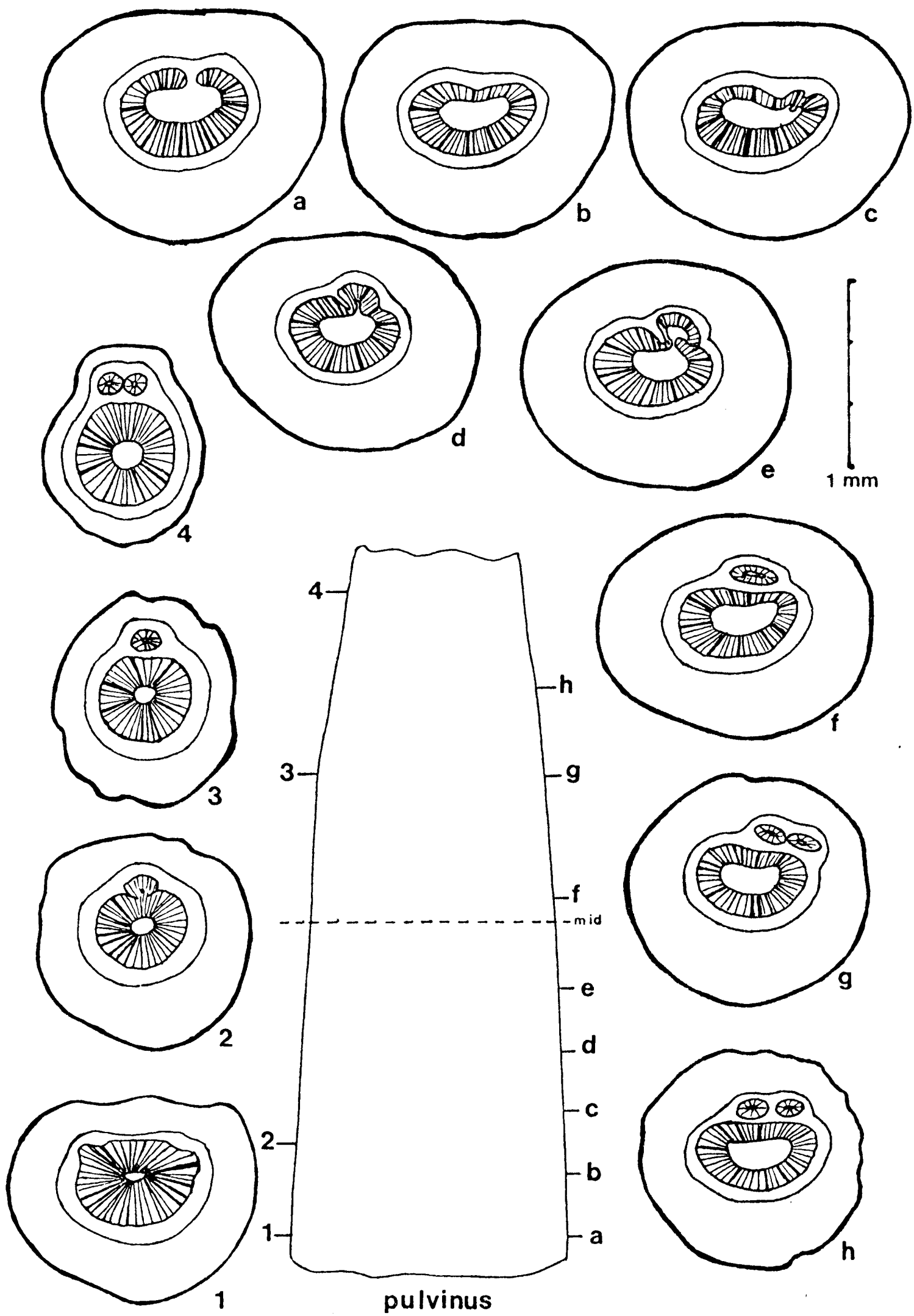


Fig. 2.22. Pulvinus vascular patterns. 1-4, *D. polyanthum* (FH Ibadan 18791, Nigeria); a-h, *D. holtzii* (Semsei 2412, Tanzania).

The invagination progressively closes and eventually connects as a single cylinder at section b. Towards the middle point of the pulvinus, the vascular cylinder becomes folded (sections c-e) at the adaxial side and later deletes and forms a separate (ridge) bundle at more or less the mid point of the pulvinus (section f). It is at this mid point where the single ridge bundle separates from the main vascular cylinder. Further towards the top the small ridge bundle gradually flattens and finally splits into 2 ridge bundles at the top point (sections g-h). The 2 ridge bundles continue as such until they reach the top of the petiole, i.e. at the first leaflet. Another example is shown at the left side of the same figure (Fig. 2.22, 1-4) where the large cylinder is already formed at the base of the pulvinus. At section 2 the small ridge bundle starts to form from the main vascular bundle and separates at section 3. This single ridge bundle progressively splits and forms 2 ridge bundles at the top of the pulvinus (section 4).

An example of a type with 2 ridge bundles at the middle point of the pulvinus is shown in Fig. 2.23, a-e. As usually happens, the base of the pulvinus begins with an invaginated vascular bundle and in this example it shows some broken segments at section a. One of the segments is crowded out, separates and forms a solitary ridge bundle at section b while at the same time the main vascular bundle begins to close the gap. Then at section c another bundle develops, this time from a segment crowded out at the other side of the main vascular bundle. Near the middle point at section d, it starts to separate as another ridge bundle. Near the top point (at section e) the 2 ridge bundles are now side by side with each other. In this case, the 2 ridge bundles did not originate from a single ridge bundle as shown in Fig. 2.22, a-h, but were formed separately from the main vascular bundle. In other species especially from Madagascar and Indo-Malesia, the 2 ridge bundles are already formed even near the abscission layer or below the

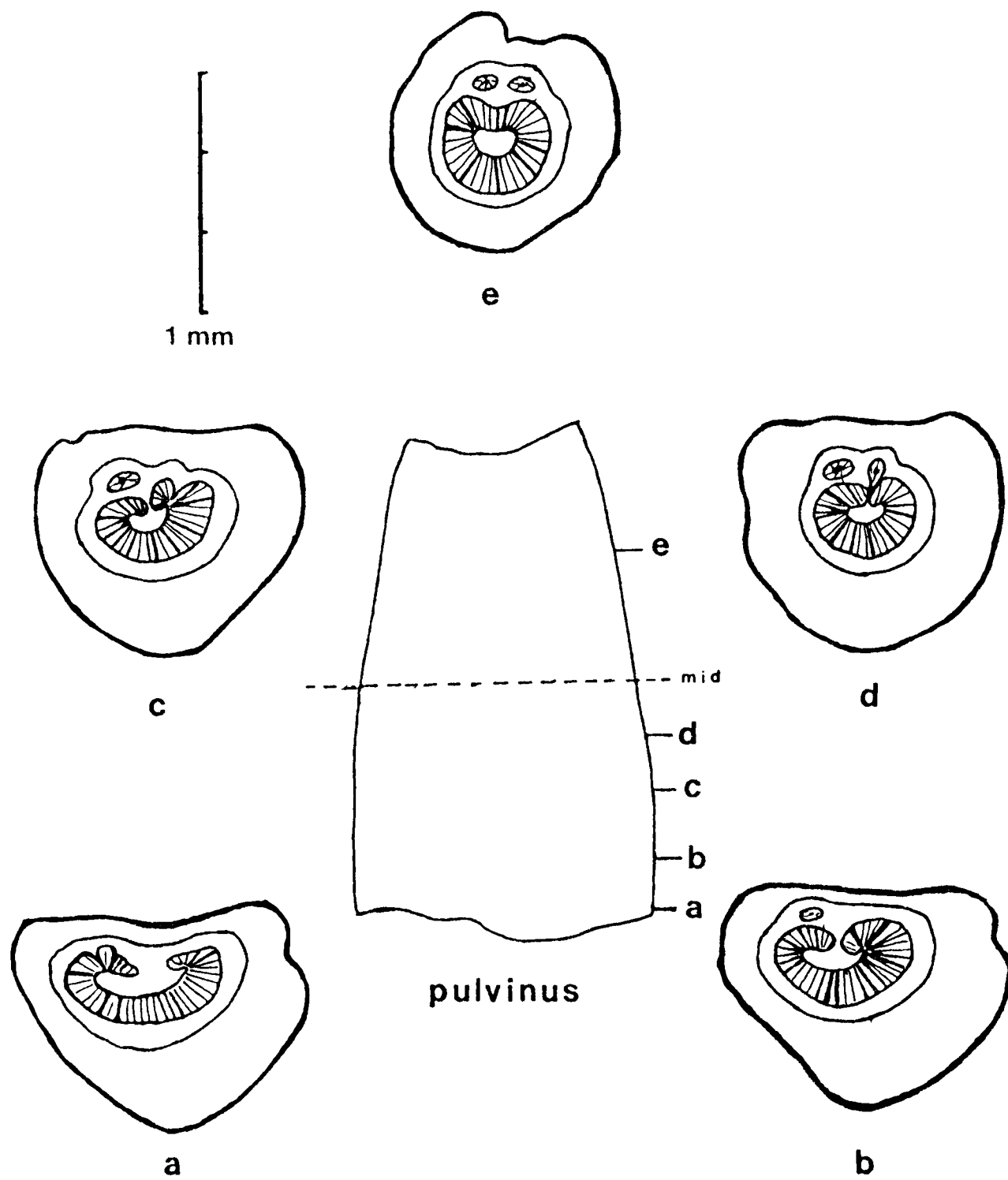


Fig. 2.23. Pulvinus vascular pattern. *D. dinklagei* (J. de Wilde 3132, Ivory Coast).

middle point of the pulvinus. Table 2.1, column 15 shows that the African species are mostly with 1 ridge bundle while the Madagascar and Indo-Malesian ones are with 2 ridge bundles at the middle point of the pulvinus.

It must be emphasized that it is sometimes difficult to determine accurately the middle point of the pulvinus. There are samples where the base or abscission layer is not clearcut. In some samples the swelling of the pulvinus is not pronounced and the top point in such cases is difficult to determine. There are also cases where species possessing 1 ridge bundle occasionally exhibit 2 ridge bundles, and vice-versa. The results recorded, therefore, are not absolute but rather represent the predominant occurrence of 1 or 2 ridge bundles halfway up the pulvinus.

2.2.2. Twigs

Twigs are terete. The older parts are always variously set with light-coloured lenticels. The lenticels are densely or sparsely set and the quality varies even in duplicates of the same collection. The younger parts are usually hairy, the hairs becoming rather dense towards the inflorescence branches. Surfaces are generally smooth or sometimes furrowed. Furrows though could be caused by shrinkage during drying rather than an inherent characteristic.

The anatomical features of the twigs are in agreement with those described by Metcalfe and Chalk (1950) in caesalpinoid species. The axial parenchyma shows two types of inclusions, i.e. silica and oxalate crystals. This complements the result found in mature wood (see below).

2.2.3. Wood

2.2.3.1. The timber and its utilization

Trees of Dialium are common but scattered in the forest. The size

and shape of the timbers are amenable to sawing. Logs are extracted from the forest for small-scale commercial utilization, usually for special purposes like tool handles, furniture, crossties, high grade construction, etc. (Chudnoff, 1979). In the Malesian region where there is still an abundant supply of timber (especially coming from trees belonging to the Dipterocarpaceae), Dialium trees are often left in logged-over areas because they have high density (45-) 50-60 lbs. per cubic foot, air dry) and specific gravity (0.65-) 0.80-0.90) values (Balan Menon, 1955; Burgess, 1966; Chudnoff, 1979). In addition, their wood contains silica and/or oxalate crystals which cause dulling of cutting edges such as saw teeth. These natural wood properties and characteristics discourage exploitation.

2.2.3.2. Anatomical features

The anatomy of mature wood of some Dialium species has already been studied by some workers, e.g. Moll and Janssonius (1914) on D. indum; Balan Menon (1955) on D. indum, D. kunstleri and D. platysepalum; Lecomte (1925) on D. cochinchinense; Fouarge, et al. (1953) on D. excelsum and D. pentandrum and Normand (1950) on D. dinklagei and D. guineense. The above species studied are only a few representatives of Dialium in Indo-Malesia and Africa. It would, therefore, be desirable to look at Dialium wood involving more species and more materials for study. Results of the observation in this study are presented below.

The external gross characteristics as well as the minute structures of the wood are uniform (except inclusions in axial parenchyma) in all species. Data on measurement of the samples examined is summarised in Table 2.3. A short descriptive summary of the wood of the three subgenera is shown in Table 2.2. The gross feature and minute structure descriptions follow.

Table 2.2. Comparative wood anatomical features in Dialium.

Subgenera/ Region	Vessels/Pores	Rays	Axial Parenchyma	Inclusions
AROUNA/ AF and AM	Diffuse, mostly solitary with radial multiples of 2-3; perforation simple; intervessel pitting alternate, often vestured.	Generally stored, homocellular or sometimes with upright marginal cells often twice higher than the rest of the body cells. Long rays (connected end-to-end) commonly present.	Apotracheal, banded, bands mostly 2-3 cells wide; parenchyma strands mostly 4-celled, storied.	Silica in axial parenchyma. In addition also a few oxalate crystals in chambered strands mixed with the predominantly silica inclusions.
DIALIUM/ WM and SL	- ditto -	- ditto -	- ditto -	Exclusively containing oxalate crystals in chambered strands.
DANSERA/ WM and MA	- ditto -	- ditto -	- ditto -	Silica inclusions only except <u>D. occidentale</u> which rarely has oxalate crystals.

2.2.3.2.1. Gross features

The colour of the sapwood is white, yellowish or creamy white. The sapwood is especially well-marked from the heartwood. The heartwood is generally uniform brown or reddish brown when freshly cut but eventually darkens upon exposure, sometimes becoming almost black with age. The texture is fine to moderately coarse. The grain is generally interlocked, wavy or sometimes straight. The radial surface usually displays a "ribbon" figure and the tangential surface shows slightly dark markings or "ripple marks" caused by storied elements especially rays and axial parenchyma. Pores are not visible with a naked eye.

2.2.3.2.2. Minute structures (Figs. 2.24 and 2.25)

Pores (vessels) diffused, c. 50-70% solitary and with radial multiples of usually 2-3 or sometimes more, a few occluded usually wholly or sometimes partially with gummy deposits; shape usually roundish to sometimes oval; moderately small to medium-sized or sometimes moderately large with tangential diameter of c. (75-) 120-190 (-310) μ m, generally few to moderately few, sometimes moderately numerous, rarely numerous (D. ovoideum) c. 3-5 to 9-11 or 10-20 (D. ovoideum) per square mm. Vessel members generally moderately short to medium-sized, rarely very short, c. (140-) 250-425 (-650) μ m; perforation simple; intervessel pittings alternate, usually vestured, medium-sized, c. 9-11 (-13) μ m in diameter; vessel ray pittings the same as intervessel pittings. Rays storied, usually numerous or sometimes very numerous, c. 9-11 (-18) per mm, essentially homocellular, procumbent but sometimes marginal cells twice higher than the body cells present; seriation generally (1-) 2-3 (-4) with triseriate parts mostly only at the widest portion of the rays or biseriates with few triseriate parts, rarely 5-seriates; height

Table 2.3 Measurement (averages) of minute structures of Dialium wood.

Species	Region	Sample	Pores	(vessels)	Vessel	Member	R	a	y	s	Parenchyma			Fibre length
			1	2	3	4	5	6	7	8	9	10	11	12
schlechteri	AF	1	126	6-10	250	13	10-13	2-3	210	30	2-3	3-5	sc	1000-1200
bipindense	AF	1	170	3-6	320	9	8-10	3-4	240	35	3-6	4	sc	1000-1200
guianense	AM	2	140	4-8	350	9-11	8-9	2-3	230	35	2-4	4	sc	1000-1300
dinklagei	AF	5	145	3-5	340	9-11	9-11	2-3	300	32	2-5	4	sc	1000-1300
orientale	AF	2	75	8-15	280	9-11	11-14	2	225	18	2-4	4	s	1100-1250
excelsum	AF	1	155	5-8	350	11	9-11	3	280	35	1-3	4-7	s	1000-1200
polyanthum	AF	4	135	5-8	340	9-11	9-12	2-3	275	32	2-5	4	sc	900-1300
pachyphyllum	AF	3	140	6-9	335	9	10-13	2-3	270	27	2-4	3-6	sc	900-1100
englerianum	AF	1	140	5-8	330	9	9-11	2-4	250	29	2-5	4-8	s	1000-1200
guineense	AF	3	120	3-5	275	9-11	10-12	2-3	230	22	2-3	4	sc	1000-1250
zenkeri	AF	1	130	4-8	300	9-11	9-11	2-3	250	26	4	4-6	s	1000-1200
platysepalum	WM	6	180	4-7	425	9-11	9-11	2-3	275	25	2-4	4	c	1000-1100
ovoideum	SL	1	90	10-20	315	9	13-17	2	240	25	2-3	4	c	1000-1100
cochinchinense	WM	2	150	4-8	420	9-11	9-11	2-3	320	35	2-4	4	c	1000-1200
indum	WM	4	190	9-11	290	9-11	8-11	2-3	270	25	2-4	4	c	1000-1100
madagascariense	MA	1	80	4-8	310	9-11	13-15	2-3	250	20	2-3	4	s	900-1100
orientale	MA	1	70	4-8	270	9-11	13-15	2-3	220	22	2-3	4	s	1000-1200
unifoliolatum	MA	1	80	4-8	300	9-11	13-15	2-3	220	22	2-3	4	s	1000-1100
kunstleri	WM	3	130	4-6	300	9-11	8-11	2-3	275	25	2-3	4	s	950-1400

1 - pore diameter in μm ; 2 - number of pores per mm square; 3 - length of vessel member in μm ; 4 - intervessel pit diameter in μm ; 5 - number of rays per mm square; 6 - ray seriation; 7 - height of rays in μm ; 8 - width of rays in μm ; 9 - number of cells wide or parenchyma band; 10 - number of cells per axial parenchyma strand; 11 - cell inclusion in axial parenchyma strand (sc - predominantly silica with few oxalate crystals; s - silica only; c - oxalate crystals only); 12 - fibre length in μm . Region abbreviations (see legend in Table 2.1).

c. (100-) 210-320 (-560) μ m, sometimes 2 or more rays connected end-to-end (confluent) to form long rays usually exceeding 600 μ m in height present; width c. (10-) 20-35 (-55) μ m. Parenchyma basically apotracheal, banded, usually one side of the band touching the pores, usually 2-3 cells wide, sometimes 5, rarely 7 or 9 and the broadest part usually near the pores, usually broken or discontinuous and irregularly spaced from each other; strands usually 4-celled, sometimes 3- or rarely 7- or 8-celled; inclusions silica (subgenus Dansera), or predominantly silica together with oxalate crystals (subgenus Arouna) or only oxalate crystals in chambered strands (subgenus Dialium). Fibres short, c. (800-) 900-1100 (-1500) μ m, usually thick-walled with very narrow lumen, non-septate, usually storied, pits simple.

Abnormal tissues have been recorded for some Malesian species by Balan Menon (1955) as composed of phloem cells in the form of short arcs of about 0.65 cm wide extending to several metres longitudinally. Balan Menon must have seen and observed this phenomenon on logs or sawn timbers but I have not been able to observe them in the field. I have not detected abnormal tissues under the microscope. Koompassia (a closely related genus of W Malesia) wood is well known for abnormal tissues known as "included phloem".

Photomicrographs of wood sections representing one species for each subgenus are shown in Figure 2.24. The structures are uniform in both cross and tangential sections. They differ only in their inclusions in axial parenchyma, i.e. profuse silica together with scattered occurrence of oxalate crystals in long chambered strands in D. dinklagei (Fig. 2.24, A & B): oxalate crystals in chambered strands in D. indum (Fig. 2.24, C & D) and in D. platysepalum (Fig. 2.25, A); and only profuse silica in D. procerum (Fig. 2.24, F). Axial parenchyma cells contain usually one silica grain (in some cases two), and as seen in SEM, they are usually globular with granular surface (Fig. 2.25, C & D).

Fig. 2.24. Photomicrographs of Dialium wood, transverse
x 30, radial x 70 and tangential x 70. A-B, D. dinklagei
(Letouzey 11440, Cameroon); C-D, D. indum (FMS 161,
Peninsular Malaysia); E-F, D. procerum (FRI 16234,
Peninsular Malaysia).

c = crystals; s = silica

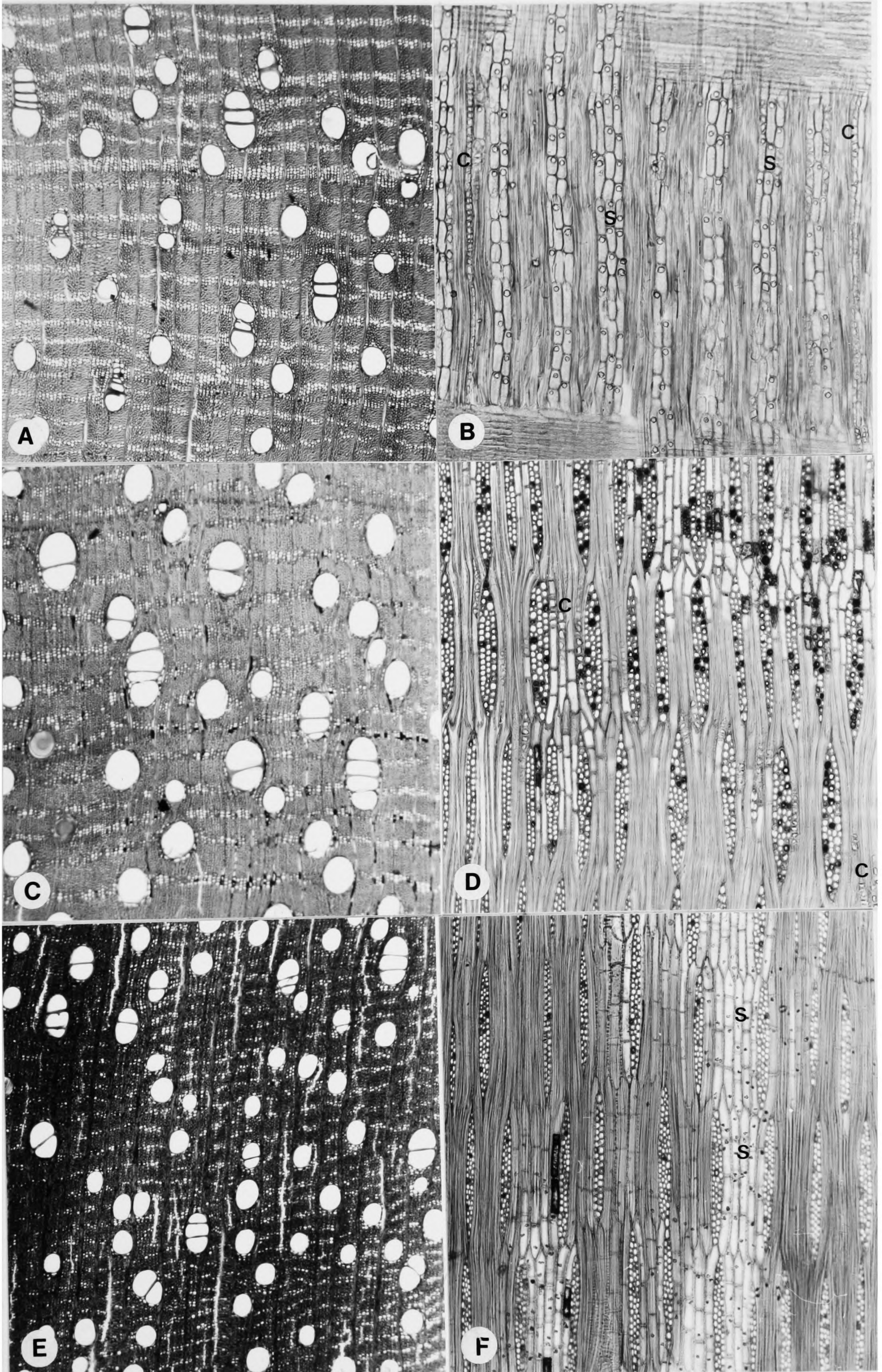
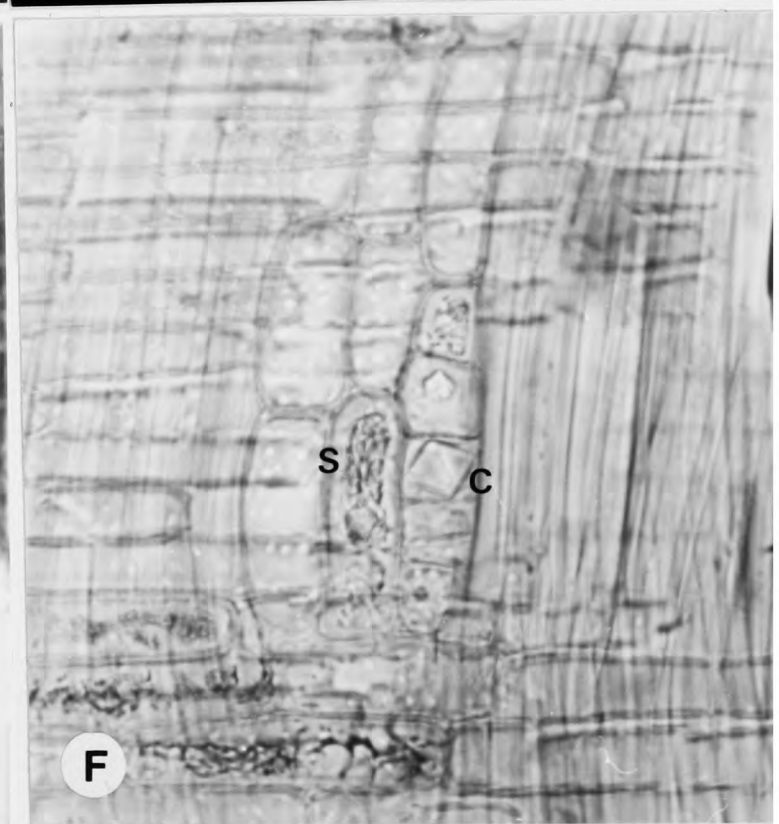
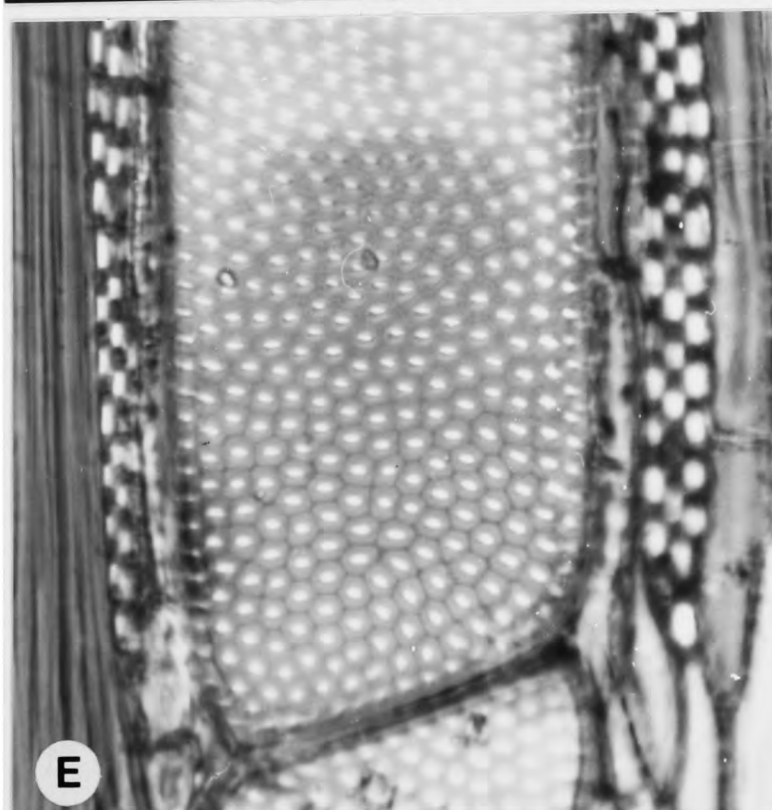
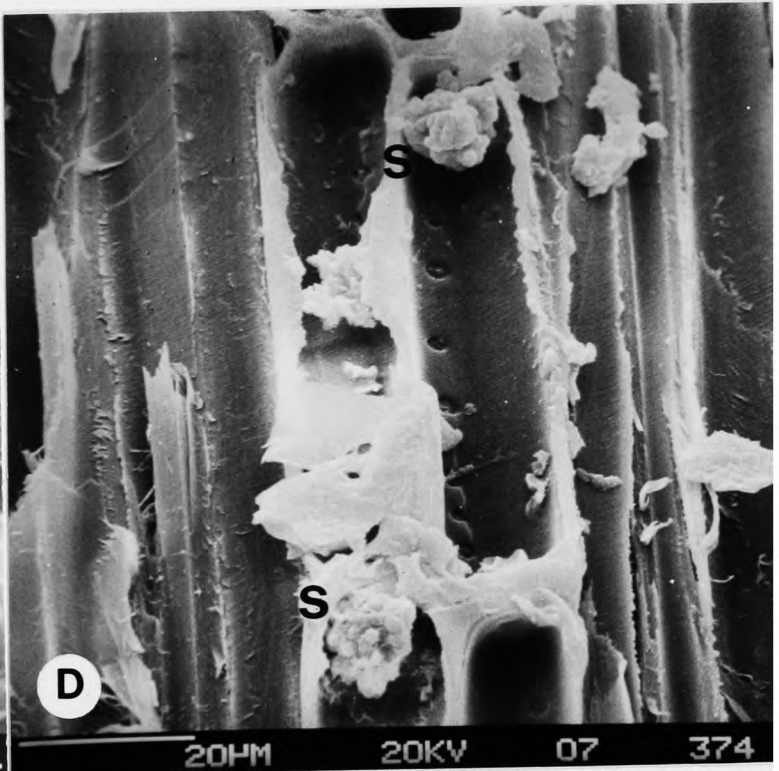
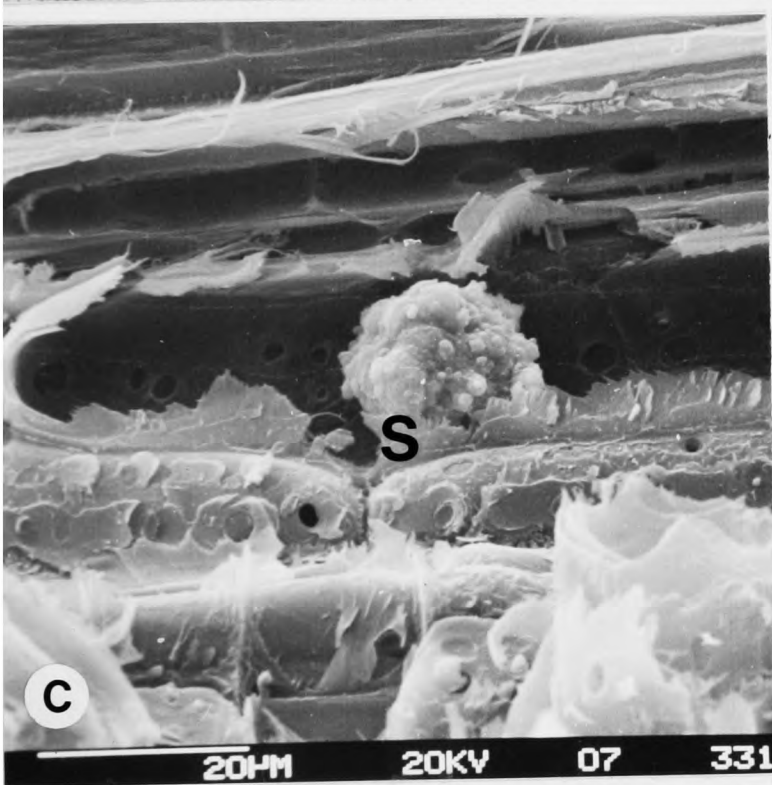
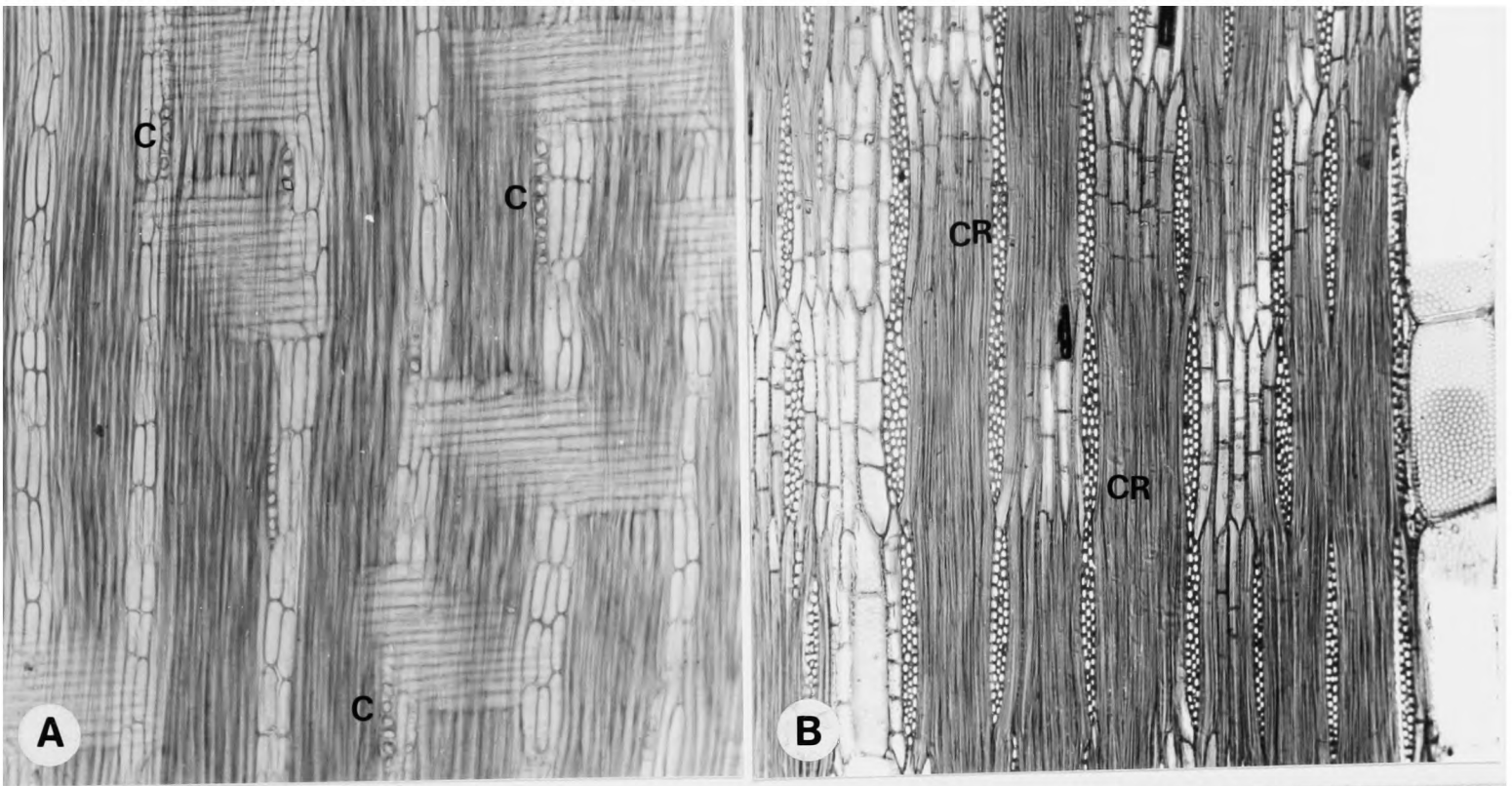


Fig. 2.25. Light and SEM photomicrographs of Dialium wood, radial A and F, x 70 and x 340, respectively and tangential B and E, x 70 and x 340, respectively. A, D. platysepalum (Normand 604, Sumatra); B, D. procerum (FRI 16234, Peninsular Malaysia); C, D. guianense (Krukoff B6262, Brazil); D-E, (same as B); F, D. dinklagei (Letousey 11440, Cameroon).

c = crystals; cr = confluent rays; s = silica



Other features common to Dialium wood are occurrence of long confluent rays (Fig. 2.25, B), i.e. connected end-to-end becoming 2 to 3 times longer than ordinary rays; sharply angular ends of axial parenchyma strand (Fig. 3.6, C) and alternate intervessel pittings (Fig. 2.25, E). The rays are homocellular, i.e. where the marginal cell is of the same height as the body cell. This is not strictly so, however, because in all species examined, the rays always have some marginal cells twice higher than the body cells.

An unusual inclusion was observed in one sample of D. dinklagei (Fig. 2.25, F). Here, some axial parenchyma as well as ray cells are completely filled with rather granular blackish deposit as observed under the light microscope and as seen in the photomicrograph. This inclusion could be tanniniferous material (Metcalf and Chalk, 1950), resin or amorphous, i.e. non-crystalline bodies of silica (Amos, 1952; Koeppen, 1967).

2.3. Palynology

2.3.1. General

I have examined representative samples of all species under the scanning electron microscope (SEM). There are two general types of sculpturing patterns that can be drawn, namely: finely striate and finely to coarsely reticulate. Within these types, intergrading ones occur. In finely striate pollen, for example, striato-punctate occurs in some samples of D. polyanthum (Fig. 2.28, F). Sometimes striations cross or meet each other more or less sharply to form checker-like patterns as in D. pobeguinii and D. schlechteri (Fig. 2.26, C,D). Reticulate sculpturing ranges from rather coarse, i.e. with distinct muri as in D. kunstleri and D. madagascariense (Fig. 2.28, A & B) and D. indum (Fig. 2.27, F) to finely reticulate as in D. englerianum,

D. hydnocarpoides, D. ovoideum (Fig. 2.27, C,D & E) and D. cochinchinense (Graham and Barker, 1981).

An intergrading type between striate and reticulate patterns is shown in D. guineense (Fig. 2.27, A) which is striato-reticulate. The reticulate pattern displayed by D. zenkeri (Fig. 2.27, B) is rather different because the muri are broad and rather smooth. In D. platysepalum the sculpturing is punctate (see Fig. 2.28, E).

Except for the sculpturing of the tectum, other characters based mainly on external morphology are common to all species. I have not gone to the extent of looking at the structure of the cross-section of the pollen which may reveal important taxonomic features.¹ My reason is given in Chapter 1, section 1.2.2.

Light photomicrographs of pollen of some species were also taken. These are shown in Fig. 2.29.

2.3.2. Description of Dialium pollen (Figs. 2.26 - 2.29)

Pollen grains suboblate to oblate spheroidal, small, P/E c. 78-95%, equatorial outline trilobed, tricolporate, very rarely trisyncolporate (D. platysepalum). Size: P (14-) 16-19 (-22) μ m. E (17-) 19-23 (-26) μ m. Colpi 3/4 to equal in length to polar axis, c. 2-3 μ m wide at the equator, rather sunken, tapered to a sharp point near the pole (except D. platysepalum). Apertures circular or rather oval, c. (2-) 3-4 (-6) μ m in diameter. Sculpturing of the tectum finely striate (subgenus Arouna section Arouna), micro-reticulate (subgenus Arouna section Codarium and some species in subgenus Dialium) or coarsely reticulate with distinct muri (subgenera Dansera and D. indum) or intergrading types like striato-reticulate (D. guineense) or punctate (D. platysepalum), microperforations/lumina c. 0.1-0.3 (-0.6) μ m in diameter, [†] irregular in shape from isodiametric, circular to angled, muri (for coarsely reticulate) c. 0.2-0.4 (-0.5) μ m wide.

Fig. 2.26. Pollen of Dialium, subgenus Arouna section Arouna. A, D. guianense (Irwin, et al. 5536, Surinam); B, D. orientale (Elliot 746, Kenya); C, D. pobeguinii (Deighton 175, Sierra Leone); D, D. schlechteri (Gomes et Sousa 1650, Mocambique); E, D. pentandrum (Louis 4017 type, Zaire); F, D. tessmannii (Donis 1653, Zaire).

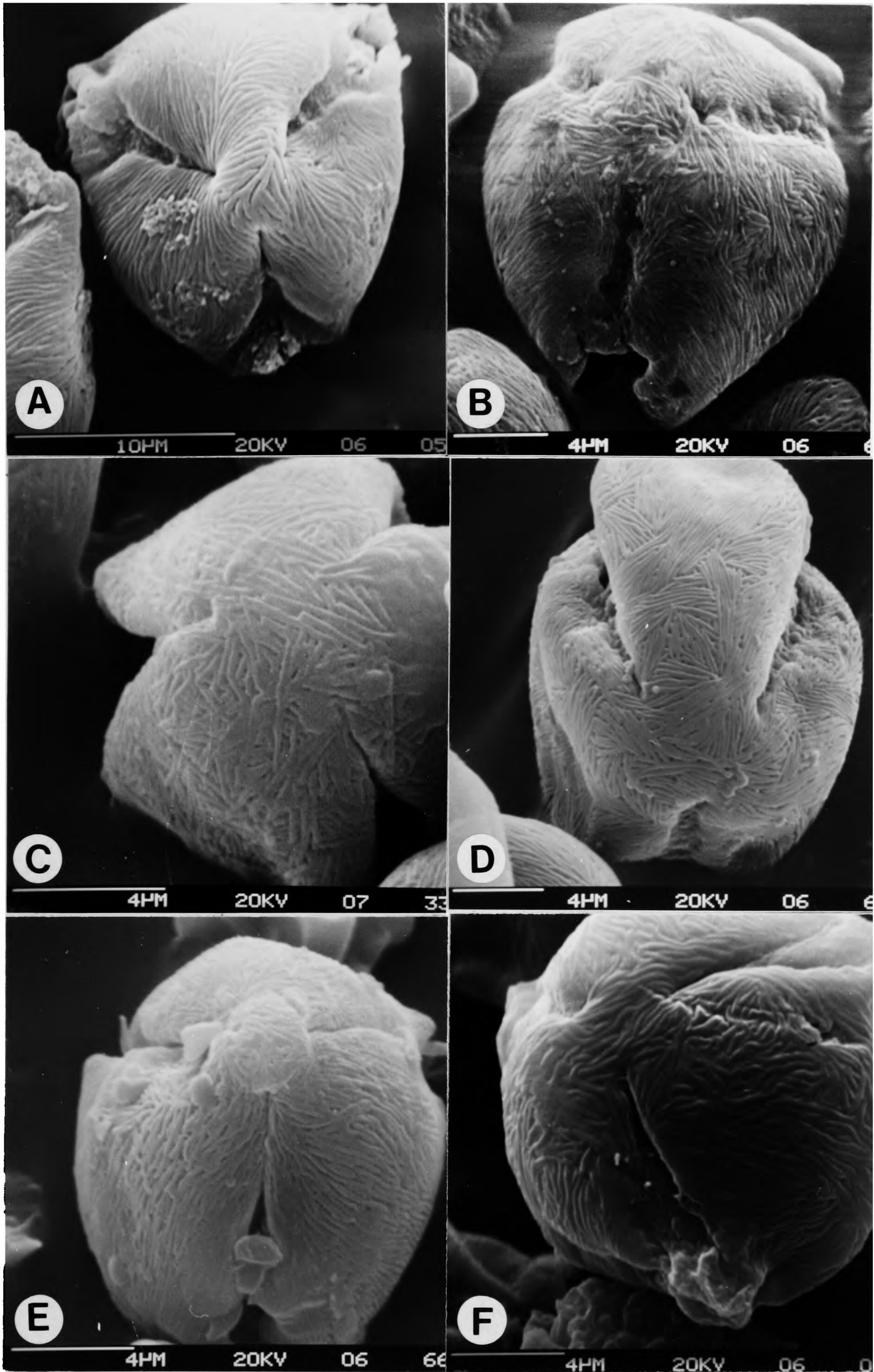


Fig. 2.27. Pollen of Dialium, subgenus Arouna section Codarium (A-C) and subgenus Dialium (D-F). A, D. guineense (Moore 165, Ghana); B, D. zenkeri (Soyaux 303, Gabon); C, D. englerianum (Barros Machada 13911B, Angola); D, D. hydnocarpoides (185T.3P.540, Sumatra); E, D. ovoideum (Kostermans 24514, Sri Lanka); F, D. indum (Reinwardt? s.n., Java).

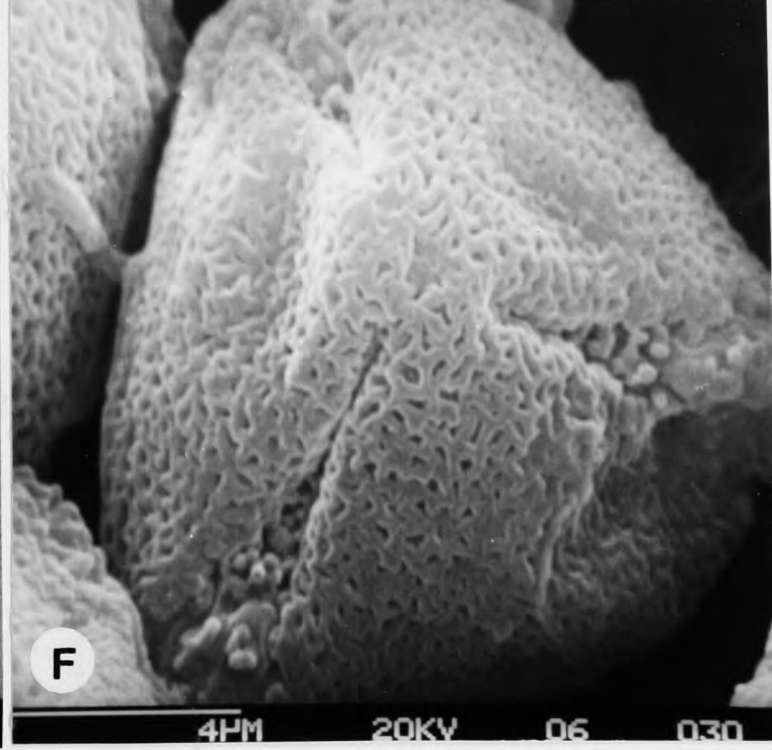
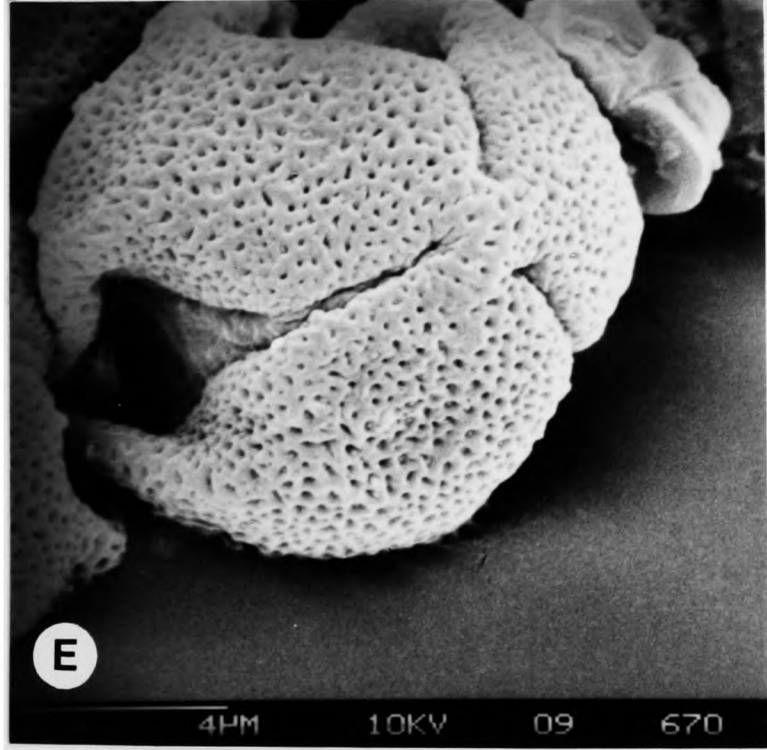
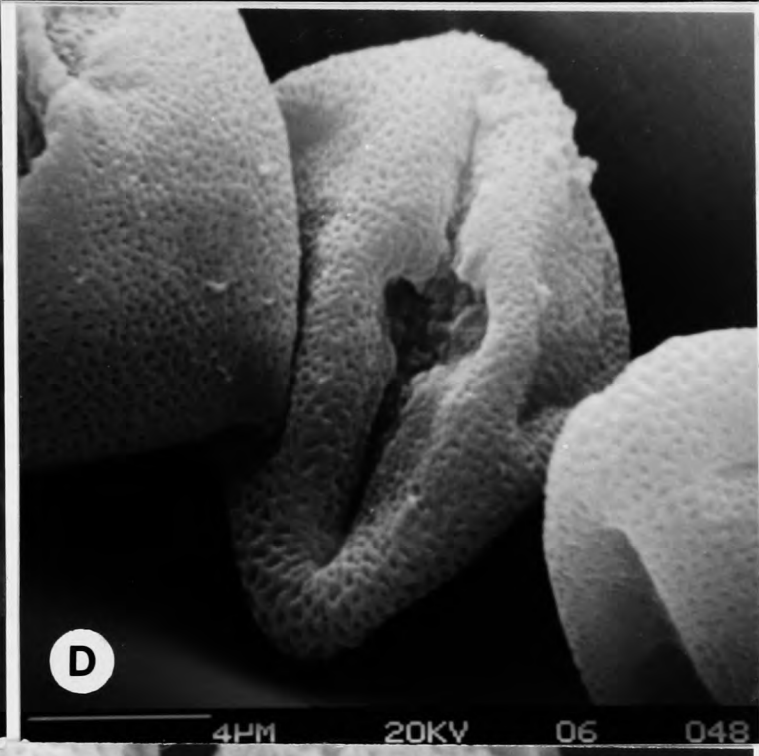
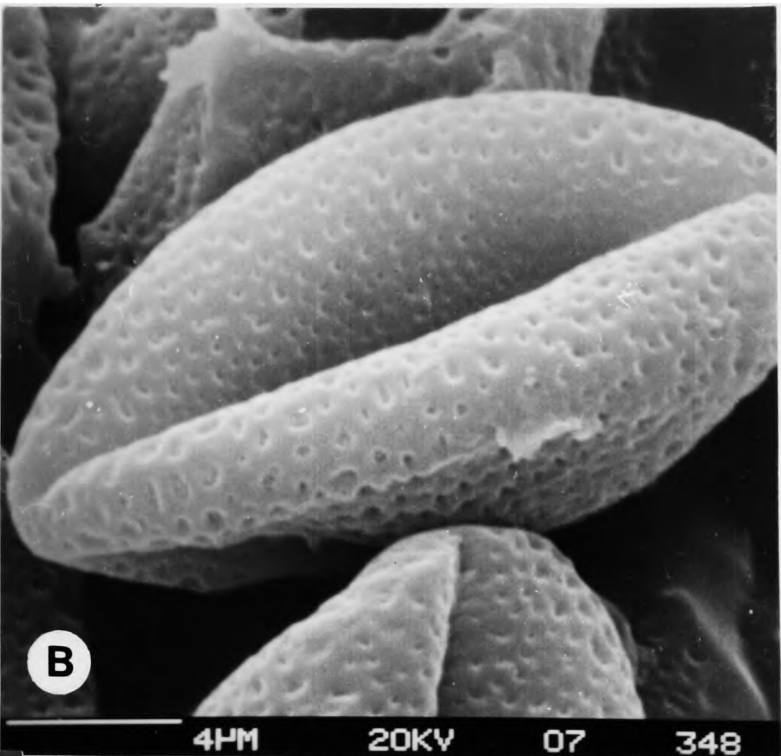
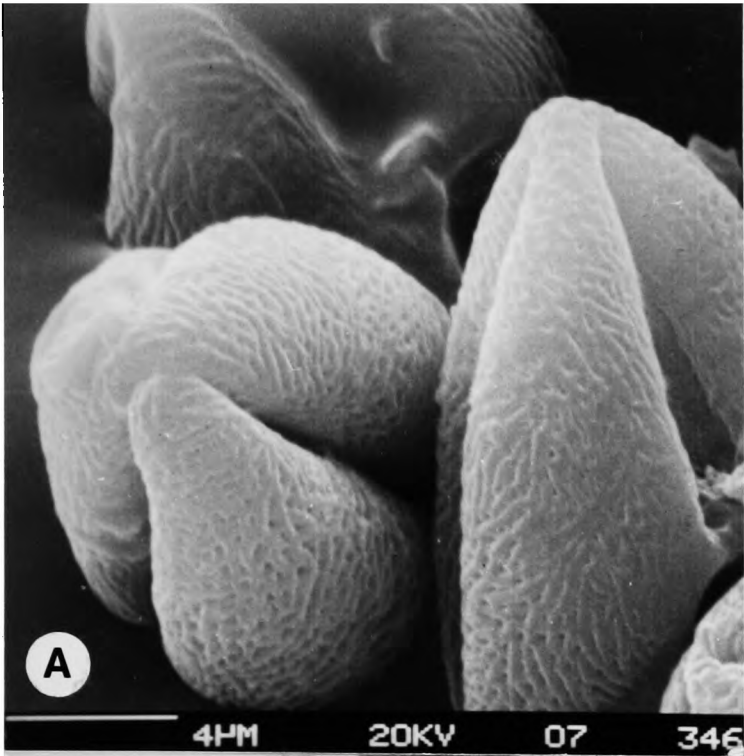
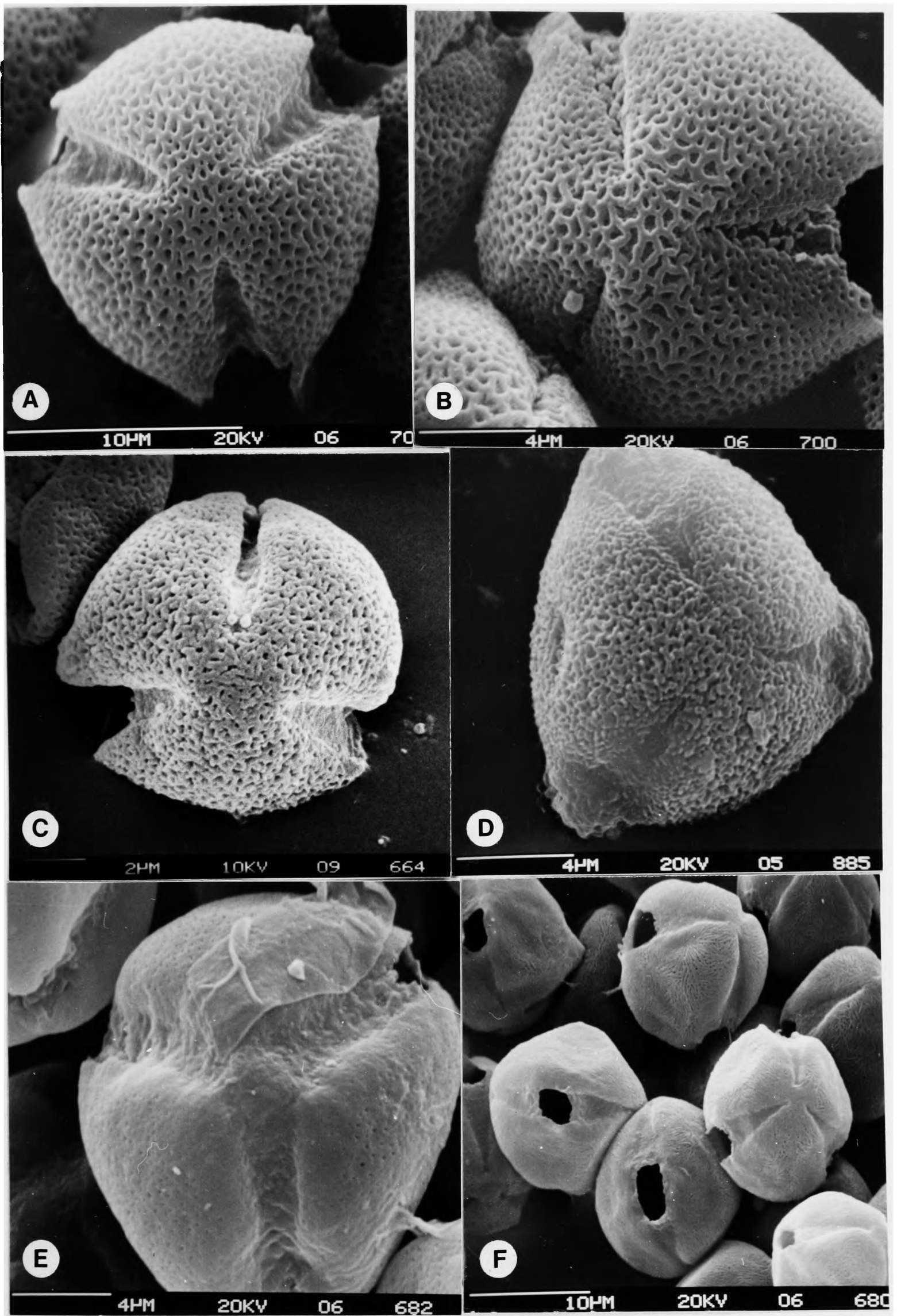


Fig. 2.28. Pollen of Dialium, subgenus Dansera (A-D), subgenus Dialium (E) and subgenus Arouna section Arouna (F). A, D. mada-
gascariense (8625 SF, Madagascar); B, D. kunstleri var. kunstleri
(SAN 65841, Sabah); C. D. occidentale var. septentrionale
(24499 SF, Madagascar); D. D. procerum (117T.3P.579, Sumatra);
E, D. platysepalum (Shouts 8337, Peninsular Malaysia); F, D.
polyanthum (Zenker 950, Cameroon).



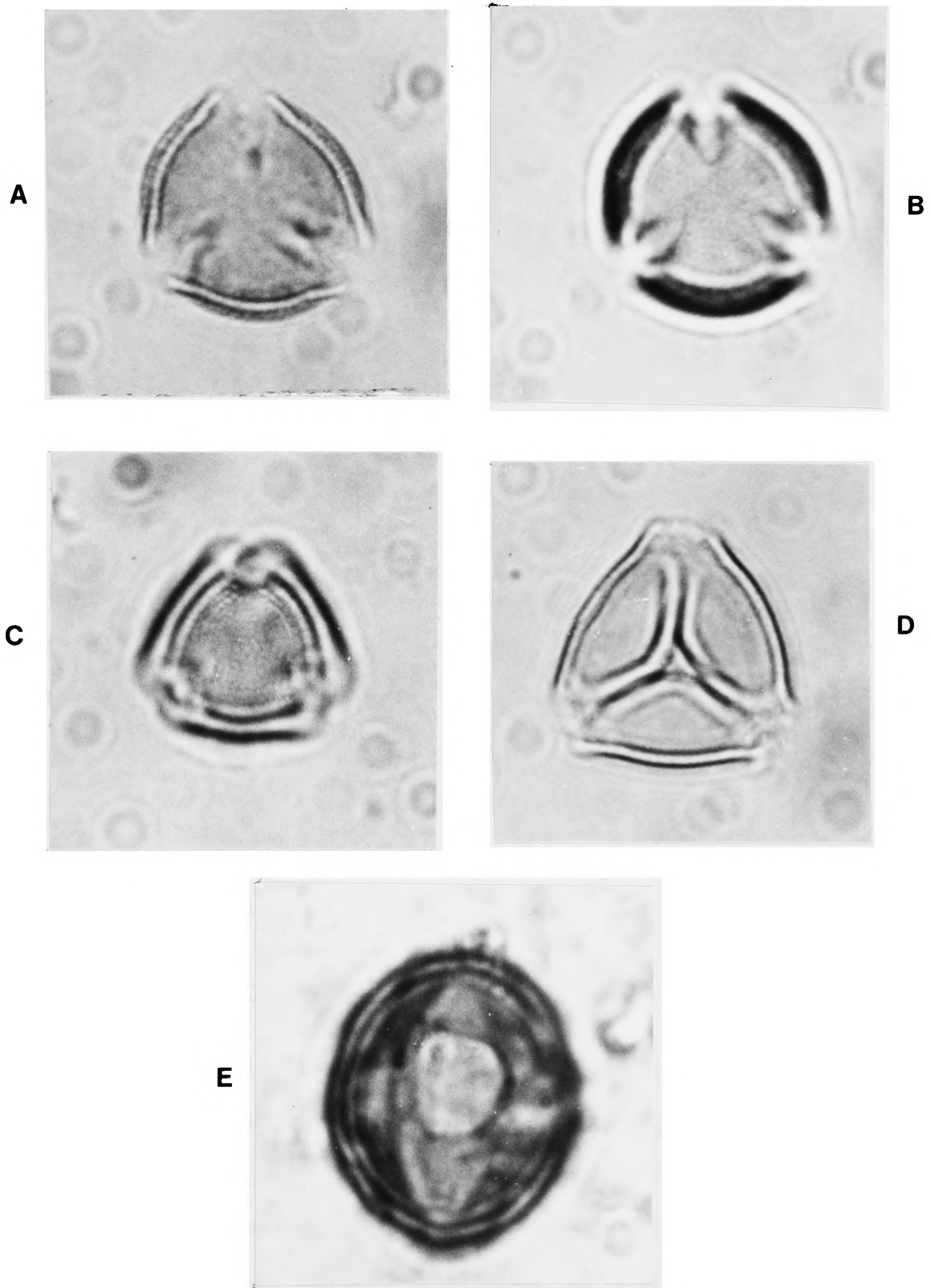


Fig. 2.29. Light photomicrographs of pollen of some Dialium species. A and B, D. madagascariense (8625 SF, Madagascar); C, D. indum (Reinwardt s.n., Java); D, D. platysepalum (Kunstler 8187, Peninsular Malaysia); and E, D. guineense (Hepper 1465, Cameroon). A, polar view showing outline of exine wall; B and C, polar surface view showing reticulate sculpturing; D, polar view showing colpi meeting at the pole (trisyncolporate); E, equatorial view showing endoaperture in surface view. All c. X2200.

The figures shown in SEM photomicrographs are arranged starting with the pollen type of subgenus Arouna section Arouna (Fig. 2.26) followed by subgenus Arouna section Codarium (Fig. 2.27, A-C), subgenus Dialium (Fig. 2.27, D-F) and subgenus Dansera (Fig. 2.28, A-D). The only species possessing a syncolporate pollen is D. platysepalum (Fig. 2.28, E). Figure 2.28, F, is D. polyanthum showing equatorial and polar views, apertures (common to all Dialium species) and the striato-punctate sculpturing pattern.

2.4. Cytology

I have not been successful in obtaining root tips from the seedlings of D. indum and D. platysepalum (both W Malesian species) I raised in the glasshouse. The published chromosome counts for the genus were obtained by Mangenot and Mangenot (1957) from D. aubrevillei (now D. polyanthum), D. dinklagei and D. guineense (Atchison, 1951; Mangenot and Mangenot, 1962). The chromosome number is $2n = 28$. Taxonomically, this count agrees with most genera in Cassieae where the basic number is $x = 14$ (Goldblatt, 1981).

2.5. Phytochemistry

Castagne (1933) was the first to publish an analysis of the chemical composition of the fruits of two Dialium species (D. pachyphyllum and D. polyanthum). This was followed in the same vein by Erhaar (1948) on the endocarp of D. indum of which he found that it has low tartaric acid content when compared with Tamarindus indica L. and concluded that it could not be recommended for commercial use.

The seeds (cotyledons) of Dialium species were studied for polysaccharides (especially amyloids) and phytohaemagglutinins (see Harborne, Boulter and Turner, 1971). These studies have interesting taxonomic implications because the results more or less conform to

the current taxonomic classification of the Cassieae, particularly Dialiinae. Toms and Western (1971: p. 380) found that Dialium cotyledons have negative reactions to the amyloid test. The presence of amyloid is indicated by blue stain when cotyledons are applied with iodine. Other genera which are now included in the new subtribe Dialiinae like Apuleia, Dicorynia, Distemonanthus, Koompassia, Martiodendron and Storckiella, also have negative reaction to the amyloid test. Phytohaemagglutinins are used to agglutinate erythrocytes. Bailey (1971: p.526) found that D. guineense seeds are non-haemagglutinating. A related genus Ceratonia is found to be also non-haemagglutinating.

There are no further published data available on the phytochemistry of Dialium. Other parts of the plants, especially the leaves, must be studied for chemical compounds which may be useful for taxonomy.

3. THE SUBTRIBE DIALIINAE

In this chapter, the morphological data of the genera in the Dialiinae are reviewed in the light of this study of Dialium which is the type genus of the newly circumscribed subtribe (Irwin and Barneby, 1981). The main purpose of the review is to find out how closely interrelated the genera in Dialiinae are and how closely the rest of them are to Dialium. The data on wood anatomy and pollen morphology are new.

3.1. General

The tribe Cassieae as circumscribed by Benthham in 1865 (for historical review see Koeppen and Iltis, 1962) has recently been subdivided into five subtribes by Irwin and Barneby (1981). The tribe had become unwieldy because of the "excessive morphological diversity" brought about by the addition of taxa, especially during the 20th century, which could no longer be accommodated properly within the tribe sensu Benthham (Hutchinson, 1964; Irwin and Barneby, 1981). The number of genera and species of each subtribe in Irwin and Barneby's scheme are as follows:

Cassiinae - 3 genera (Cassia, 30 spp.; Senna, 240 spp.; Chamaecrista 250 spp.) with 520 species

Ceratoniinae - 1 genus (Ceratonia) with 2 species

Duparquetiinae - 1 genus (Duparquetia) with 1 species

Labicheinae - 2 genera (Labichea, 9 spp.; Petalostylis, 3 spp.)

with 12 species

Dialiinae - 14 genera (Androcalymma, 1 sp.; Apuleia, 1 sp.; Baudouinia, 4 spp.; Dialium, 27 spp. presently recognised; Dicorynia, 2 spp.; Distemonanthus, 1 sp.; Eligmocarpus, 1 sp.; Kalappia, 1 sp.; Koompassia, 3 spp.; Martiodendron, 4 spp.; Mendoravia, 1 sp.; Storckiiella, 3 spp.; Uittienia, 1 sp.; and Zenia, 1 sp.) with 51 species

3.2. Concept of the Subtribe Dialiinae

As indicated in their key to the subtribal taxa, Irwin and Barneby (1981) divided the five subtribes into two major groups (i.e. Dialiinae in one group and Cassiinae, Ceratoniinae, Duparquetiinae and Labicheinae in another group) using mainly the distinguishing features of the inflorescence, the fruit (pod) and the leaves. The Dialiinae possesses the following features: inflorescence cymose-paniculate; pod either drupaceous or samaroid-discoid, indehiscent or only tardily dehiscent, 1 to few-seeded; leaves imparipinnate or reduced to a terminal leaflet. In contrast, the other four subtribes (Cassiinae, Ceratoniinae, Duparquetiinae and Labicheinae) have: inflorescence spirally racemose or, if paniculate, composed of racemose elements; fruit commonly a conventional pod, either dehiscent or indehiscent, usually several-seeded, never drupaceous, leaves paripinnate or imparipinnate. These four subtribes were further separated by flower characters (see Irwin and Barneby, 1981: p. 100).

The concept of the Dialiinae as defined by Irwin and Barneby (1981) is, I consider, firmly based on the "cymose-paniculate inflorescence and, with rare exceptions, in the indehiscent, drupaceous or samaroid fruit". This brief definition, however, indicates that the taxa in the subtribe are not very homogeneous with regard to fruit (i.e. contrasting fruit types - drupaceous or samaroid) and leaf (i.e. simple and imparipinnate or reduced to a terminal leaflets) types. What really holds the subtribe together is the "cymose-paniculate inflorescence" that its member taxa all have in common. This type of inflorescence is distinct enough to delineate the Dialiinae from the other subtribes in the Cassieae. The basic difference is that Dialiinae have an inflorescence composed of cymose units whereas the other 4 tribes have inflorescence composed of racemose units.

3.3. Review and Comparison of Characters of the Genera (see Tables 3.1 - 3.3)

The Dialiinae with 14 genera is the biggest subtribe of the Cassieae of which two are monotypic, one is ditypic and one has 3 genera. Because of its size, a revision of its taxa (excluding Dialium) would perhaps entail the same length of time as spent in the study of Dialium. For this reason it was not possible to make a detailed study. However I have looked at representative specimens of all species in it and have checked my observations against the published data. Based on my observations, I agree with Irwin and Barneby that the genera in the subtribe, which are generally recognised on the basis of flower and fruit characters, are distinct from each other. There are, however, some genera that are more closely related to each other than they are to Dialium (see Table 3.2, column 5 and Table 3.3, column 2). These genera require a thorough investigation on which to base taxonomic and nomenclatural decisions which, unfortunately, are beyond the scope of this study.

For the same reason, only illustrations of wood anatomical structures and pollen exine are shown here. Figures 3.2 - 3.3 and 3.4 - 3.6 show the wood anatomical structures and pollen exine of representatives of the Dialiinae. These features were not covered by Irwin and Barneby. They, however, discuss and illustrate flowers and fruits of representatives of the subtribe, see Irwin and Barneby (1981) Fig. 1 (p. 99) for flowers and Fig. 2 (p. 103) for fruits. There are also illustrations of flowers and fruits in the revisions of Koeppen (1963; 1967) and Koeppen and Iltis (1962) on Androcalymma and Dicorynia, and Martiodendron, respectively. These published illustrations should be consulted in amplification to the discussion presented here.

The following sections review the morphology of the vegetative parts, inflorescences, flowers, fruits and seeds. Morphological data

are augmented with data on wood anatomy, pollen morphology, cytology and phytochemistry. The more important characters are compared for their similarities and/or differences.

3.3.1. Morphology

3.3.1.1. Vegetative parts

All species in the Dialiinae are unarmed, small to big-sized trees. With the exception of species sometimes growing in savannas and drier habitats (e.g. Dialium englerianum, Dialium schlechteri), the majority of them (especially rain forest species) exhibit long and straight trunks with more or less smooth bark surfaces. In Dialium, all member species produce reddish-brown sap from the cut inner bark. This reddish-brown exudate has not been reported to occur in trees of other genera in the Dialiinae. It, however, also occurs in other legume genera, e.g. Pterocarpus (Corner, 1940; Whitmore, 1972; Rojo, 1972) and Inocarpus (Corner, 1940).

The leaves of the Dialiinae are mostly imparipinnate. The rest are unifoliolate (i.e. reduced to a terminal leaflet) or simple. Among the imparipinnate ones, Eligmocarpus is unique because its leaflets are opposite instead of alternate. The unifoliolate leaves of Dialium subgenus Dansera and Uittienia are articulate and with pulvinus. In Uittienia, however, the point of articulation is swollen and resembles a pulvinus.

The leaf blades of Dialiinae are entire. The shapes of the blades vary only slightly but are basically elliptic, oblong or ovate. In terminal leaflets the blades are usually widest above the middle; lower leaflets are generally widest below the middle and usually with an inequilateral base.

Stomata are mostly of the paracytic type. Watson (1981) noted anomocytic to actinocytic stomata in Baudouinia. As noted (see Chapter 2)

in Dialium, paracytic stomata are predominant but variations can sometimes be observed on a specimen even in a single microscope field. This has also been noted by Watson (1981) that stomata in Caesalpinoideae are preponderantly of the paracytic type and that it is invariably possible in any preparation to detect a few aberrant stomata.

Hairs are generally simple and unicellular (see Fig. 2.5 A and B). Watson (1981) observed papillae and simple hairs (sometimes with a 'gland' base) in Dicorynia guianensis Amsh. A globular papillae is also noted in Dialium englerianum (see Chapter 2). No other types of hairs have been observed.

The vascular bundles at the middle cross section of the pulvinus are of two patterns, i.e. with either 1 or 2 ridge bundles at the adaxial side (see Table 3.1, column 15). For discussion of anatomy of the pulvinus, see Chapter 5.

3.3.1.2. Inflorescences

The type of inflorescence is the principal basis for the delimitation of subtribal ranks in the Cassieae as discussed above. In Dialiinae, inflorescences are cymose-paniculate. They are either axillary or terminal. Sometimes axillary panicles occur in species which have mainly terminal panicles (e.g. Dialium indum Fig. 2.7) and vice-versa (see Dialium procerum Fig. 2.8). It is significant to note that axillary panicles have short branches (to c. 10 to 15 cm long) with fewer flowers. Those species with terminal inflorescences have longer branches which are many-flowered. Inflorescence axes are hairy and generally appear blackish to dark greyish brown when dry.

3.3.1.3. Flowers

There are two receptacle types in flowers of members of the Dialiinae, i.e. with a disc and without a disc. Only Dialium subgenus Arouna,

Uittienia and Zenia have a disc. The disc in Uittienia (Fig. 3.1, d) is thicker than in subgenus Arouna and Zenia. In the perianth, the most conservative part is the calyx. Sepals are mostly five; only two taxa, i.e. Apuleia and Dialium subgenus Dansera have 3 sepals. The majority of the genera have sepals which are strongly imbricate. In the remaining genera they are slightly imbricate (i.e. Distemonanthus, Koompassia, Martiodendron and Mendoravia) in bud.

Petals are rather variable in number and to a lesser extent in size. They are mostly 5 and, except in Dialium, all genera display more or less showy petals which are bigger than the sepals especially at anthesis (see Table 3.2, column 5-7).

The stamens are more variable in number than the petals. In Dialium, for example, they are mostly 2, then followed by 3, 5 or (8-) 10 stamens. The rest of the Dialiinae have stamens that fall within the range of numbers in Dialium except Mendoravia which has 11 to 12 stamens (see Table 3.2, column 2).

The anthers are all basifixed and sagittate at the base. There are two types of anther dehiscence, i.e. dehiscing by lateral slits and dehiscing by a terminal pore. Dialium together with Storckiella, Uittienia and Zenia dehisce by longitudinal slits and the rest dehisce by a terminal pore. Within Dialium, the shape of the anther apex provides important distinguishing characters (see Chapter 2).

The ovary is usually densely adpressed hairy and contains usually 1 to 3 ovules. Baudouinia, Eligmocarpus, Kalappia, Storckiella and Zenia have more than 4 ovules and usually produce more than 1 seed per pod. Those genera with 1 to 3 ovules often produce only 1 seed.

3.3.1.4. Fruits

The fruits are indehiscent (except Baudouinia) and are either drupaceous or samaroid-discoid, and they provide good taxonomic characters within the subtribe. Dialium is the only genus with more or less

Table 3.1. Legend

- AF - Africa; SA - South America; IM - Indo-Malesia
- MA - Madagascar; WM - West Malesia; NC - New Caledonia
- CV - China and Vietnam; EM - East Malesia; WA - West Africa
- + - 1 inner bark exudes reddish-brown sap, 2 leaves imparipinnate, 3 inflorescence essentially terminal, 4 receptacle with disc, 5 flower bud imbricate, 6 sepals 5, 7 petals not showy, 8 stamens usually 2, 9 anther dehiscence by lateral slit, 10 one to 3-ovuled, 11 fruit with crustaceous exocarp and pulpy endocarp, 12 seed with irregularly-cracked testa surface, 13 pollen sculpturing striate, 14 axial parenchyma inclusion with crystals and silica together, 15 mid pulvinus one ridge bundle.
- a - leaves simple and articulate
- +o - leaves imparipinnate and leaflets opposite
- e - leaves simple and exarticulate
- - 1 inner bark not exuding reddish-brown sap, 3 inflorescence essentially axillary, 4 receptacle without disc, 5 flower bud valvate to slightly imbricate at the base, 6 sepals 3, 7 petals showy or larger than the calyx, 8 stamens usually 5 or sometimes to 7, 9 anther dehiscence by apical pore or transverse slit, 10 ovules more than 4, 11 fruit non-crustaceous exocarp and without pulpy endocarp, 12 seed testa not as in Dialium, 13 pollen sculpturing reticulate, 14 axial parenchyma inclusion silica only, 15 mid pulvinus 2 ridge bundle
- / - 8 stamens usually 3 or 4
- o - 8 usually 10 or up to 12 stamens, 13 pollen sculpturing coarsely scabrate-punctate, 14 axial parenchyma inclusion oxalate crystals only
- na - data not available
- + - - 13 pollen sculpturing of which both striate and reticulate types occur

Table 3.1. Summary of important taxonomic characters in Dialiinae

Genera	No. Species	Region	Inner bark	Leaves	Inflo- rescence	F	1	0	w	e	r	s	Fruit	Seed	Pollen	Wood	Pul- vulus
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
DIALIUM																	
Arouna	17	AF-SA	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dialium	5	IM	+	+	+	-	+	+	+	+	+	+	+	+	-	0	-
Dansera	5	MA-WM	+	a	-	-	+	-	+	+	+	+	+	+	-	-	+
APULEIA	1	SA	-	+	-	-	+	-	-	/	+	+	-	-	-	+	na
DICORYNIA	1	SA	-	+	+	-	+	+	-	+	-	+	-	-	-	-	+
ANDROCALYMMA	1	SA	-	+	+	-	+	+	-	/	-	+	na	na	-	0	na
STORCKIELLA	3	NC	-	+	+	-	+	+	-	0	-	-	-	-	-	0	+
ZENIA	1	CV	-	+	+	+	+	+	-	-	+	-	-	-	-	na	na
KALAPPIA	1	EM	-	+	+	-	+	+	-	0	-	-	-	-	-	0	+
DISTEMONANTHUS	1	WA	-	+	+	-	-	+	-	-	-	+	-	-	-	+	+
KOOMPASSIA	3	W-EM	-	+	+	-	-	+	-	-	-	+	-	-	+	0	-
MARTIODENDRON	4	SA	-	+	+	-	-	+	-	-	-	+	-	-	-	0	na
ELIGMOCARPUS	1	MA	-	to	-	-	+	+	-	0	-	-	-	-	-	0	-
UITTENIA	1	WM	-	a	-	+	+	+	-	-	+	+	-	-	-	0	+
BAUDOUINIA	4	MA	-	e	-	-	+	+	-	0	-	-	-	-	-	na	na
MENDORAVIA	1	MA	-	e	-	-	-	+	-	0	-	+	-	-	0	0	nil

drupaceous fruit. Uittienia could possibly have a drupaceous fruit as well. There are, however, differences between the fruits of the two genera. In Dialium the fruit (see Fig. 2.18, b) has a thin crustaceous exocarp which is usually hairy and easily crushed or sometimes detached from the adjacent mesocarp. Furthermore, it has a pulpy and edible endocarp which entirely envelops the seed. Also, the fruits are many in one infructescence and the pedicels only slightly increased in diameter (c. 2-4 mm thick) from flowering to fruiting stage.

By contrast, the fruit of Uittienia (Fig. 3.1, f and g) does not have a crustaceous exocarp but instead has a thick (c. 4-5 mm) and hard pericarp which when dry is uncrushable by hardest pressing between two hands. Usually, only one fruit develops from an inflorescence. The original slender few-flowered axillary panicle becomes a thick, one-fruited infructescence. To support the big and more or less globose fruit (c. 4-6 cm x 4-6 cm in diameter), the pedicel increases in thickness to more or less a centimetre from the original thin (c. 1-2 mm) pedicel in the flowering stage. As a result, the stalk of the mature fruit is much thicker than the twig that bears it.

The fruits of the other genera are flattish or compressed and sometimes with membranous wings, as in Apuleia, Koompassia, Martiodendron and Storckiella (see Irwin and Barneby, 1981; p. 103, Fig. 2). These types of fruits predominate in the subtribe (see Table 3.3).

3.3.1.5. Seeds and seedlings

The seeds are usually compressed and reniform in shape with the exception of Uittienia seed. In Uittienia the seed is more or less globose, i.e. following the shape of the pericarp. The specimen examined (Kostermans 5476) is in a bad condition and appears to be devoid of testa. The testa of Dialium seed has been described in Chapter 2. It has an irregularly-cracked surface pattern (see Fig. 2.19). This testa

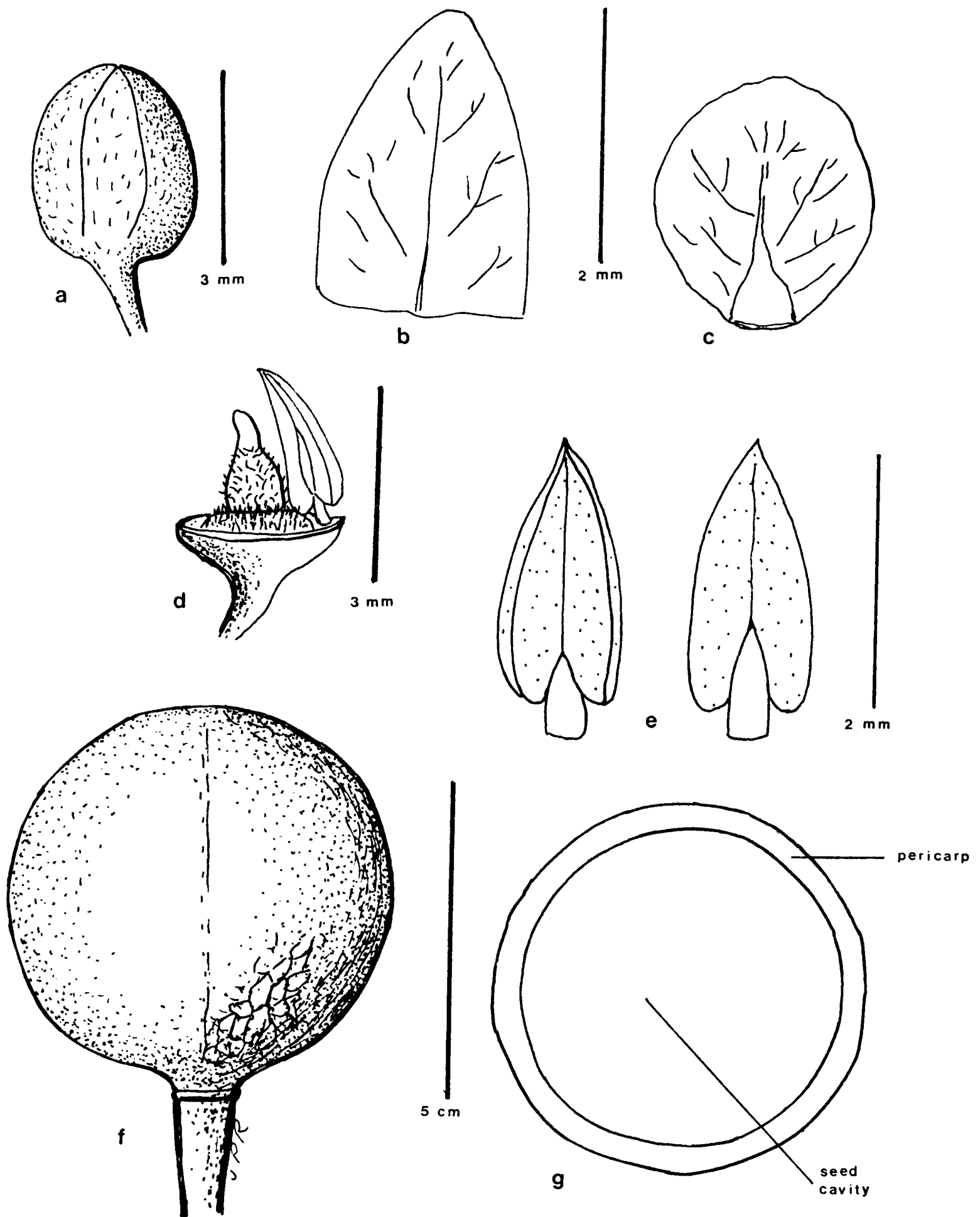


Fig. 3.1. Flower and fruit of Uttienia modesta Steenis. a, unopened bud; b, sepal; c, petal; d, receptacle with ovary and one stamen (i.e. 5 sepals, 5 petals and 4 stamens removed); e, anther adaxial and abaxial sides; f, fruit; g, a transverse section of the fruit. (flower, Kostermans 13413A; fruit, Kostermans 13231, all from Borneo).

surface pattern has been described by Steyaert (1953), Brennan (1967) and Capuron (1968) for seeds of species in Zaire (Congo), east tropical Africa and Madagascar, respectively. Testa of seeds of other genera has not been observed because of lack of material for observation. In published descriptions of seeds of the rest of the genera in Dialiinae, testa surface pattern is usually not included in the description or sometimes only noted as smooth.

Seedling morphology and development have been observed in Dialium (see Chapter 2). The germination or seedling development in Dialium belongs to the "epigeal" (Ng, 1978) or to the "Sloanea subtype A" (Vogel, 1980) types. These germination types have cotyledons exposed (i.e. the testa shed off) above the ground on a long hypocotyl. The former type does not indicate whether the cotyledons are foliar or haustorial while the latter has haustorial or storage cotyledons. Both types of seedling development fall under the "phaneroepigeal" type, a new terminology by Duke and Polhill (1981) indicating cotyledons exposed (i.e. phanerocotylar) and borne above the ground (i.e. epigeal). Seedling development of the rest of the Dialiinae has not been studied and no information could be compiled from literature. Duke and Polhill (1981), however, noted that the Cassieae and the Caesalpinieae generally have phaneroepigeal seedlings with foliar cotyledons.

3.3.2. Wood anatomy (Figs. 3.2 - 3.3)

Anatomy of mature wood of some Dialiinae has been studied, notably by Koeppen (1963, 1967) on Androcalymma and Dicorynia, Koeppen and Iltis (1962) on Martiodendron, Balan Menon (1955) on some W Malesian Dialium and Koompassia and Normand (1950) on Distemonanthus. Wood characteristics and properties have been noted by Record and Hess (1943) on Apuleia, Dicorynia and Martiodendron and Chudnoff (1979) on Distemonanthus and Koompassia. The systematic comparison of caesalpinoid wood with the rest of the Leguminosae have been presented by Baretta-Kuipers (1981).

Data on measurement of structures (vessels, rays and parenchyma in the cross and tangential sections) are obviously not comparable between mature and juvenile wood. I have, therefore, only noted in the juvenile wood inclusions in ray and axial parenchyma (see Table 3.1, column 14) which I consider equivalent to those in the mature wood.

Similarities and/or differences of wood structural features are given below. Each paragraph starts with a summarised description of Dialium wood. This is then followed by comparative descriptions of wood of other genera in the subtribe.

The vessels/pores are diffused, solitary and sometimes in radial multiples of mostly 2-3; the perforations are simple; the intervessel pittings are 8-11 μ m, alternate and mostly vestured. All Dialiinae wood have vessels/pores, perforations and intervessel pitting characteristics similar to Dialium wood.

Rays are storied, occasionally semi-storied, homocellular to sometimes weakly heterocellular with upright marginal cells usually twice higher than the rest of the body cells. Long rays connected end-to-end are common. In Martiodendron the rays are similar to Dialium. In Apuleia, Dicorynia and Distemonanthus the rays differ with Dialium by being distinctly heterocellular (Fig. 3.2 B; Fig. 3.3, E) and long rays being uncommon. Koompassia differs from Dialium by having heterocellular rays; Androcalymma by being non-storied and Storckiella by frequent occurrence of uniseriate rays with biseriate parts (Fig. 3.3, D).

Parenchyma are apotracheal, banded, the bands mostly 2-3 cells wide and discontinuous or broken especially when touching the pores. Strands are mostly 4-celled, usually storied like the rays. The ends of strands on the tangential section are sharply angled (Fig. 3.3, C) instead of gable-like in papilionaceous wood (Reinders-Gouwentak, 1955). The parenchyma patterns of Storckiella and Apuleia are similar to Dialium. Dicorynia, Distemonanthus (Fig. 3.2, C), Koompassia (Fig. 3.3 A),

Fig.3.2. Photomicrographs of Dialiinae wood, transverse x 30, radial x 340, tangential (D and F) x 70 and x 340 respectively. A-B, Apuleia leiocarpa (CFI 9706, Brazil); C-D, Distemonanthus benthamianus (FPRL 18605, Sierra Leone); E-F, Martiodendron excelsa (FPRL 15973, British Guiana).

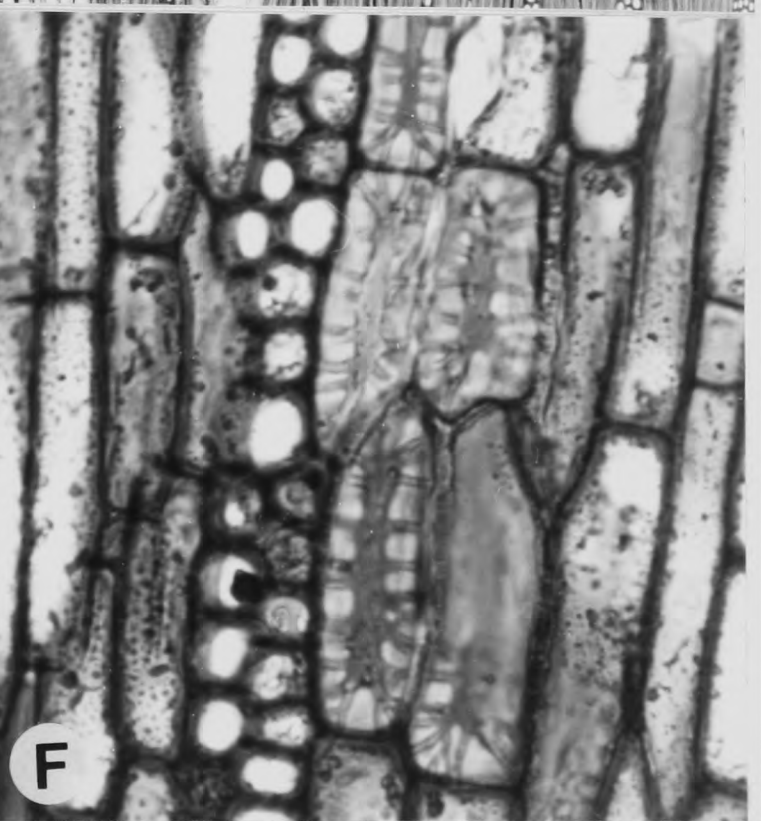
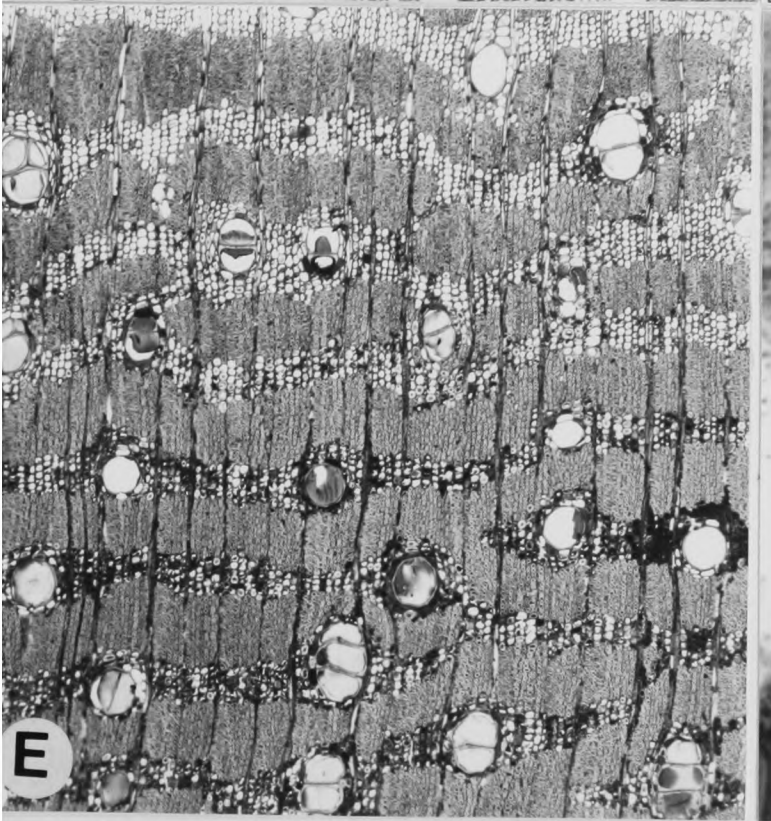
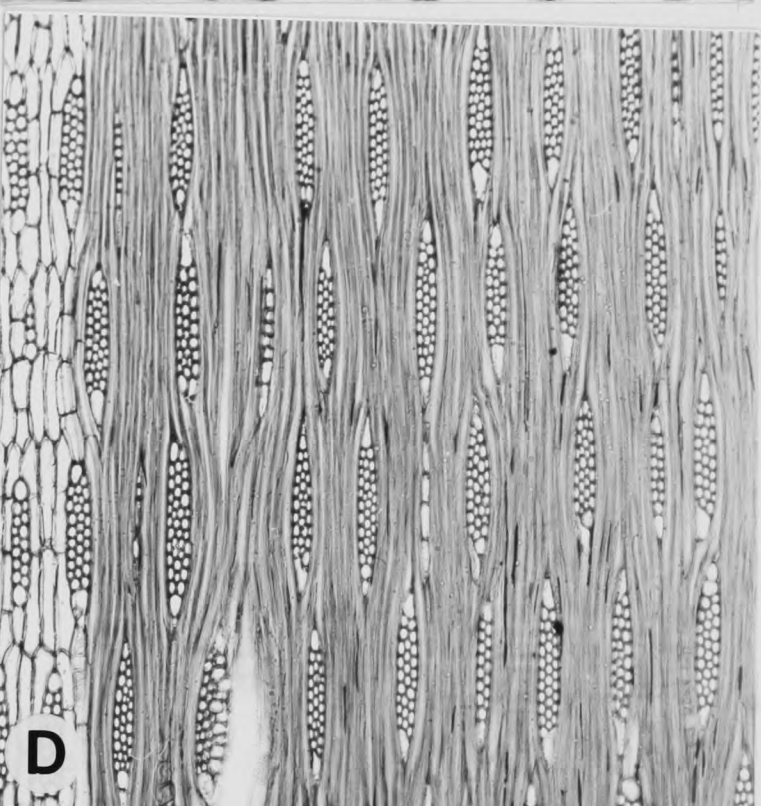
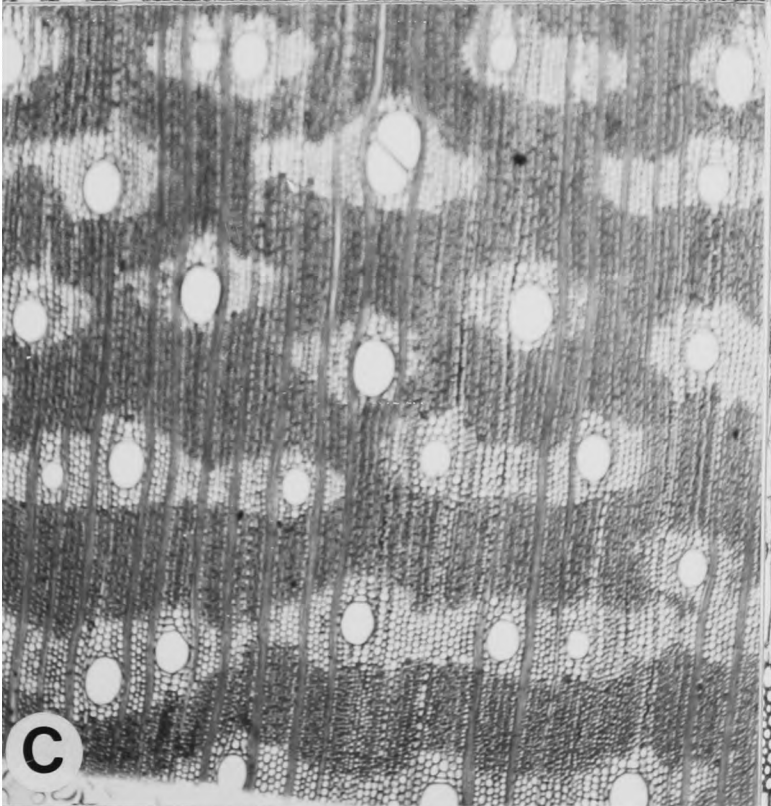
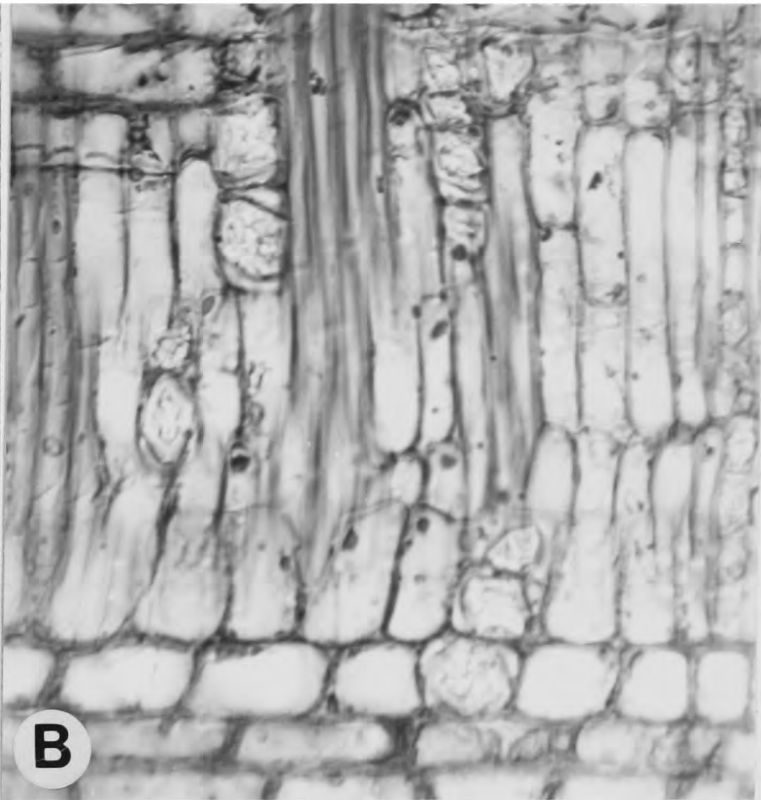
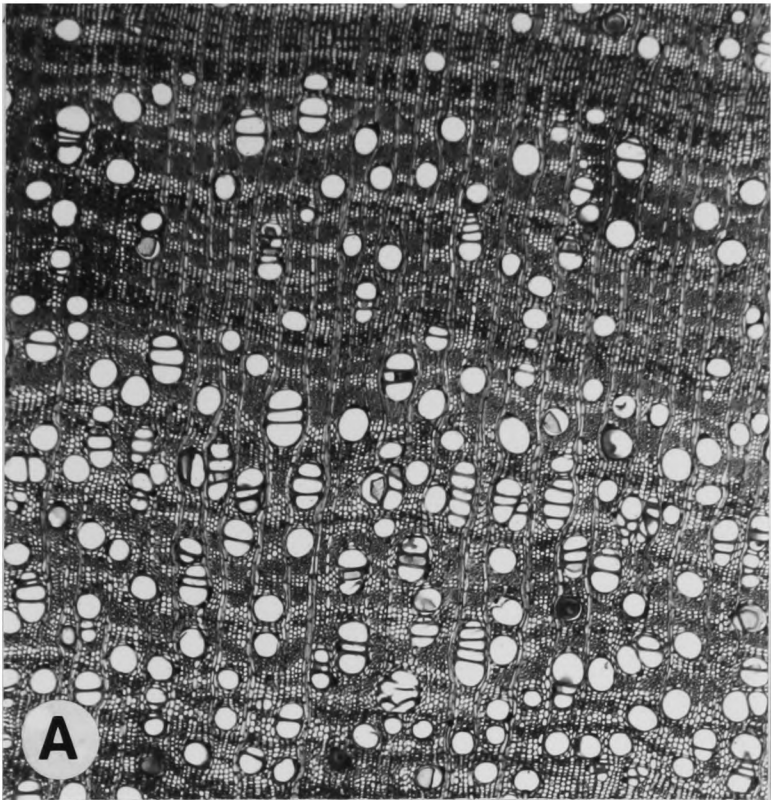
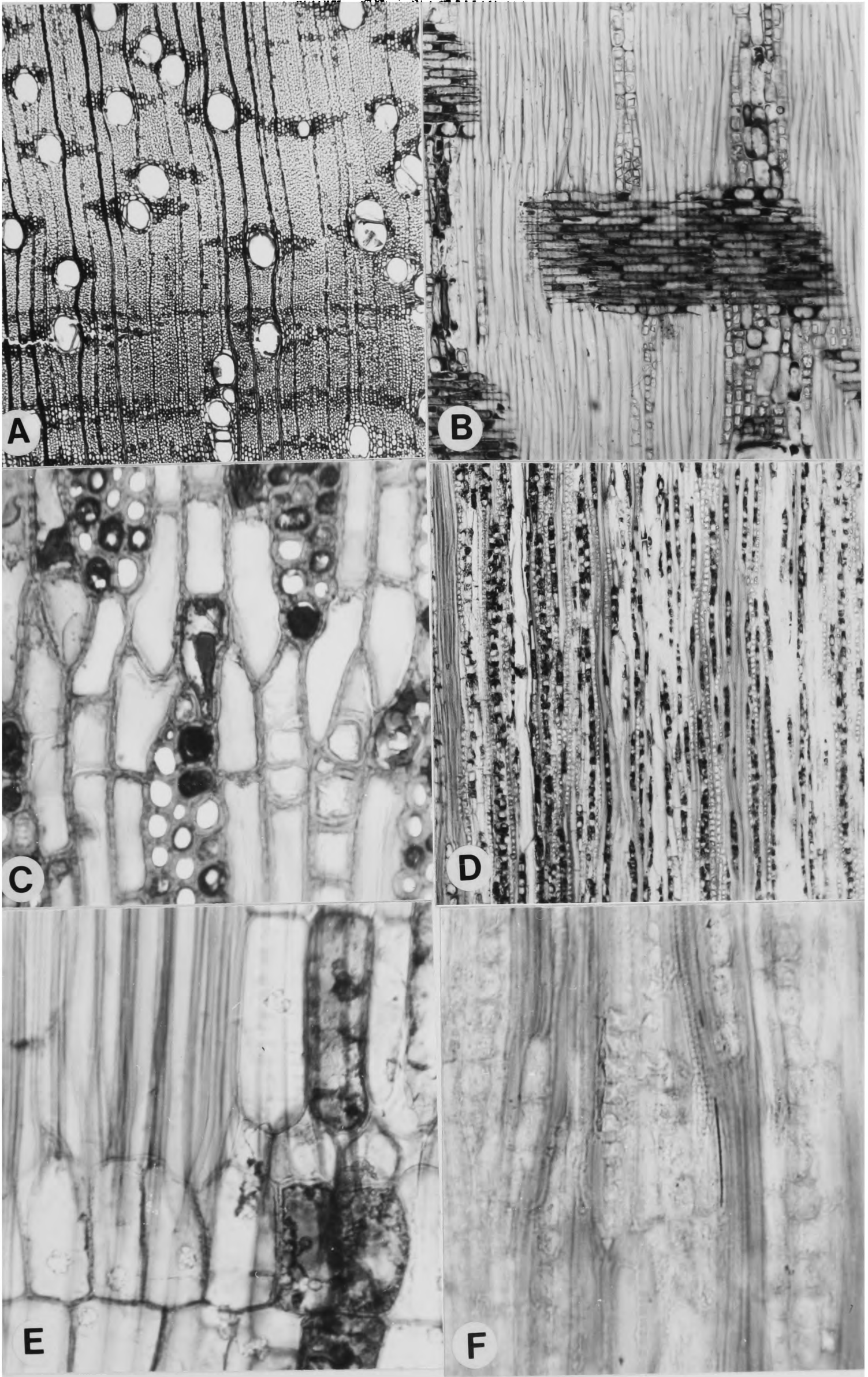


Fig. 3.3. Photomicrographs of Dialiinae wood, transverse
x 30, radial (B and E) x 70 and x 340 respectively,
tangential (C, D and F) x 340, x 70 and x 340, respectively.
A-B, Koompassia grandiflora (Craven & Schodde 1058a, New
Guinea); C, Dialium indum (FMS 161, Peninsular Malaysia);
D, Storckiella pancheri (Vieillard 402, twig, New Caledonia);
E, Dicorynia guinanensis (Y 45576, Surinam); F, Eligmocarpus
cynometroides (McWhirter 204, twig, Madagascar).



Androcalymma and Martiodendron (Fig. 3.2, e) differ from Dialium in having paratracheal aliform to banded rather than apotracheal banded parenchyma. Androcalymma and Martiodendron (Fig. 3.2, F) possess sclerotic parenchyma which do not occur in other Dialiinae wood. Koompassia sometimes have long strands which may extend from 8 to 15 cells long instead of the average 4 cells usual in the subtribe.

Inclusions or deposits in axial parenchyma are either exclusively with oxalate crystals in chambered strands, exclusively with silica or both silica and oxalate crystals occur together in the same wood. Oxalate crystals are abundant in Kalappia, Koompassia, Martiodendron, Storckiella and Uittienia which conform with those in subgenus Dialium. Crystals are rather few in Eligmocarpus and Androcalymma. Koeppen (1967) found few oxalate crystals in one sample of Dicorynia. In Apuleia (Fig. 3.5, B) and Distemonanthus the crystals do not only occur in axial parenchyma but also in marginal cells. Silica inclusions are present in Apuleia, Dicorynia and Distemonanthus which agree with those of subgenera Arouna and Dansera in Dialium. Dicorynia (Fig. 3.3 E), however, also has silica inclusions in marginal cells. A unique combination of inclusions is found in the wood of Apuleia where oxalate crystals occur in ray parenchyma and both silica and crystals are present in axial parenchyma.

Mature wood samples of Baudouinia, Eligmocarpus, Kalappia, Mend-oravia and Uittienia were not available but twigs from herbarium materials were studied by me.

3.3.3. Pollen morphology (Figs. 3.4 - 3.5)

The pollen morphology of the Cassieae has recently been studied by Graham and Barker (1981). The pollen grains of Duparquetiinae and Ceratoniinae are different from the other three subtribes (Cassiinae,

Dialiinae and Labicheinae). In Duparquetiinae, Graham and Barker observed that the grains have three prominent meridionally elongated ridges, superficially resembling protruding pores when viewed in equatorial optical section. The pores are two which are located one at each pole, and running through these pores around one edge of two of these ridges is a continuous colpus. In Ceratoniinae, the grains are typical of the Cassieae (i.e. size small, shape oblate to oblate-spheroidal, sculpture pattern generally reticulate) but they are tetracolporate, although a new species referred to Ceratonia has tricolporate grains (Ferguson, 1980).

The pollen of the three other subtribes, Cassiinae, Dialiinae and Labicheinae does not vary very markedly. Their pollen grains are tricolporate and typically oblate to oblate-spheroidal. Subtle differences occur in the sculpture patterns which range from finely to rather coarsely scabrate-punctate to finely reticulate. In Dialiinae, two distinct types of sculpturing occur, i.e. finely striate and reticulate. This study confirms these observations by Graham and Barker (1981). There are, however, subtle variations which are shown below.

The general pattern of sculpturing is reticulate, ranging from rather rough and distinct muri in Uittienia (Fig. 3.4, A) to smooth and finely reticulate in Baudouinia fluggeiformis Baill. (Fig. 3.4, F). Storckiella pancheri Baill. and Martiodendron excelsum (Benth.) Gleason (Fig. 3.5, B,C) pollen grains are finely reticulate to somewhat finely scabrate-punctate. Pollen grains of Dicorynia, Androcalymma, Kalappia (Fig. 3.4, A-E) and Eligmocarpus (Fig. 3.5, A) are finely reticulate. Pollen of Zenia (Fig. 3.5, D) is punctate. The 3 species of Koompassia have different sculpturing patterns, i.e. finely striate in K. malaccensis Maingay (Graham and Barker, 1981: p. 814), reticulate with broad muri in K. excelsa (Becc.) Taub. (Fig. 3.4, B) and reticulate with narrow muri in K. grandiflora Kosterm. (Fig. 3.5, E).

Fig. 3.4. Pollen of Dialiinae. A, Uittienia modesta (Kostermans 13413A, Borneo); B, Koompassia excelsa (For. Dept. 20363, Peninsular Malaysia); C, Dicorynia guianensis (Boschbeher 44, Surinam); D, Androcalymma glabrifolium (Krukoff 9005 type, Brazil); E, Kalappia celebica (bb. 33693, Celebes); F, Baudouinia fluggeiformis (de la Bathie 5503, Madagascar).

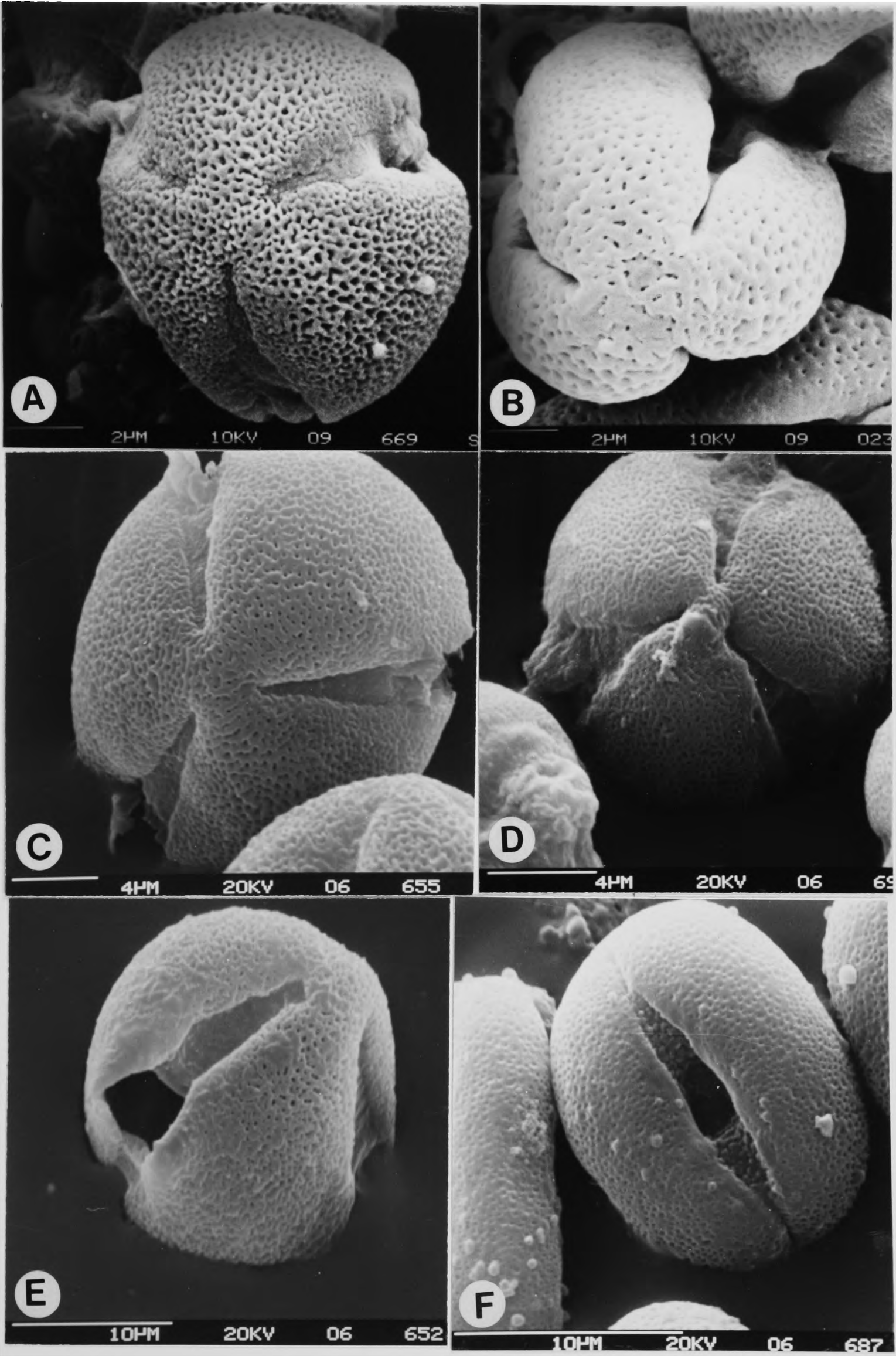
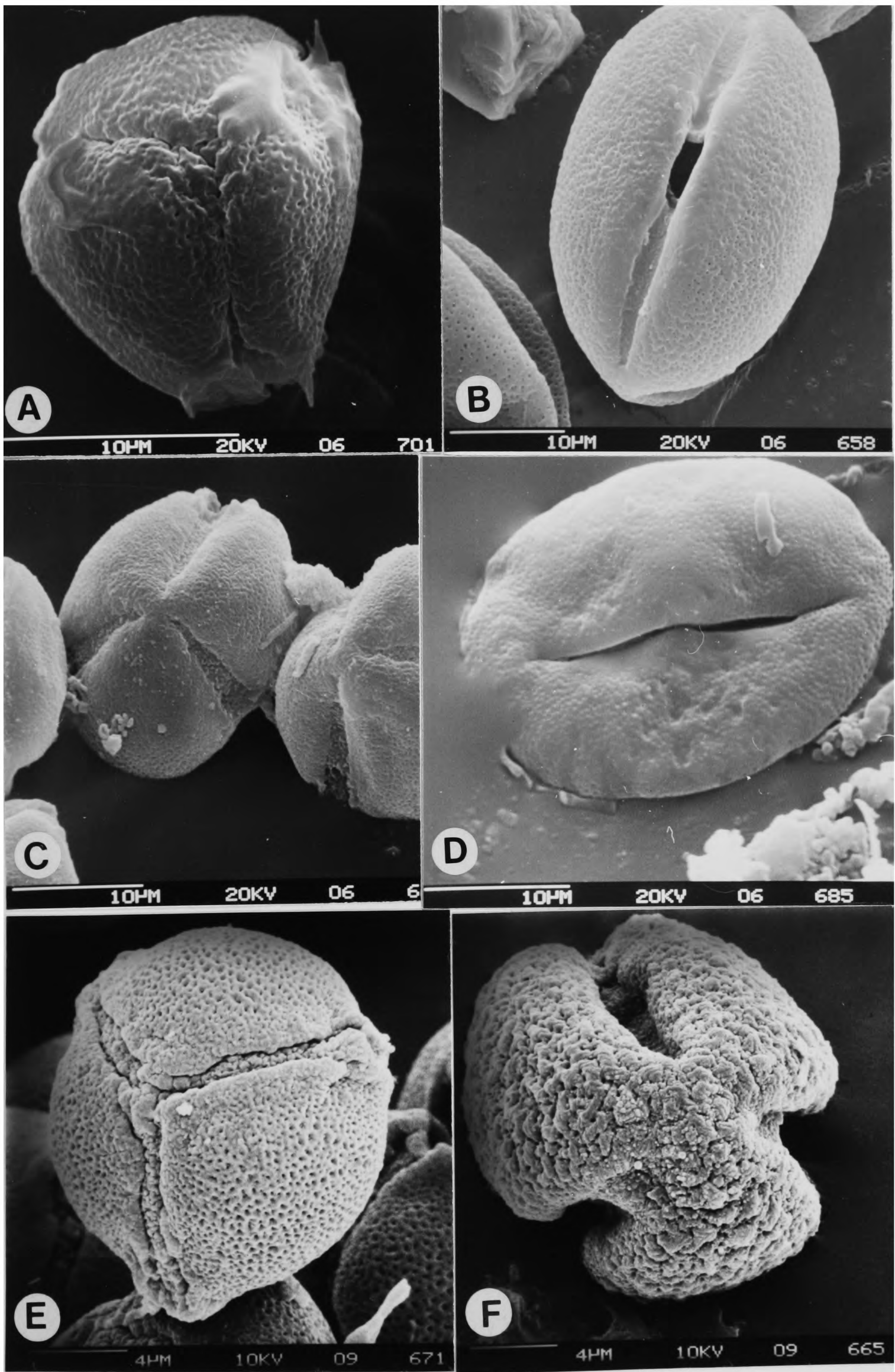


Fig. 3.5. Pollen of Dialiinae. A, Eligmocarpus cynometroides (20501 SF type, Madagascar); B, Storckielia pancheri (Franc 32, New Caledonia); C, Martiodendron excelsa (Samuels 243, Surinam); D, Zenia insignis (Poilane 25752, N Vietnam); E, Koompassia grandiflora (Kostermans 492, New Guinea); F, Mendoravia dumaziana (McWhirter 212, Madagascar).



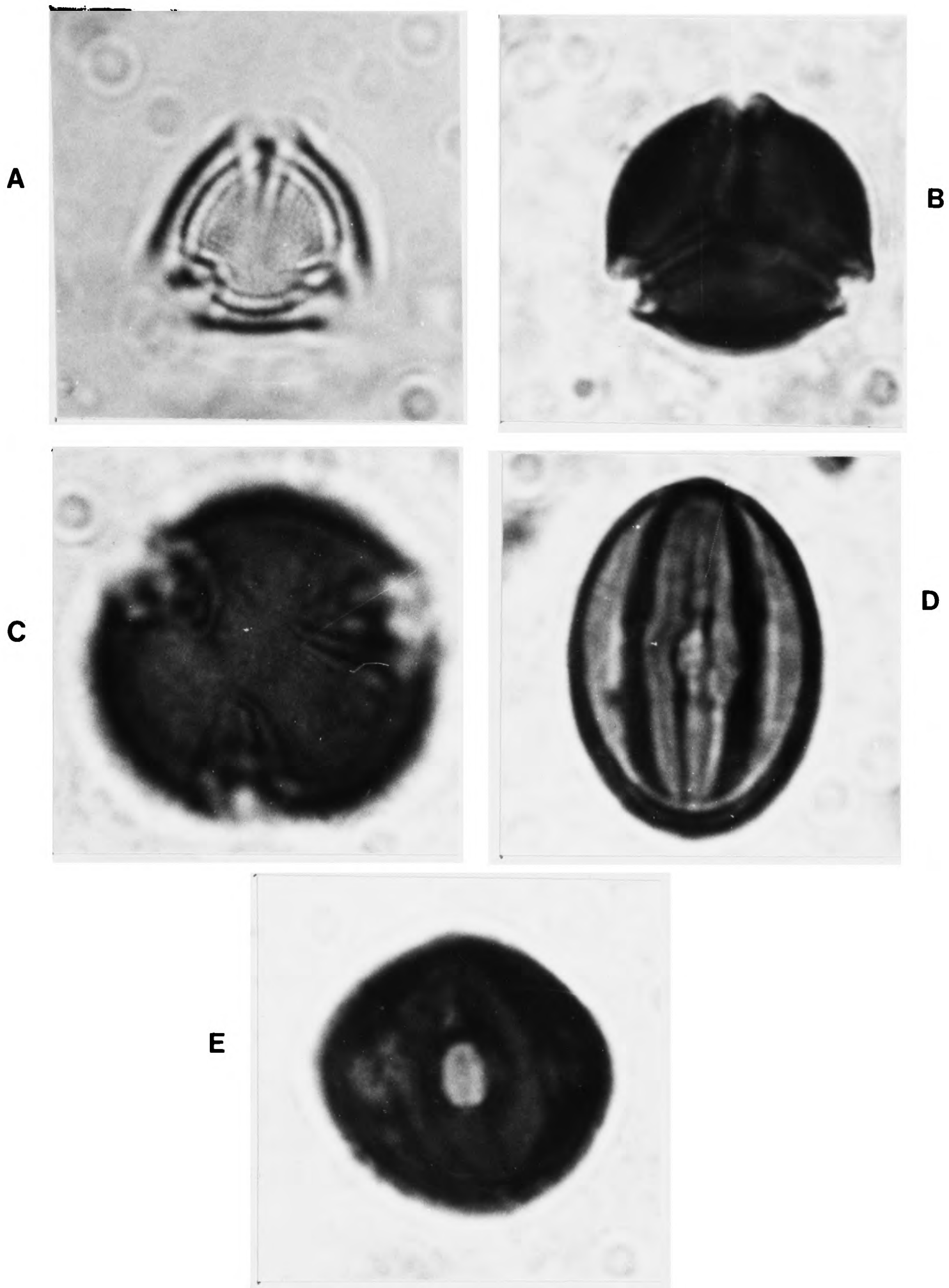


Fig. 3.6. Light photomicrographs of pollen of some Dialiinae species. A, Zenia insignis (Foillane 25752, N Vietnam); B, Koompassia grandiflora, (Kostermans 492, New Guinea); C, Distemonanthus benthamianus (Green and Vigne 9, Ghana); D, Kalappia celebica (bb. 33693, Celebes); E, Uittienia modesta (Kostermans 14313A, E Borneo). A, polar view showing reticulate sculpturing; B, polar view showing colpi meeting at the pole (trisyncolporate); C, polar view; D, equatorial view showing colpus and outline of endoaperture; E, equatorial view showing endoaperture in surface view. All c. X2200.

The only pollen sculpturing pattern in Dialiinae that deviates markedly from the rest is the one displayed by Mendoravia dumaziana Capuron (Fig. 3.5, F) which is coarsely scabrate-punctate. This type of sculpturing is typical of some species of Bauhinia, e.g. B. schlechteri Harms, B. scandens Roxb. and B. curtisii Prain (Graham and Barker, 1981) in the tribe Cercideae. Overall, the pollen sculpturing of the Dialiinae is more or less similar to Dialium.

The pollen of the majority of the Dialiinae is tricolporate with the colpi generally c. 3/4 or sometimes almost equal in length to the polar axis. However, in Dialium platysepalum it is trisyncolporate. Some pollen grains in Baudouinia, Eligmocarpus (Fig. 3.5, A) and Koompassia grandiflora (Fig. 3.5, E) are also trisyncolporate.

Light photomicrographs of pollen of some Dialiinae species were also taken. These are shown in Fig. 3.6.

3.3.4. Cytology

Chromosome counts are only available in the following genera, namely: Apuleia ($2n = 28$), Dialium ($2n = 28$), Distemonanthus ($2n = 26$), and Storckiella ($2n = 28$). Of the genera already studied (Goldblatt, 1981: p. 432) in the Cassieae, the number $n = 14$ predominates.

3.3.5. Phytochemistry

The only data in Dialiinae are those given by Toms and Westerns (1981) who found that cotyledons of Apuleia, Dialium, Dicorynia, Distemonanthus, Koompassia, Martiodendron and Storckiella are negative to amyloid test.

3.4. Relationships of the Genera in Dialiinae (Table 3.1 - 3.3)

Similarities and/or differences of some important taxonomic characters of the genera in the Dialiinae have been shown in the preceding

sections and subsections. These are summarised in Table 3.1. The tables 3.2 and 3.3 show relationships of the genera in terms of the taxonomic characters of the flowers and the fruits.

An important taxonomic character of the subtribe is the reddish-brown sap that exudes from the inner bark when cut. This taxonomic character in the inner bark occurs only in Dialium. It could possibly occur in other genera in the subtribe but so far, it is only observed in Dialium.

The vegetative characters of the genera in the Dialiinae are uniform. Generally, the leaves are imparipinnate; the pulvinus present; the hairs simple and unicellular; the stomata paracytic. There are a few exceptions in the genera Baudouinia, Eligmocarpus, Mendoravia and Uittienia. Baudouinia and Mendoravia have simple and exarticulate leaves while Eligmocarpus, although possessing imparipinnate leaves, have opposite leaflets. Baudouinia has also been found to have some anomocytic and actinocytic stomata (Watson, 1981). These three genera which are endemic to Madagascar, have already been noted by Irwin and Barneby (1981) to merit further taxonomic investigation. Uittienia has unifoliolate leaves with a pulvinus similar to Dialium subgenus Dansera but it has also a swollen point of articulation which resembles a pulvinus.

The inflorescence is uniformly cymose-paniculate. This is the unifying taxonomic character that holds the subtribe together.

The differences in taxonomic characters of the flowers and fruits are discussed below with reference to Tables 3.2 and 3.3. In the Dialiinae, distinction between genera is rather difficult because flowers and fruits do not vary much (see again Tables 3.2 and 3.3) in morphological features (except for example in details especially of the androecium). The majority of the genera share a common type of flower (i.e. petaliferous and with petals longer than the sepals, as

Table 3.2. Inter-relationships of genera in Dialinae based mainly on the diagnostic key of Irwin and Barneby (1981) using floral characters.

RECEPTACLE	Receptacle of flower plane or subconvex, the stamens hypogynous				Receptacle of flower concave, the stamens perigynous	
PETALS	Flowers apetalous or, if petals present, these are shorter than the petals				Flowers petaliferous, the petals longer than the sepals	
SEALS	3	5	5	3	5	
	DIALIUM subgen. Dansera*	DIALIUM subgen. Arouna.** DIALIUM subgen. Dialium	DICORYNIA		DISTEMONANTHUS (zygomorphic)	
	2					
	3			APULEIA (actinomorphic)		
	4		ANDROCALYPTIA			
S T A M E N S						
5			UTTIENIA** ZENIA** KALAPPIA*** KOOMPASSIA MARTIODENDRON			
10 to 12			BAUDOUINIA ELIGMOCARPUS MENDORAVIA		STORCKIELLA (actinomorphic)	

* Section Dansera has 6 stamens; ** Hypogynous disc present; *** 2-4 staminode present

shown in Table 3.2, columns 5-7) and a common type of fruit (e.g. samaroid or dry discoid fruits, as shown in Table 3.3, column 2). The distinction of genera is even more difficult if we consider that (with the exception of Baudouinia, Eligmocarpus, Mendoravia and Uittienia) those with petaliferous flowers (i.e. regardless of receptacle type) also display more or less the same type of fruit, i.e. samaroid or dry discoid (see Table 3.3, column 2). Moreover, these genera have wood with axial parenchyma that contains oxalate crystals (except Dicorynia, see Table 3.1, column 14) and have pollen with reticulate exine (except one species of Koompassia which is finely striate; see Table 3.1, column 13). Therefore, based partly on the flowers (petaliferous), fruits (dry discoid or samaroid), oxalate crystal inclusions in axial parenchyma and pollen sculpturing (finely reticulate), these genera, viz. Androcalymma (fruit unknown), Apuleia, Dicorynia, Distemonanthus, Kalappia, Koompassia, Martiodendron, Storck-iella and Zenia can be seen to be a homogeneous group in the Dialiinae. For convenience in discussion, I call this group the 'Androcalymma group'.

The genera Baudouinia, Eligmocarpus and Mendoravia may be regarded as 'anomalous' as was pointed out by Irwin and Barneby (1981) because their fruits (i.e. pseudolomentaceous, crumpled pod valves and late dehiscent bean-like pod, respectively) differ considerably from the indehiscent drupaceous or samaroid-discoid fruits commonly displayed by the rest of the genera in Dialiinae. Aside from their obvious differences in fruit types, they also deviate from the other genera by their type of leaves and number of stamens (see Table 3.1, column 2 and 8). Eligmocarpus, although imparipinnate, has opposite leaflets. Its flowers have 10 stamens and are dimorphic which make it unique in the subtribe as regard this stamen character. Baudouinia and Mendoravia have both simple and exarticulate leaves which are also peculiar

Table 3.3. Grouping of genera in Dialiinae based on the data of Irwin and Barneby (1981) using fruit characters.

Drupaceous	Samaroid or dry discoid	Others
DIALIUM - Pod a sort of indehiscent, 1- or 2-seeded nut, sometimes strongly, sometimes scarcely compressed laterally, consisting of a crustaceous exocarp and a pulpy, when ripe mealy reddish-brown endocarp enveloping the seed.	APULEIA DICORYNIA DISTEMONANTHUS KALAPPYA KOOMPASSIA MARTIODENDRON STORCKIELLA ZENIA	BAUDOUINIA - pseudolomentaceous pod ELIGMOCARPUS - crumpled pod valves MENDORAVIA - late dehiscent bean-like pod UITTIENIA* - Pod indehiscent, rounded, c. 4-6 x 4-6 cm, the pericarp thick, c. 4-5 mm thick, very hard when dry and more or less wrinkled or rough outside. ANDROCALYPTA - fruit unknown

* - Fruit description supplied in this study

in the subtribe. Their stamens are isomorphic but they are 6-10 or 11-12, respectively, which also deviate from the usually 5-merous stamens in most genera in the subtribe. In so far as flower and fruit characters are concerned, Baudouinia, Eligmocarpus and mendoravia are taxonomically quite remote from Dialium and the rest of the genera in the subtribe.

The flowers of Uittienia are 5-merous and petaliferous (see Fig. 3.1, a-e). In this respect, it belongs to the 'Androcalymma group' of genera mentioned above. However, its fruit (see Fig. 3.1, f and g; also description and discussion in subsections 3.3.1.4 and 3.4.1, respectively) is different from either that of Dialium or the other genera in the subtribe. On the basis of fruit type, therefore, Uittienia can be also considered as another 'anomalous' genus. This was not noted by Irwin and Barneby (1981).

The pollen grains of Dialiinae are relatively uniform (Graham and Barker, 1981). They differ in their exine sculpturing which is of three types, namely: reticulate, striate or scabrate punctate. The majority of the genera have reticulate pollen. Striate pollen occurs only in subgenus Arouna (Dialium) and in Koompassia (K. malaccensis). Only Mendoravia has scabrate-punctate exine which is more related to some species of Bauhinia (Graham and Barker, 1981) of the tribe Cercideae. As confirmed in this study, reticulate pollen is the main pollen type of Dialiinae, and the Cassieae as a whole (Graham and Barker, 1981).

Wood structure features of the Dialiinae are also uniform, i.e. storied structure, multiseriate rays and banded parenchyma. They differ slightly in some aspects such as inclusions in axial parenchyma (i.e. silica and oxalate crystals in Apuleia, Dialium, Dicorynia and Distemonanthus; oxalate crystals only in the rest of the genera) and in other features like the sclerotic parenchyma displayed by Androcalymma and Martiodendron or the unusually long parenchyma strands in Koompassia

(both minor characters and not mentioned in Table 3.1). But the fundamental structures like storied structure, multiseriate rays and banded parenchyma are the same in all the genera of the Dialiinae. In terms of wood structure, therefore, the Dialiinae can be considered as a homogeneous group as has already been noted by Reinders-Gouwentak (1955), Koeppen (1980) and Baretta-Kuipers (1981).

Based on the gross morphological features of the flowers and fruits and in conjunction with the vegetative, pollen and wood anatomical characters discussed above, the Dialiinae can be arranged into three groups as follows:

1. Dialium (unique in its drupaceous fruit with crustaceous exocarp and pulpy endocarp, flowers generally apetalous, reddish-brown sap exuding from the cut inner bark)
2. Androcalymma, Apuleia, Dicorynia, Distemonanthus, Kalappia, Koompassia, Martiodendron, Storckia and Zenia (samaroid-discoid fruits, petaliferous flowers, stamens generally 5, oxalate crystal inclusions in axial parenchyma)
3. Baudouinia, Eligmocarpus and Mendoravia (different fruit types from the above two groups, stamens more than 5, leaves simple and exarticate or imparipinnate with opposite leaflets)

Uittienia does not fit these groups. However, it matches group 2 except for its fruit which is unique as described in subsection 3.3.1.4.

3.4.1. The status of Uittienia in the Dialiinae

As a result of this review, it was found out that the genus Uittienia differs from Dialium (to which it had been reduced as a subgenus) in fruit characters.

The genus Uittienia van Steenis (1948) had been reduced to a subgenus of Dialium by Steyaert (1953) based on the characters of the flower, i.e. having a receptacle with a disc similar to that of subgenus

Arouna (one of three subgenera presently recognised in Dialium).

On the same basis, Uittienia was reaffirmed by Irwin and Barneby (1981) as a distinct subgenus in Dialium. This cannot be maintained in this study because, although there are similarities in the characters of the flowers of both subgenus Arouna (Dialium) and Uittienia, their fruits are entirely different (see description of Uittienia fruit in subsection 3.3.1.4, and Fig. 3.1, f and g).

The fruit of Uittienia (which is globose and measures at least 4-6 x 4-6 cm with c. 4-5 mm thick pericarp which does not have crustaceous exocarp) deviates from the drupaceous fruit of Dialium or from the samaroid-discoid fruits exhibited by the majority of the genera in the Dialiinae. Its fruit, therefore, can be regarded as another one of the exceptions of fruit types in the Dialiinae such as those of Baudouinia (pseudolomentaceous), Eligmocarpus (crumpled pod valves) and Mendoravia (late dehiscent bean-like pod).

Dialium has fruits which are uniformly drupaceous but with a crustaceous exocarp and a pulpy endocarp. This fruit type is common to all species of Dialium regardless of what subgenera they belong to. It means that before any taxon is considered to be congeneric with Dialium, that particular taxon should first be examined to see whether its fruit is similar to that of Dialium. Unfortunately, neither Steyaert (1953) nor Irwin and Barneby (1981) saw the fruit of Uittienia before they decided a change of its status to a subgenus of Dialium. Since the fruit of Uittienia is taxonomically different from that of Dialium, it has to be reinstated as a distinct monotypic genus in the Cassieae belonging to the same subtribe Dialiinae.

The genus Dansera (van Steenis, 1948) was, at the same time with Uittienia, also reduced to a subgenus of Dialium by Steyaert (1953). It is retained as a subgenus because the conservative features of its fruit, seed and the inner bark are the same as those of Dialium (see Chapter 5, section 5.1).

3.4.2. Dialium in relation to the other genera in Dialiinae

As it is the type genus, it is appropriate to discuss last Dialium in relation to the rest of the genera in Dialiinae. Aside from the fruit type mentioned above (in comparing Dialium with Uittienia), how closely related is Dialium to the rest of the genera in the subtribe? Can it be sufficiently separated as a distinct genus when compared with the other genera in Dialiinae? What is its place in the taxonomic sequence of the Dialiinae?

As has already been discussed above, there are genera that are more closely interrelated (i.e. those genera called the 'Androcalymma group') than they are to Dialium. Also, there are genera that are quite distinct taxonomically not only from Dialium but also from the rest of the genera in the subtribe. Their differences are centred on the characters of the flowers and the fruits. Can Dialium, therefore, be sufficiently separated from the rest of the genera in the subtribe? The answer is, yes based on the following taxonomic features which are common to all its species:

1. reddish-brown sap that exudes from the inner bark when cut (see subsection 3.3.1.1 and Table 3.1, column 1). Within the Dialiinae, only species in Dialium possess this taxonomic character of the inner bark.

2. drupaceous fruit with crustaceous exocarp and pulpy endocarp. Only species in Dialium exhibit this fruit character (see Table 3.1, column 11 and Table 3.2, column 1).

3. testa with irregularly-cracked surface pattern. There are no other published records of seed testa in Dialiinae that display this characteristic feature (see Table 3.1, column 12).

4. apetalous flowers or, if petals present, these are shorter than the sepals (see Table 3.2, column 3-4). No other genera in the

Dialiinae have apetalous flowers. The rest of the genera in the Dialiinae are petaliferous (their petals longer than the sepals) regardless of the type of receptacle.

The above taxonomic characters are unique to Dialium. Any taxa not possessing all the above characters do not belong to Dialium.

Irwin and Barneby (1981) have arranged their enumeration of the subtribes in the Cassieae and the genera in the Dialiinae by placing first in the sequence the taxa which possess a receptacle with a disc. Thus in the Cassieae the subtribe Ceratoniinae precedes Dialiinae of which only three out of 14 genera have a disc, i.e. Dialium, Uittienia, and Zenia. In Dialiinae, Zenia precedes Dialium, then followed by the other genera whose member species have flowers without a disc. Irwin and Barneby could have arranged the taxa of the Dialiinae in the above sequence for convenience. Nevertheless, they could have followed Polhill, et al. (1981) who have indicated that in the legumes, flowers with a nectary presented in an exposed disc which is a common feature of the relictual genera of Cassieae, are precedent over those with a nectary in a floral tube (hypanthium). In agreement with Polhill, et al. (1981) above, any genus in the Dialiinae with a disc could be arranged first in the taxonomic sequence. Since the arrangement has already been implied by Irwin and Barneby (1981), there is no need to point out which of the three genera (i.e. Dialium, Uittienia and Zenia) is placed first in the taxonomic sequence of the Dialiinae.

4. ECOLOGY AND DISTRIBUTION

4.1. Ecology

4.1.1. Dialium

The majority of Dialium species occur in rain forests. In these areas they grow in different forest formations as outlined by Whitmore (1975: p. 121). In ever-wet dry land areas they range from lowland to about 600 metres elevation or occasionally reaching 1000 metres. These areas actually fall under the tropical lowland evergreen rain forest formation (Whitmore, 1975). In W Malesia some species also occur in other lowland areas such as in peat (D. patens = D. indum) and fresh-water swamps (D. platysepalum, and heath forest (D. kunstleri). In littoral areas, D. schlechteri (E Africa) and D. unifoliolatum (Madagascar) are usually found. Actually, only very few species grow in rather harsher habitats such as in monsoon forests and savannas. But even in these seasonally dry areas the species are moisture-loving. For example, D. angolense, D. englerianum and D. guineense (all African species) are known to grow in savannas or scrub woodlands but in these areas they are usually found in river fringes or growing in deep soils. D. englerianum, the only species exclusively inhabiting "savane boisée" or savanna woodlands, grow in deep soils or in areas where moisture is not limiting for its growth. D. guineense is found in savanna forest formation but it is actually a species of rather lower rainfall parts of a high forest, often in areas associated with water courses (Taylor, 1960: p. 137). On the other hand, D. angolense is generally a species of the "galeries forestières" (Steyaert, 1952).

All Dialium species of Peninsular Malaysia appear to be deciduous (Corner, 1940: p. 394). I have not been able to confirm this in the field. Also, I have not found any observation in field notes indicating individuals to be deciduous. But this is understandable because at the time of collection, trees are usually in bloom or in fruit and in the herbarium the flowers or fruits are usually associated with mature leaves. It is only in D. schlechteri where I have observed some specimens with flowers together with very young leaves. This may indicate that this species is truly deciduous, perhaps for a longer period. D. schlechteri happens to be the only subtropical species in the genus.

The types of soils that Dialium species grow on are only occasionally mentioned in field notes. Some observations are "sandy or quartzitic", "brown to yellowish silt to sandy loam", "clay-sandy", "calcareous and sandy", and "alluvium with sandstone substratum". These soils fall under the different soil types reviewed by Burnham (1975) and used by Whitmore (1975: p.121) in his table (Table 10.1) on the main forest formations of the tropical rain forests of the Far East.

The flowering and fruiting periods appear to vary from one species to another but they usually occur throughout the year with noticeable peak months.

4.1.2. Dialiinae

Dialiinae, like Dialium is composed mostly of rain forest species. At least 10 out of 14 genera are found in rain forests, to wit: Dialium, Androcalymma, Apuleia, Dicorynia, Distemonanthus, Kalappia, Koompassia, Martiodendron, Storckiella, and Uittienia.

In the study of Capuron (1968) on caesalpinoid genera of Madagascar, species of the three genera (i.e. Baudouinia, Eligmocarpus and Mendoravia)

endemic to the island, have not been mentioned by him to be found in rain forest areas. However, all species belonging to these genera inhabit coastal places. According to Koechlin, Guillaumet and Morat (1974), the eastern coastal region of Madagascar extending from Vohemar to Fort Dauphin is a rain forest, i.e. 'foret dense humide sempervirente'. This narrow coastal region has been indicated by Whitmore (1975: p. 3, fig. 1.1) as a rain forest. Apuleia, although found in the Amazon region, also occurs in NE Argentina near the border with Paraguay, but this area could be a pocket of rain forest (Whitmore, pers. comm.). Zenia (a monotypic genus of S China and N Vietnam) could also be found in rain forest. In southernmost China (Fukien, Kwangtung and part of Yunnan and Kwangsi) rain forest also occurs (Whitmore, 1975).

Aside from Dialium, Androcalymma, Dicorynia, Distemonanthus and Martiodendron are known riparians and usually composed of big-sized trees. Koompassia species are usually found in lowlands and peat swamps and also mostly composed of big-sized individuals. Koompassia excelsa, for example, is known to be the third tallest tree in the world after Sequoia sempervirens, the giant redwood of California and Eucalyptus regnans, the blue gum of Australia (Richards, 1952: p. 4; Whitmore, 1972: p. 264).

Trees of Dicorynia shed their leaves after fruiting (Bena, 1960; p. 126). There are no other records of deciduousness of trees in other genera but herbarium materials of Apuleia in flowers are usually with young unopened leaves which signify its species to be deciduous.

4.2. Distribution

4.2.1. The distribution patterns of Dialium (Fig. 4.1)

For the proper understanding of the distribution patterns of Dialium, 3 maps are drawn: Fig. 4.1, showing the overall range

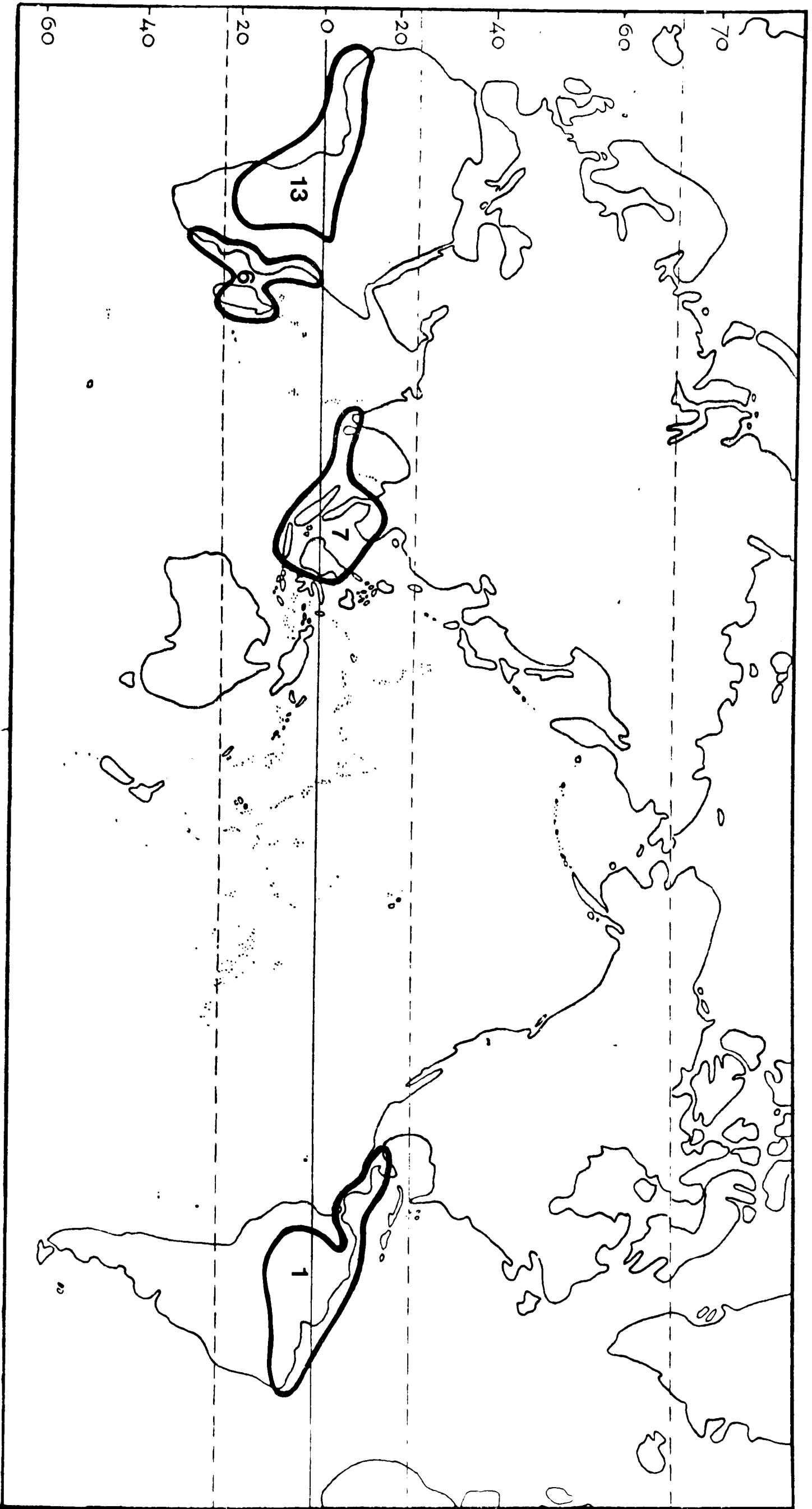


Fig. 4.1 Distribution of Dialium. Figures refer to number of species within the delimited area.

of the genus and Figs. 4.2 and 4.3, showing the distribution patterns at the subgeneric level.

From Fig. 4.1, it is of course evident that Dialium is a pantropical genus (but not extending beyond Makassar Strait east of Borneo), although as earlier stated, one species, i.e. D. schlechteri is extra-tropical. Other than this, all species inhabit the tropics from c. 19°N in S Mexico and Belize to 23°S in Madagascar.

The genus has reached the Pacific coast. It did not cross the Andes but probably crossed over the low mountain ranges of Central America. The wide-spread D. guianense extended northwestward along the Atlantic coastal fringes of Central America and reaching S Veracruz, Mexico at c. 19°N, 94°W. In the Pacific coast, it now survives in a small pocket of rain forest in Costa Rica at Golfo Dulce (Allen, 1956: p. 192). There is no other record of D. guianense occurring elsewhere in the Pacific coast.

The easternmost limit lies west of the original Wallace's line of 1863-1890 (George, 1981), i.e. E Borneo. There has not been any species of Dialium discovered east of Wallace's line. A plant described by Rumphius in Amboina which was interpreted by Merrill (1917: p. 257) to be D. indum could have been introduced there from Java.

4.2.1.1. Subgenus Arouna (Fig. 4.2)

Subgenus Arouna (divided into sections Arouna and Codarium) has the widest area of distribution as well as the highest number of species. The greatest concentration of species (not only of subgenus Arouna but also of the whole genus) is in tropical Africa

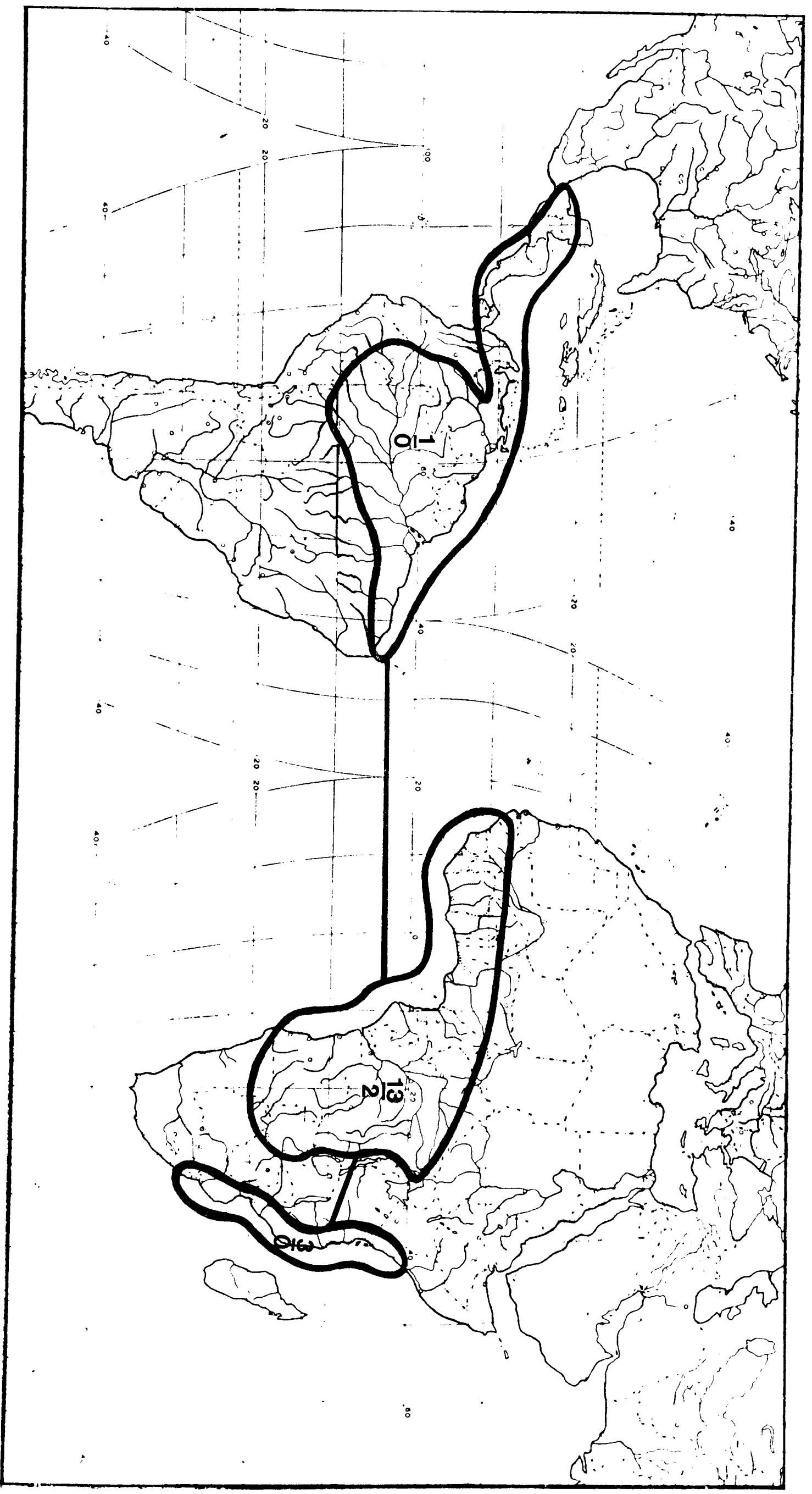


Fig. 4.2. Distribution of *Dialium*, subgenus *Arouna*. Figures above and below the hyphen refer to number of species and varieties, respectively.

west of the Lake Districts. Here, 13 species (1 with varieties) – exist. Branching out from this centre, 3 species are disjunctly distributed in the eastern coastal region of Africa and 1 species (D. guianense) across the Atlantic.

At subsectional level, subsection Pirula (section Arouna) has the same distributional pattern as the subgenus or section Arouna because the American D. guianense and E African D. holtzii, D. orientale and D. schlechteri belong to it. Subsection Indumentosa (section Arouna) and section Codarium are both confined within the area of section Arouna, i.e. minus its E African and transatlantic extensions. In this respect, sections Arouna and Codarium are sympatric in this particular area (west of the Lake Districts). It is for this reason that in this area their distributional limits can not be defined separately.

4.2.1.2. Subgenus Dialium (Fig. 4.3)

The distribution pattern of this subgenus is centred in W Malesia (i.e. including southern parts of Thailand, Laos, Cambodia, and S Vietnam). One species (D. ovoideum) or possibly 2, is disjunctly found in Kerala-Sri Lanka area. The subgenus is homogeneous and composing only of 5 species, of which 4 are confined in W Malesia. The subgenus together with section Dansera define the easternmost limit of Dialium, i.e. in E Borneo.

4.2.1.3. Subgenus Dansera (Fig. 4.3)

As can be noted in Fig. 4.3, the distribution pattern of this subgenus (divided into sections Hova and Dansera) is bicentric. Section Hova with 3 species (1 with varieties) is endemic to Madagascar. Section Dansera with only 2 species (1 with varieties) is disjunctly found in W Malesia and occupy a lesser area there than subgenus Dialium.

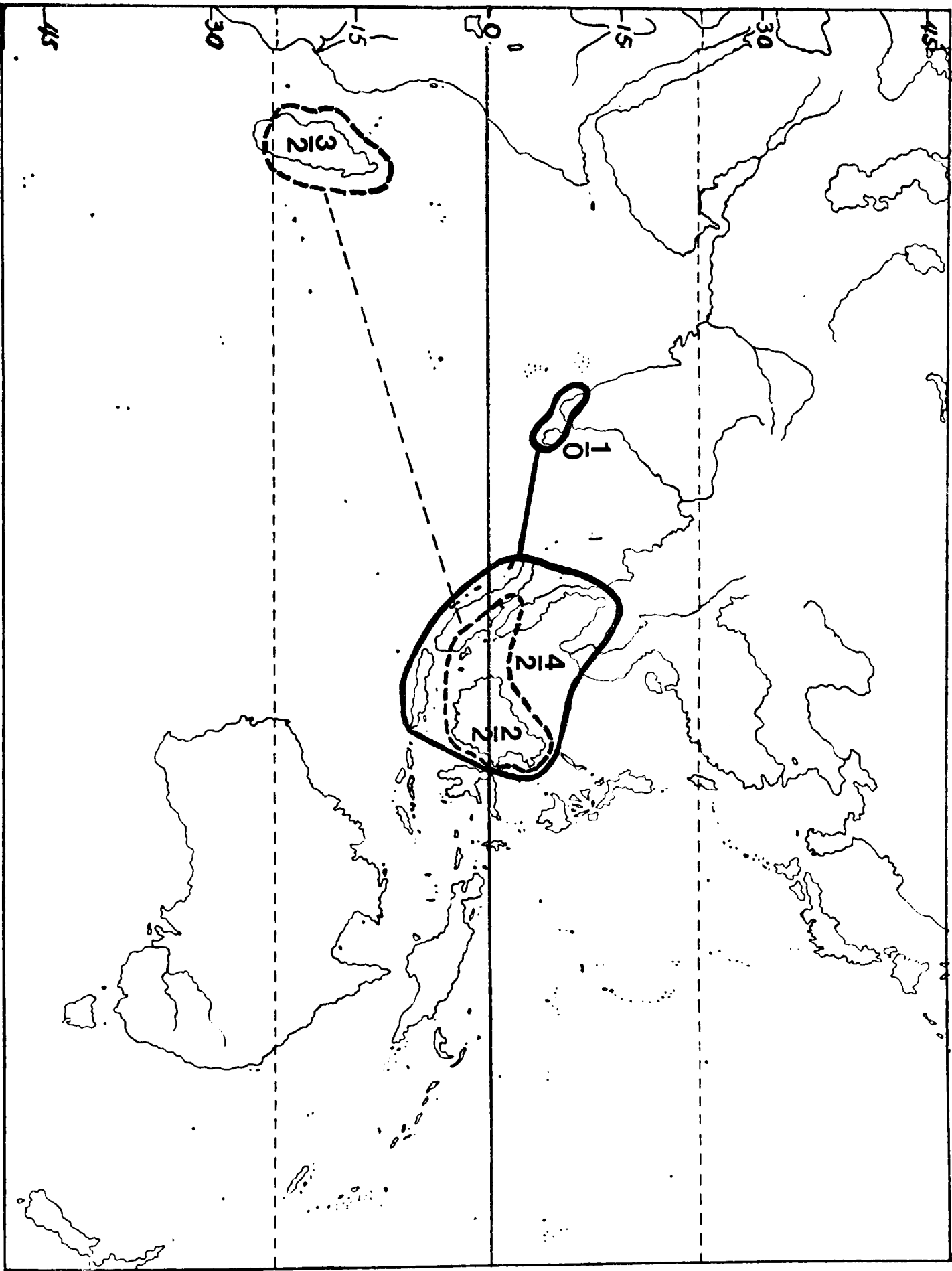


Fig. 4.3. Distribution of *Dialium*, subgenus *Dialium* (—) and subgenus *Dansera* (-----). Figures above and below the hyphen refer to number of species and varieties, respectively.

4.2.2. The distribution patterns of Dialiinae (Fig. 4.4)

The range of Dialiinae can be superimposed within the distribution pattern of Dialium with the exception of 4 genera, i.e. Eligmocarpus, Kalappia, Storckiella and Zenia. These genera exclusively lie outside the range of Dialium in the north, the south and the east. In the north Zenia is found in N Vietnam and in Kwangsi (southern province of China at c. 22° - 24° N). Towards the south in Madagascar, Eligmocarpus is found in and around Fort Dauphin region where it coexists with Mendoravia, although the latter genus extends within the range of Dialium at c. 23° S. In S America Apuleia, although also found within the area of Dialium in the Amazon, disjunctly extends to NE Argentina bordering/Paraguay at c. 26° - 28° S. Towards the east, Kalappia barely extends outside the range of Dialium in Malesia (i.e. east of Wallace's line) where it is restricted to Celebes. Uittienia is found just across the Makassar Strait from Celebes where it is restricted in S Borneo which is within the range of Dialium. A species of Koompassia (K. grandiflora) is disjunctly found in W New Guinea (Irian Jaya). Its relative (K. excelsa) is widely distributed in W Malesia. The easternmost genus is Storckiella where its species occur in Fiji and New Caledonia, and recently discovered to occur also in N Queensland, Australia (B. Hyland, per.comm.).

Excluding Dialium, Africa is poor in Dialiinae, i.e. with only one genus (Distemonanthus). But east and west of Africa, Dialiinae is relatively rich. To the east (which is by far the richest) 8 genera exist, i.e. 3 in Madagascar (Baudouinia, Eligmocarpus, and Mendoravia), 3 in Malesia (Koompassia, Kalappia and Uittienia), 1 in N Vietnam and S China (Zenia) and 1 in Fiji-New Caledonia-Queensland (Storckiella). Across the Atlantic 4 genera (Apuleia, Androcalymma, Dicorynia and Martiodendron) are found and occupy the same area with Dialium in the Amazon.

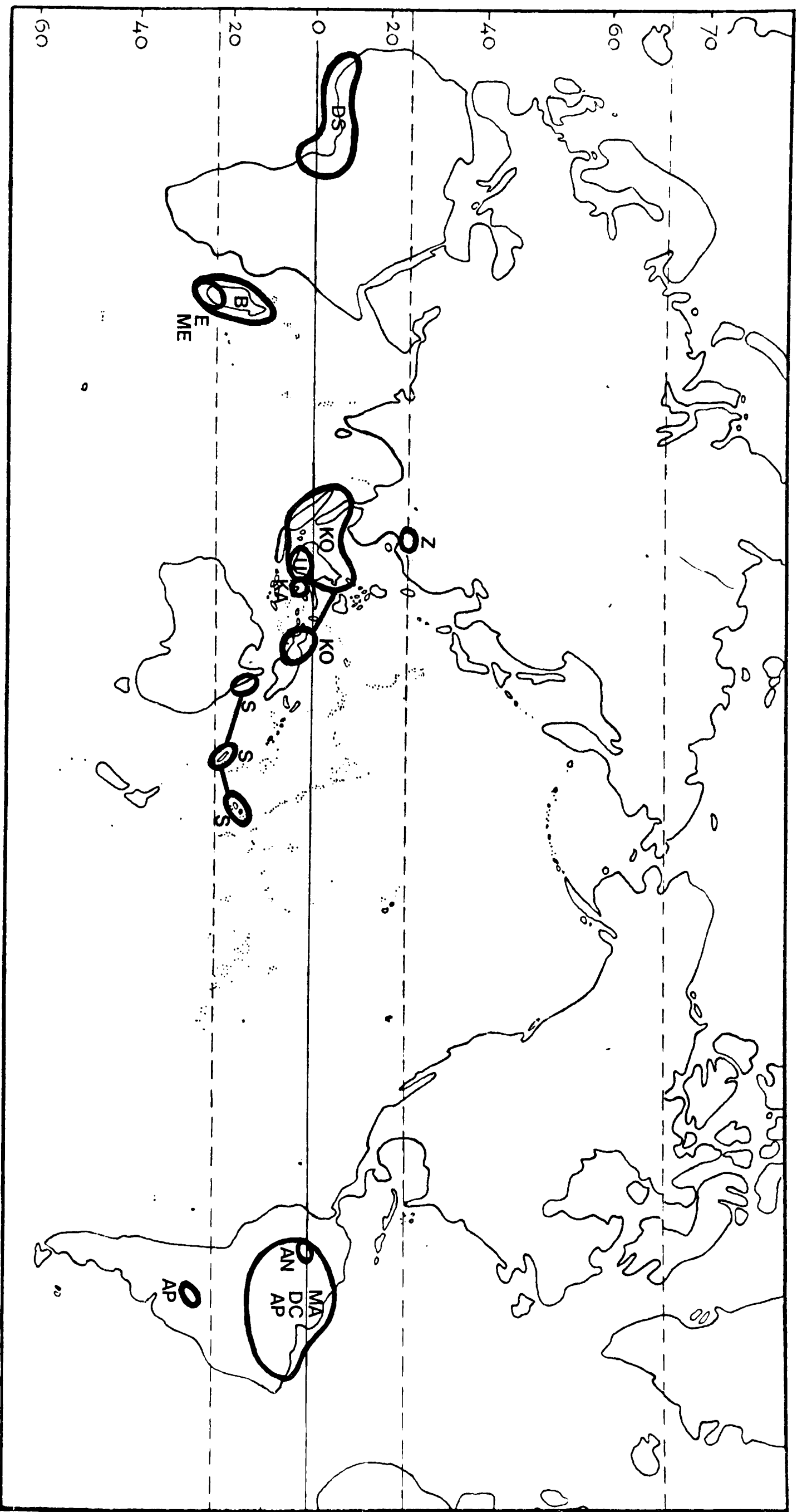


Fig. 4.4. Distribution of Dialiinae. DS - Distemonanthus, B - Baudouinia, E - Eligmocarpus, ME - Mendoravia,

Z - Zenia, KO - Koompassia, U - Uittienia, KA - Kalappia, S - Storckielia, AN - Androcallymma, AP - Apuleia,

DC - Dicorynia, and MA - Martiodendron.

PART III. GENERAL DISCUSSION AND CONCLUSIONS

5. RELATIONSHIPS OF THE TAXA WITHIN DIALIUM

5.1. The Generic Concept (see Table 3.1 and subsection 3.4.2.)

Before the recent classification of the Cassieae into five subtribes and consequently Dialium, together with 13 other closely related genera, into one subtribe (Irwin and Barneby, 1981), the concept of Dialium used to be mainly centred on the taxonomic characters of the flower. The reductions earlier of genera Arouna (Aublet, 1775) and Codarium (Vahl, 1804) to sections of Dialium (Bentham, 1865; Taubert, 1892; Harms, 1915) based on the taxonomic features of the flower attest to this. Steyaert (1953) himself also relied heavily on the characters of the flower when he reduced the genera Dansera and Uittienia of van Steenis (1948) to Dialium even though, for Uittienia, he did not see fruiting material. In the present concept, the characters of the flower are only of secondary importance for generic distinction especially when we view Dialium as a member of a subtribe composed of taxonomically closely related genera.

As already discussed in Chapter 1 (section 1.3.) and Chapter 3 (section 3.4) the present study confirms the observations of Irwin and Barneby (1981) that floral features particularly in perianth and androecium are very variable within Dialium and as such, taxonomic characters from them cannot be considered 'basic determinants' of the genus. The concept of the genus, has to be based on conservative characters common to all species which alone carry phylogenetic messages (Irwin and Barneby, 1981) at the generic level. These conservative characters are restated (see Table 3.1 and subsection 3.4.2.) as follows:

1. reddish-brown sap that exudes from the inner bark when cut
2. drupaceous fruit with crustaceous exocarp and pulpy endocarp
3. testa with irregularly-cracked surface pattern
4. flowers apetalous or, if petals present, these are shorter than the sepals.

The above conservative characters, especially the first 3, distinguish Dialium from the rest of the Dialiinae. As far as can be gathered from literature and from field notes of representative specimens observed, no other genus in the Dialiinae possess any of the above characters which are unique to Dialium. As stated in Chapter 3 (subsections 3.3.1.1 and 3.4.2) there are other legumes which exude reddish-brown sap from the cut inner bark, but this is not in combination with characters of the fruit and testa stated above. Also, the characteristic irregularly-cracked testa surface can be found in some seeds of Cassia, though sometimes associated with areoles (Brenan, 1967). Again, this character of the testa is not in combination with the characters of the inner bark and the fruit.

I consider that Steyaert (1953) was correct in reducing genus Dansera to a subgenus of Dialium based on the above characters. The Madagascan section Hova (subgenus Dansera) and the W Malesian section Dansera (subgenus Dansera) have been noted by Capuron (1968) and van Steenis (1948), respectively, to exude reddish-brown sap from the cut inner bark. A collection (Jacobs 5221, from Sarawak) of D. procerum (subgenus Dansera) was noted to exude reddish-brown sap. The fruits of subgenus Dansera possess the same conservative features mentioned above as have been verified in this study.

In contrast, however, Steyaert (1953) was wrong (as were Irwin and Barneby (1981) maintaining it) by reducing genus Uittienia to a subgenus in Dialium because, with the exception of the receptacle with a disc, it does not possess any of the first three conservative characters mentioned above. There is reason, therefore, to exclude it from Dialium and to reinstate it (as stated in Chapter 3, subsection 3.4.1) to its previous status as a monotypic genus belonging to subtribe Dialiinae.

At the generic level, there appears to be no single good taxonomic character in the flower that can be considered common to all member

species of Dialium except to say that the majority of them are apetalous (63%), and if they do have petals (37%), these are shorter or at least do not exceed the length of the sepals in the mature stage. This 'generic' character puts Dialium quite distinct from the rest of the Dialiinae which are all petaliferous, with the petals longer than the sepals (see discussion in Chapter 3, section 3.4). Other than the above, the rest of the floral characters especially in perianth and androecium are only useful for the delimitation of lower level taxa, i.e. especially at subgenus and section. These floral features together with anatomy and palynology, will now be discussed in connection with the delimitation of infrageneric taxa.

5.2. Characters for the Delimitation of Infrageneric Taxa

5.2.1. Morphology (refer to Fig. 5.1, and Tables 2.1, 5.1 and 7.1)

The gross morphological features from the flower listed below are important to the taxonomy of the genus at the infrageneric level. They are listed according to importance of taxonomic characters they provide for the delimitation of infrageneric taxa, i.e. for subgenera (items 1 and 2), for sections (items 3 and 4) and for subsections (item 5).

- (1) the type of receptacle
- (2) the number of sepals
- (3) the shape of the anther (particularly the apex) and the type of dehiscence
- (4) the number of petals and stamens
- (5) the shape of the filaments

The subgeneric classification of Steyaert (see Table 5.2) based on the presence and absence of a disc in the receptacle is maintained in the present investigation. However, this study shows that the presence of a disc is not by itself adequate to reduce a taxon to Dialium. Relying solely on the presence of a disc, Steyaert (1953) and Irwin

and Barneby (1981) fell into a trap by reducing Uittienia to a subgenus of Dialium. This of course happened because they did not examine fruiting material which was already available in the 1950s (Kostermans 5476, collected in 1951). But certainly, the subgeneric division of Dialium based on the presence and absence of a disc is maintained in this study because, coupled with other taxonomically important characters, it corresponds very well with geographical distribution, i.e. those with disc (subgenus Arouna) are found in Africa and Neotropics and those without disc (subgenera Dansera and Dialium) are found in Madagascar and Indo-Malesia.

The number of sepals is important to distinguish the two subgenera Dansera and Dialium which have no disc. It is possible to just merge these two subgenera into a single subgenus because both are without a disc. But the number of sepals correlates again with geographical distribution. Those with 3 sepals (subgenus Dansera) are found in Madagascar and disjunctly in W Malesia while those with 5 sepals (subgenus Dialium) are strictly Indo-Malesian (see Fig. 4.3). Moreover, this gross morphological character is supported partly by the anatomical evidence of the wood and in the type of exine sculpturing (all reviewed in the next section). So, the subgenera Dansera and Dialium, as recognised by Steyaert (1951, 1953) and Irwin and Barneby (1981) mainly on sepal number and with the addition of data from this study, are maintained as separate taxa equivalent in rank with subgenus Arouna.

At the level of the section, the shape of the anther apex is taxonomically useful. The sections Arouna and Codarium (all in subgenus Arouna) for which I have added new distinguishing taxonomic characters, are based on the shape of the anther which is obviously correlated with the type of sculpturing of the exine. Section Arouna possesses finely striate pollen while section Codarium has a finely (and striato-) reticulate pollen. The palynological evidence supports strongly the

foundation of these amplified sections. The sections (Recta and Geniculata) of Steyaert (1951) were founded on the basis of the shape of the filaments, i.e. either straight or geniculate. While morphologically sound and practical from the identification point of view, these characters are not supported by others, e.g. the sculpturing of the exine which I consider should be given a higher taxonomic value than the shape of the filament. This is because in Dialium, the pollen shows less plasticity (more conservative) of characters than the androecial parts (e.g. number of petals, number and shape of the stamens). However, at the next lower level (subsection) the shape of the filaments can be applied in conjunction with the shape of the fruit in delimiting subsections in section Arouna. On this basis, I retain subsections Indumentosa and Pirula of Steyaert (1951) under section Arouna.

The type of anther dehiscence is also taxonomically useful when applied infragenerically to African (plus the only Neotropical) species. For example, species in section Arouna have anthers that dehisce basipetally while those in section Retusa have anthers that dehisce evenly along the slits. Type of anther dehiscence, however, cannot be applied in the sections of subgenus Dansera and in subgenus Dialium because their species have anthers that dehisce uniformly along the slits. In this connection, the African section Codarium (subgenus Arouna) is closely linked to subgenera Dansera and Dialium because their anthers have the same dehiscing pattern (i.e. evenly along the slits). Also, their pollen has the same reticulate sculpturing of the exine (see Figs. 2.27 and 5.1).

The shape of the anther especially at its abaxial side is as useful as anther dehiscence to distinguish sections in the African (i.e. subgenus Arouna) and to a lesser extent in the Madagascan and Indo-Malesian subgenera (Dansera and Dialium) (see Figs. 2.15 and 2.16). In subgenus Arouna the species in section Arouna have anthers humped

while the species in section Codarium have them flattish at the abaxial side (see Fig. 2.15). This humped shape of the anther is also found in one species (i.e. D. occidentale) of section Hova (subgenus Dansera) in Madagascar which occurs on the west side of the island. D. occidentale used to be a subspecies of D. madagascariense (which occurs on the opposite side of the island) but on the basis of this distinction plus its very small anther (see description of species number 23 and Figs. 2.13, A and 2.16, F), I have now accorded it the status of species. It is thus closely related to the African species (excepting section Codarium). The two species (D. madagascariense and D. unifoliolatum) of E Madagascar (section Hova) on the other hand, have anthers with flattish abaxial and adaxial sides which is similar to their relatives (D. kunstleri, see Fig. 2.16 D and D. procerum) in W Malesia (section Dansera). The shape of the anther in the Indo-Malesian subgenus Dialium is more similar to D. englerianum (section Codarium, Africa) than to the species in subgenus Dansera (Madagascan and W Malesian).

The number of petals and stamens is variable in the African species and cannot be used to delimit sharply the infrageneric taxa there. By contrast, all the species in the Indo-Malesian subgenus Dialium, have 2 stamens and are without a petal. In subgenus Dansera (Madagascar and W Malesia), the number of petals and stamens can separate sectional categories, i.e. section Hova (Madagascar) with 3 petals and 2 stamens and section Dansera (W Malesia) with zero petals and 6 stamens. In subgenus Dansera, therefore, the number of petals and stamens correlates with geographical distribution (see Fig. 4.3).

5.2.2. Anatomy and palynology

In addition to gross morphological characters, it is also possible to delimit the infrageneric taxa on anatomical and pollen features.

I consider that taxonomic characters from the following features are important.

1. the number of ridge bundles (adaxial side) at the middle cross section of the pulvinus
2. the type of inclusions in the axial parenchyma of the secondary xylem
3. the type of sculpturing of the pollen exine

5.2.2.1. Pulvinus vascular bundles

Variations in the structural patterns found in the vascular body of a petiole of a normal leaf, especially in woody dicotyledons, have long been recognised to be of taxonomic value (Howard, 1974 for historical review; Howard, 1979). The systematic value varies from one taxon to another. In some cases families can be recognised; in other instances genera, species or varieties can be distinguished on the basis of the petiole vascular patterns. However, these patterns appear to be most useful in the interpretation of taxa at the generic level (Howard, 1963; 1974; 1979).

Comparative anatomical studies, mostly on the family level, have been undertaken to provide evidences for phylogenetic relationships of taxa. Some of these studies which included, among others, anatomical examination of the petioles were those Decker (1967) on Luxemburgieae (Ochnaceae), Dickison (1967; 1975) on Dilleniaceae and Cunoniaceae, Schofield (1968) on Guttiferae, Stern, Brizicky and Eyde (1969) on Columelliaceae, Stern, Sweitzer and Phipps (1970) on Saxifragaceae, Stone (1970) on Juglandaceae and Sweitzer (1971) on Ulmaceae. Most of these studies concluded that anatomical variations present in the family provide valuable evidence for generic definition and separation. These anatomical variations, however, do not always have obvious ecological or evolutionary interpretations.

Anatomical variation of the leaf, including petiole, often relates closely with genera or species but occasionally with families. The work of Baas (1975) on the vegetative anatomy of Aquifoliaceae suggested the view that the great variability of several characters within a genus (in Aquifoliaceae) implies that the systematic value of these characters is restricted in discussions of affinities above the genus level. Of equal importance is the study of Jansen and Baas (1973) on the comparative leaf anatomy of Kokoona and Lophopetalum (Celastraceae) which concluded that the separation of the two genera by morphological-taxonomic herbarium study is supported by the differences in vascular anatomy of the distal end of the petiole. This is more complex in Lophopetalum than in Kokoona, but other taxonomic characters of the leaf, viz., stomata, hairs, etc. gave no positive results. Dickison and Baas (1977) used petiole vascular patterns (among other vegetative characters examined) to suggest close relationship of Paracryphia (Paracryphiaceae) to genus Sphenostemon (Trimeniaceae). The study of Rojo (1978) on the petiole anatomy and vascular patterns of Philippine Shorea (Dipterocarpaceae) concluded that the vascular bundles, in combination with other anatomical features, generally agree with the sectional categories of the genus as defined by Ashton (1978) based on morphological herbarium study. Metcalfe and Chalk (1950) extensively used petiole anatomy in their study of the dicotyledons and also reviewed studies on petiole anatomy up to that period.

In Leguminosae, Watari (1934) studied the vascular patterns of petioles of some species cultivated in Tokyo. One of his findings was that the presence or absence of the ridge bundle is irregular even in one and the same genus. In usual cases, however, he pointed out that the ridge bundles are separated from the petiolar stele at the transitional region between the pulvinus and the slender part of the

petiole. This is confirmed in Dialium where the critical separation of the ridge bundles occurs more or less halfway up the pulvinus. This led, in this study, to the arbitrary selection of the middle cross section of the pulvinus as the point where variations in number or ridge bundles were taken and compared.

In this study, it is found that species in subgenus Arouna (Africa) have generally one ridge bundle at the mid point of the pulvinus while species in subgenera Dansera (Madagascar and W Malesia) and Dialium (Indo-Malesia) have them generally two.

5.2.2.2. Wood inclusions and other anatomical features

The use of wood anatomical diversity for taxonomic purposes has been reviewed by Metcalfe and Chalk (1950, 1979) and very recently by Baas (1982). According to Baas, the potential use of wood anatomical diversity for taxonomic purposes had already been hinted by various authors in the first decade of the nineteenth century. However, critical studies based on extensive research materials had begun in the second half of the nineteenth century. Among the more important studies, Baas (1982) cites the work of Sanio (1863), Boerlage (1875), Vesque (1881) and de Bary (1884). This period culminated with the work of Solereder in 1899 which was translated into English by Boodle and Fritsch and revised by Scott (1908). Solereder's work had led to the preparation (Metcalfe, 1976) of the 'Anatomy of the Dicotyledons' by Metcalfe and Chalk (1950) which not only summarised the data accumulated during the first half of the twentieth century but also included major original observations and taxonomic comments (Baas, 1982).

The important contribution of comparative wood anatomy to taxonomy (aside from identification and assessment of the chemical, mechanical and physical properties of wood as a building material) is not only on the use of specific characters such as vestured pits (Bailey, 1933),

crystals (Chattaway, 1955; 1956) and silica (Amos, 1952) for their taxonomic value but also on the phylogenetic significance of some wood anatomical features. Bailey (1954) and his students from 1918 (Bailey and Tupper, 1918) onwards have assessed the phylogenetic significance of wood anatomical features such as vessels and tracheary elements (Metcalfe and Chalk, 1950; Davis and Heywood, 1973; Heywood, 1976). This has greatly influenced the use of anatomical characters as additional evidence in modern systems of classification, for example by Cronquist (1968), Thorne (1976), Dahlgren (1980) and Takhtajan (1980).

The value of wood anatomical features to taxonomy has been elaborated extensively by Metcalfe and Chalk (1950, 1979), Brazier (1975), Stern (1978) and Baas (1982). As it has been previously expressed in a similar vein by other workers, Baas (1982) states that "if at all there is a generally applicable principle in systematic taxonomy, it is the rather negative one that no absolute gener^{a/}isations can be made on the value of any single character. In this respect the wood anatomical approach does not differ from any other source of inquiry in plant taxonomy." A good review on the role of wood anatomy in taxonomy is given by Davis and Heywood (1973).

In this study, wood anatomical features especially the inclusions in the axial parenchyma are taxonomically important. Inclusions and other features of Dialium wood are discussed below.

The occurrence of silica, oxalate crystals or both silica and crystals in the same wood in the axial parenchyma is taxonomically important at the infrageneric level. For example, subgenus Arouna possesses both silica and crystals in the same wood (see Fig. 2.24, B). Subgenus Dansera has only silica (except D. occidentale of W Madagascar) inclusions (see Fig. 2.24, F) while subgenus Dialium (Indo-Malesian) exclusively has oxalate crystal inclusions (see Fig. 2.24, D). These

types of inclusion are taxonomically correlated with geographical distribution, i.e. subgenus Arouna (African and Neotropics - both silica and crystals in the same wood), subgenus Dansera (Madagascar and W Malesia - silica only, except D. occidentale) and subgenus Dialium (Indo-Malesia - oxalate crystals only). This anatomical feature confirms the infrageneric divisions based on morphological grounds.

The occurrence of silica inclusions mostly in axial parenchyma has recently been recorded by Koeppen (1980) based on an extensive survey of 382 genera in the Leguminosae. Koeppen found that silica inclusions are present only in 8 of the genera surveyed and they all belong to the subfamily Caesalpinioideae. Out of these 8 genera, 4 are under the tribe Cassieae (i.e. Apuleia, Dialium, Dicorynia and Distemonanthus) and which all belong to the new subtribe Dialiinae of Irwin and Barneby (1981).

The occurrence of oxalate crystals (usually rhomboidal) mostly in chambered strands in timbers was studied by Chattaway (1956). Out of the 77 leguminous species investigated in that study, 32 belong to Caesalpinioideae, 29 to Papilionoideae and 16 to Mimosoideae. The presence of oxalate crystals in leguminous wood was also recently reported by Baretta-Kuipers (1981). She noted that occurrence of rhomboidal crystals in chambered strands is common throughout all three subfamilies investigated, thus confirming Chattaway's finding.

Anatomists have recognised that the wood anatomical features in the Leguminosae are close to each other and there are no sharp distinctions even at the subfamily level (Solereeder, 1908; Senn, 1943; Metcalfe and Chalk, 1950). Identification of leguminous wood especially at genus and species level is so difficult that the wood anatomist is often frustrated because of the close similarity of their external features and anatomical characters (Koeppen, 1980). Nevertheless, some generalised anatomical features such as those found by Reinders-

Gouwentak (1955) based on storeyed structure features are helpful to recognize taxa at the subfamily level.

Recently, Baretta-Kuipers (1981) found that the ray structure (i.e. type and height in tangential section) and number of cells per axial parenchyma strand could help establish phylogenetic relationships in the three subfamilies of the Leguminosae. The more heterogeneous and higher the rays are and the more cells the parenchyma strands have, the less they are specialised and hence the more primitive. Using these criteria, Baretta-Kuipers found that the wood of the Caesalpinioideae is the most primitive, the Papilionoideae as intermediate and the Mimosoideae as the most advanced. She, however, noted that the storeyed structure (e.g. in rays and axial parenchyma cells) is an advanced character. Storeyed structures are absent in Mimosoideae and therefore it is considered to be primitive in this respect. On the other hand, Koeppen (1980) found that the presence of silica inclusions, together with their distribution in the tissues of the wood of the Leguminosae, constitute a reliable diagnostic character, which is useful not only for purposes of identification but also has taxonomic implications. Koeppen found that silica inclusions are restricted only to species belonging to the three tribes of the Caesalpinioideae, viz., Caesalpinieae (3 genera), Detarieae (1 genus) and Cassieae (4 genera). In Cassieae, silica inclusions are found in species of Dialium (subgenera Arouna and Dansera), Apuleia, Dicorynia and Distemonanthus as stated earlier.

From the findings of the above workers, there can be no doubt that anatomical features in leguminous wood can be used to advantage in taxonomic delimitation especially in tribal and subfamilial lines. In the present study, however, the wood anatomical features especially the inclusions in the axial parenchyma, are used to delimit lower level taxa, i.e. within the Dialiinae, particularly in dividing Dialium into infrageneric taxa.

The anatomical features of Dialium wood are indeed very uniform (see Table 2.2). It is impossible to identify a piece of Dialium wood down to the species level, but by using the characters present in the axial parenchyma the possibility of identification is now for the first time narrowed down to the infrageneric level. In as much as the type of inclusion is correlated with geographical distribution, it would be possible to indicate whether a piece of Dialium wood comes from Africa, Madagascar or Indo-Malesia, but provided of course that the anatomical features of the family or the tribe is first taken into consideration.

5.2.2.3. Pollen

Pollen characters have been increasingly used by taxonomists to support delimitation of taxa based on external gross morphology, and recently particularly heightened by the use of the scanning electron microscope (SEM) and transmission electron microscope (TEM) to look at the surface sculpture patterns and structural features of the exine at high resolution. The application of SEM in systematics has been fully dealt with in Heywood (1971 b). Even under ordinary light microscope, external ornamentation of pollen shows patterns which are distinctive to particular groups of plants (Erdtman, 1966). A rather significant account of pollen morphology of the Leguminosae had been presented by Erdtman (1966). Fasbender (1959) extensively studied the pollen of mainly American genera of the Amherstieae, Cynometreae and Sclerobieae using particular pollen characteristics. She found that pollen characters support the traditional taxa but some needed rearranging based on palynological grounds. The above studies have been augmented recently by the systematic studies of the three subfamilies by Guinet (1981) on Mimosoideae, Graham and Barker (1981) on Caesalpinioideae and Ferguson and Skvarla (1981) on Papilionoideae (see Polhill and Raven, 1981).

Graham and Barker (1981) in their study of caesalpinoid taxa revealed considerable variations in sculpturing patterns of the exine. They have emphasized light and scanning electron microscopy of surface features (size, shape, apertures, sculpture patterns) which they considered most likely to provide data readily available to help solve problems of tribal classification in the Caesalpinioideae. They pointed out that the perforate tectum is the most common structural feature of the angiosperm and is particularly widespread throughout the Leguminosae. They emphasized that similarity in the pollen structure (including sculpture patterns) in unrelated taxa in Caesalpinioideae does not imply that they are taxonomically related because these patterns must have developed through parallelism and convergence caused by pollination mechanism, etc.. At the level of the tribe, however, they recognised that the different features may prove useful in separating taxa into subgroups. In this study, the pollen sculpturing patterns have proved to be taxonomically useful in delimiting infrageneric taxa.

The sculpturing pattern of the exine has already been partly discussed above particularly to strengthen the infrageneric division of the taxa based on gross morphological data. At the subgenus level, it supports strongly the division of the genus into three subgenera (Arouna, Dansera and Dialium). At the level of section, it also strongly supports the division of subgenus Arouna into the amplified sections Arouna and Codarium, the former with finely striate pollen, the latter with finely (and striato-) reticulate pollen.

The rather coarsely reticulate pollen of the Madagascan species (subgenus Dansera section Hova) makes them to be more closely related to the finely reticulate pollen of the Indo-Malesian species (subgenus Dialium and subgenus Dansera section Dansera) than to the finely striate pollen of the African species (subgenus Arouna).

5.3. Definition of Infrageneric Taxa

The taxa are defined according to the outline in Table 5.1 based on the important taxonomic characters discussed in the previous sections. The outline of the proposed subdivision (Table. 5.1) is semi-diagrammatically illustrated in Fig. 5.1. For comparison, the outline of the previous classification (Steyaert, 1951) of the African species is presented in Table 5.2. See also Table 7.1 (i.e. inter-relationships of the species.).

5.3.1. Key to the infrageneric taxa

KEY TO SUBGENERA, SECTIONS AND SUBSECTIONS

1. Receptacle with a disc much wider than the ovary (Africa- Neotropics)
..... I. Subgenus Arouna
2. Anthers with pointed apex on the adaxial side, usually humped on the abaxial side, and with basipetally dehiscent slits
..... A. Section Arouna
3. Filaments straight to slightly curved; fruits $\pm$ globose; petals 0 or sometimes 1 a. Subsection Pirula
3. Filaments geniculate; fruits $\pm$ compressed; petals 1 (Africa) b. Subsection Indumentosa
2. Anthers with retuse apex, $\pm$ flattish on both abaxial and adaxial sides, and with evenly dehiscent slits (Africa)
..... B. Section Codarium
1. Receptacle with disc absent, narrow or about as wide as the ovary.
4. Sepals 5; petal 0; stamens 2 (Indo-Malesia).....
..... II. Subgenus Dialium

4. Sepals 3; petals 3 or 0; stamens 2 or 6 (Madagascar -
W Malesia) III. Subgenus Dansera

5. Petals 3; stamens 2; anther apex deeply cleft
(Madagascar) C. Section Hova

5. Petals 0; stamens 6; anther apex not cleft (W Malesia)
..... D. Section Dansera

5.3.2. The infrageneric taxa defined (see Table 5.1 and Fig. 5.1)

The traditional gross morphological characters are combined with the data on wood anatomy and pollen in defining each infrageneric taxon recognised by me. Definitions are restated in Part IV (Taxonomy) where they are nomenclaturally treated.

Subgenus AROUNA. Receptacle with well-developed disc much wider than the ovary. Flower buds trulloid-ovoid (except D. englerianum, D. pentandrum and D. schlechteri). Sculpturing of the exine finely striate (section Arouna) or finely (and striato-) reticulate (section Codarium). Secondary xylem axial parenchyma cells predominantly containing silica inclusions and often together with few oxalate crystals in short chambered strands.

Section AROUNA (subgenus Arouna). Anthers with pointed apex on the adaxial side, usually humped on the abaxial side and with basipetally dehiscing slits. Sculpturing of the exine finely striate. Filaments more or less straight or geniculate. Fruits (sub)globose to compressed.

Subsection PIRULA (Section Arouna). Filaments straight to slightly recurved at the top. Fruits ellipsoidal to (sub)globose. Petals 0 or 0-1.

Subsection INDUMENTOSA (section Arouna). Filaments geniculate. Fruits more or less compressed. Petals 1.

Section CODARIUM (subgenus Arouna). Anthers with retuse apex, the abaxial side more or less flattish, and with evenly dehiscent slits. Sculpturing of the exine finely (and striato-) reticulate. Filaments more or less straight. Fruits ellipsoid-ovoid to sometimes more or less discoid.

Subgenus DIALIUM. Receptacle with disc absent, narrow or as wide as the ovary or rarely with a flattish top (D. hydnocarpoides). Sepals 5. Petal 0. Stamens 2. Sculpturing of the exine finely reticulate. Secondary xylem axial parenchyma cells exclusively containing oxalate crystals in long chambered strands. Leaves imparipinnate, usually more than 2 pairs.

Subgenus DANSERA. Receptacle with disc absent. Sepals 3. Petals 3 or 0. Stamens 2 or 6. Sculpturing of the exine rather coarsely reticulate. Secondary xylem axial parenchyma cells containing silica (except D. occidentale which rarely contains crystals). Leaves unifoliate or imparipinnate to 2 pairs (rarely 3 pairs).

Section HOVA (Subgenus Dansera). Sepals 3. Petals 3. Stamens 2. Anther apex deeply cleft. Leaves unifoliate or trifoliate.

Section DANSERA (subgenus Dansera). Sepals 3. Petal 0. Stamens 6. Anther apex not cleft. Leaves unifoliate or (1-) 3-5 (- rarely 7) leaflets.

Although the division of the genus into infrageneric taxa more or less conforms with previous classifications, there are differences which are explained below (see also Fig. 5.1 and Table 5.1).

Table 5.1. Proposed subdivision of Dialium. The taxa have been provided with numbers and letters as arranged in the taxonomic text (Part IV). See also the key to infrageneric taxa.

Genus	Subgenus	Section	Subsection
Dialium			I. Arouna (Aublet) Stey. _____
			A. Arouna¹ _____ b. Codarium² _____ a. Pirula Stey. b. Indumentosa Stey.
			II. Dialium _____
			III. Dansera (Steenis) Stey. _____
			C. Dansera D. Hova (Irwin & Barneby) Rojo

- 1) Section Arouna (Aublet) Taubert in Engl. & Prantl, Pfl. Fam. iii, 3 (1892) 155.
- 2) Section Codarium (Sol. ex Vahl) Benth. in Benth. & Hook., Gen. Pl. 1 (1865) 574.

The subgenus Hova Irwin and Barneby (1981). This study disagrees giving the Madagascan species a separate grouping with a rank of subgenus because their characters (except androecial parts) are in general agreement with those of subgenus Dansera. I now reduce this to a section of subgenus Dansera.

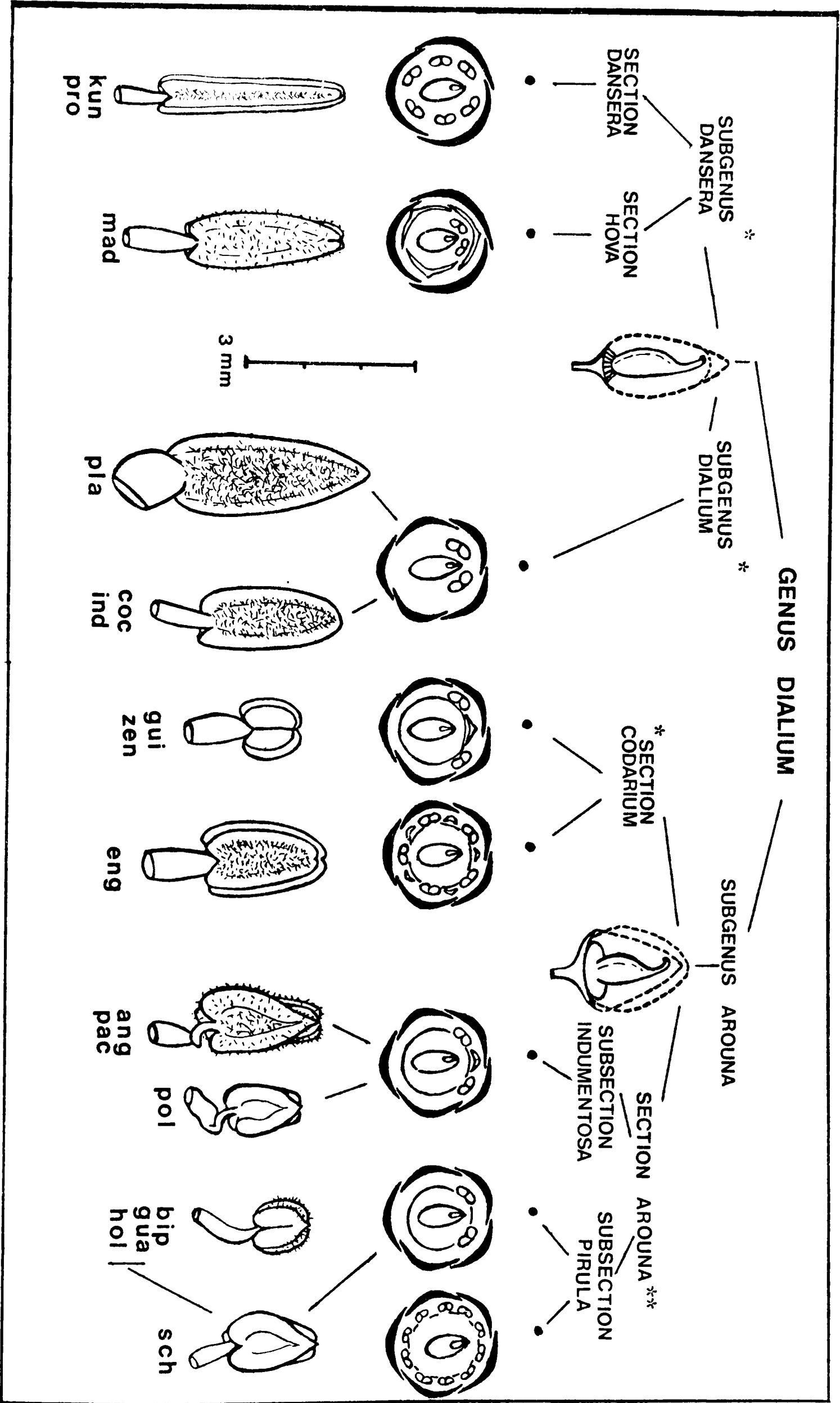
The subgenus Uittienia (van Steenis) Steyaert (1953). Steyaert reduced this genus of van Steenis to a subgenus of Dialium. This was reiterated by Irwin and Barneby (1981). They obviously did not see the flowers and fruits (see Fig. 3.1 and description of the fruit in Chapter 3). This taxon has to be taken out from Dialium and restored as a monotypic genus in the Cassieae as van Steenis originally intended. Without this taxon, Dialium becomes a group of closely related infra-generically divisible taxon.

The section Recta (subgenus Arouna) Steyaert (1951). This section which Steyaert divided into subsections and in turn split into series and subseries (see Table 5.2) is based principally on the straightness of the filaments. This cannot be maintained (at the level of section) because it is composed of species which possess different types of exine sculpturing and anther apex. For this reason, I now reduce those species with striate pollen and with acute anther apex (on the adaxial side) to subsection Pirula Steyaert of section Arouna. Those species with finely (and striato-) reticulate pollen and with retuse anther apex are now placed by me to the newly amplified section Codarium.

The section Geniculata (subgenus Arouna) Steyaert (1951). This section (also split by Steyaert into subsections and series) is based on geniculate filament. It also cannot be maintained at the level of section because species under it possess the same types of exine sculpturing and anther apex as species in subsection Pirula. However, because of the distinctive geniculate filament, the group is kept separate from subsection Pirula (i.e. with straight filament). I now

Fig. 5.1. Dialium and its infrageneric taxa illustrated.

sch - schlechteri, bip - bipindense, gua - guianense,
hol - holtzii, pol - polyanthum, ang - angolense,
pac - pachyphyllum, eng - englerianum, gui - guineense,
zen - zenkeri, coc - cochinchinense, ind - indum, pla - platysepalum,
mad - madagascariense, kun - kunstleri and
pro - procerum. The direction of evolutionary trends at
the sectional and/or subgenus level is from the right to
the left. The scale refers only to the size of the anthers
which are adaxially illustrated.



* - pollen reticulate; ** - pollen finely striate

reduce species in this section to subsection Indumentosa Steyaert of section Arouna.

The series and subseries (see Table 5.2) of sections Recta and Geniculata stated above are based on rather trivial characters which are best put in the species descriptions rather than giving them infra-generic status. A more coherent classification of African Dialium is shown in the semi-diagrammatic representation in Fig. 5.1 and presented in a table (Table 5.1).

5.4. Phytogeography of Infrageneric Taxa (see Figs. 4.1 - 4.3)

My definitions of the taxa are based solely on the data from morphology, anatomy and palynology. It can be seen that these taxa have correlated geographical ranges and this is expressed at the infra-generic level. This clearly suggests they are natural groups. We may now base a discussion about phytogeography of infrageneric taxa within Dialium on a combination of morphological-anatomical features and geographical patterns which are first tabulated as follows:

<u>Taxa</u>	<u>Taxonomic characters</u>	<u>Distribution</u>
Subgenus <u>Arouna</u>	Disc present, sepals 5, silica and oxalate crystal inclusions both present in the wood	Africa and Neotropics
Section <u>Arouna</u>	Anther apex adaxial side acute, pollen finely striate	Africa and Neotropics
Section <u>Codarium</u>	Anther apex retuse, pollen finely reticulate	Africa only
Subgenus <u>Dialium</u>	Disc absent, sepals 5, pollen finely reticulate, only oxalate crystal inclusions in the wood	Indo-Malesia

<u>Taxa</u>	<u>Taxonomic characters</u>	<u>Distribution</u>
Subgenus <u>Dansera</u>	Disc absent, sepals 3, pollen rather coarsely reticulate, only silica (except in one species) inclusions in the wood	W Malesia and Madagascar
Section <u>Hova</u>	Petals 3, stamens 2	Madagascar
Section <u>Dansera</u>	Petals 0, stamens 6	W Malesia

In their review of the biogeography of the Leguminosae, Raven and Polhill (1981) stated that the time of origin of the legumes is unknown, although fossil woods (Müller-Stoll and Madel, 1967, as cited by Raven and Polhill, loc. cit.) and pollen (Muller, 1981) indicate the presence of Mimosoideae and Caesalpinioideae in the Maastrichtian (65-70 million years ago). Also, they have indicated that despite little support from the fossil record (Raven and Axelrod, 1974; Muller, 1981), the Caesalpinieae, Cassieae and Cercideae almost certainly differentiated prior to the close of the Cretaceous. Furthermore, Raven and Polhill (1981) found that on the basis of present-day distribution most archaic genera of the legumes are concentrated in the Old World, with Africa as the prime centre for radiation and evolution in the family. This means that the Leguminosae is a Gondwanic family and the above background would serve as a reference point on the discussion of the possible spread of Dialium west and east of Africa.

In the context of worldwide distribution, the subgenera (and partly the sections outside Africa) are allopatric with the exception of subgenus Dansera section Dansera which overlaps with the Indo-Malesian subgenus Dialium in W Malesia. The sympatric distribution of section Dansera and subgenus Dialium in W Malesia (see Fig. 4.3) is unique because, among other characters, their floral morphology is quite different; the former has 3 sepals and 6 stamens and the latter has 5 sepals and 2 stamens. This leads to the conjecture that the differences in their morphology could not have been the result of

evolutionary change within the area they now occupy. This is because their close affinities (at the subgeneric level) are not with each other but with their relatives in Madagascar and Africa, i.e. section Dansera to section Hova in Madagascar and subgenus Dialium to subgenus Arouna (particularly section Codarium) in Africa.

In terms of geographical distances (i.e. assuming that there are no great natural barriers like high mountains and strong sea currents), it would be safe to assume that the nearer the infrageneric taxa are to each other, the more likely they are to have closely similar morphology. Yet, this is not the case because section Hova (subgenus Dansera) in Madagascar is morphologically closer to section Dansera in W Malesia than to subgenus Arouna in nearby Africa. On the other hand, despite the great distance, section Codarium (subgenus Arouna) in Africa is morphologically closer to subgenus Dialium in Indo-Malesia than to section Hova (Madagascar).

Dispersal of Dialium fruits (seeds) by monkeys has been recorded by Ridley (1930) while Pijl (1982) noted their dispersal by ground mammals. However, Dialium species could possibly be disseminated by long distance dispersal by water. In fact, some species in W Malesia, i.e. D. platysepalum (Corner, 1978) and D. indum (Whitmore, 1972) and Africa, i.e. D. polyanthum and D. zenkeri (Steyaert, 1952), inhabit water fringes or swampy areas. Also, sea currents could possibly disperse the fruit because it floats. However, in the absence of any record, long distance dispersal would remain unlikely, at least for species found east of continental Africa (i.e. Madagascar and Indo-Malesia). For example, there are no species in Madagascar that are found across E Africa and vice-versa. Also, in Malesia the genus has not crossed the narrow Makassar Strait from Borneo to Celebes nor is it recorded to occur in the neighbouring islands to the north (Palawan,

Sulu archipelago, Mindanao) or the south-east (Bali) of Borneo.

Assuming that Celebes is botanically poorly collected, Dialium (if species occur there) could not have escaped the discerning eyes of Dutch botanists and foresters because of its prominent habit. Therefore, the present-day occurrence of Dialium in both Madagascar and Indo-Malesia could not be explained by long distance dispersal.

Explanation should be sought from other dispersing agents. For example, it would fit quite sensibly if we explain the distribution patterns in concert with geographical history. For this purpose, an assumption should be taken to account for the occurrence of the subgeneric taxa of Dialium east of continental Africa -- that they could have been brought about by means of the movements of great land masses by continental drift (Wegener, 1924).

As reviewed by Whitmore (1981: p. 70), there were several early attempts to relate the distribution of plants in the Malay archipelago to the geographical history of the region along Wegenerian lines, but abandoned because of disagreement and lack of precision in the palaeogeographical interpretation. However, the idea of Laurasian/Gondwanic collision has become acceptable again especially when viewed against the background of the modern theory of plate tectonics which has developed since the 1960s (Whitmore, 1981). This idea particularly finds support from the papers, especially by Schuster (1972, 1976), Raven and Axelrod (1972, 1974), Johnson and Briggs (1975) and more recently by van Steenis (1979: p. 156). Van Steenis' acceptance of the theory of plate tectonics is particularly of interest because he (van Steenis, 1950, 1962) was among those who abandoned relating the ranges of Malesian plants to the geographical history of the area.

The theory of continental drift or plate tectonics has recently been used to test the validity of the Wallace's line (see George, 1981) using some examples from both flora and fauna extant in Wallacea (the

island region in central Malesia which lies between Wallace's line and Weber's line) and Malesia as a whole (Whitmore, 1981). Accordingly, many plants and animals in Malesia probably could have arrived from one of three sources, i.e. Laurasia, Gondwanaland via India and Gondwanaland via Australia. With this theory in mind, it is clear to imagine that species in subgenus Dansera section Dansera and subgenus Dialium could have reached W Malesia by way of the northwest route from Gondwanaland via India. In fact, there exists one species (possibly two) of subgenus Dialium (D. ovoideum) in Kerala and Sri Lanka.

The distribution of Dialium guianense (a species very closely related to the W African species in subsection Pirula) in the Neotropics is not very easy to interpret. It could either have arrived there by means of long distance dispersal (particularly sea current) or by drifting on the continental fragment. If long distance dispersal is to be considered, there are examples of plants (of the same species) occurring in the tropics of both sides of the Atlantic which possibly could have been dispersed by water.

In leguminous plants, Ridley (1930), Amshoff (1939), and Polhill (1981: p. 240) noted this distribution pattern (i.e. on both sides of the Atlantic) in Andira inermis (Wright) DC., Dalbergia ecastaphyllum (L.) Taubert and Machaerium lunatum Tul. Other examples are two species of Pterocarpus (Rojo, 1972), i.e. P. officinalis Jacq. and P. santalinoides DC., and Sophora occidentalis L. (Ridley, 1930; Thorne, 1973). Dalbergia ecastaphyllum and Sophora occidentalis are sea-current-borne plants (Thorne, 1973) and probably Machaerium lunatum. The two species of Pterocarpus above are riparian - their fruits (the seed-bearing part thickened and corky and the wing reduced to a mere keel) could easily be transported by sea currents. Andira inermis is also a riparian species with fruits capable of long distance dispersal by water. Because of the adaptability of their fruits to water transport,

there can be no doubt that the above examples of leguminous species must have been distributed to their present range over long distance by sea currents.

There are also non-leguminous plants (of the same species) found on both sides of the Atlantic, e.g. Rhipsalis baccifera (J. Miller) N.T. Stearn (a highly specialised cactus dispersed by birds), Tristichia trifaria (Bory and Willd.) Sprengel of the Podostemaceae (dispersed by water) and Pitcairnia feliciana L'Heritier (dispersed possibly by birds) (Thorne, 1973).

In all the above-mentioned plants, there has not been any actual experiment nor any record to show which direction they have dispersed or from where they have originated. The plants are all well developed on both sides of the Atlantic. In this connection, it has been suggested by Thorne (1973) that for the above taxa, interchange can be two-way between two continents rather than one-way between a source and a receptive continent or archipelago. As Thorne noted, "the two continents (Africa and S America) present numerous similar ecological niches that surely facilitate establishment of disseminules from the opposite continent. The continents have been there a long time, much longer than history of seed plants requires", such that long distance dispersal by sea currents is the most logical means by which the above leguminous plants have spread.

Within the leguminous plants above, dispersal seems to have occurred both ways. In contrast, we consider the species in Velloziaceae (Ayensu, 1973). Ayensu theorised that on the basis of correlation of morphological and anatomical characters, the Velloziaceae of Madagascar-Africa are more primitive than those in S America and, therefore, even if there is high preponderance of species of a taxon in a geographical region (as Velloziaceae in S America), it does not necessarily represent a place of origin. So, for Velloziaceae, long distance dispersal (particularly by birds) is held likely to be one-way (Ayensu, 1973) from

Madagascar-Africa to S America.

Dialium guianense in the Neotropics is without doubt distributed there from Africa. Africa (especially the west, see Fig. 4.2) is not only the centre of diversity of Dialium but also the area where the most archaic taxa (subgenus Arouna) of the genus are found.

The conclusions that can be drawn from the above discussion on the relationship of morphological-anatomical features and geographical distribution of the infrageneric taxa of Dialium are the following:

1. For the infrageneric taxa east of tropical Africa, the more likely cause of dispersal could probably have been by drifting on the land masses. This is supported by the fact that the two subgeneric taxa (subgenera Dansera and Dialium) have overlapping ranges in W Malesia, and one of the two subgenera (subgenus Dansera) has a bicentric distribution, i.e. one section in Madagascar (Hova) and another one in W Malesia (Dansera). The two subgenera could not have been among those taxa originating from eastern Asia-Australasia, an area which is suggested to be the origin and centre for radiation of the angiosperms (Smith, 1973; Takhtajan, 1969), because their archaic relatives can be found in Africa (i.e. subgenus Arouna). Moreover, the prime centre for radiation and evolution of the legumes is in Africa (Raven and Polhill, 1981).

2. The widely distributed and only species (D. guianense) of Dialium in the Neotropics could probably have been dispersed one-way there by sea currents from W Africa. This is because, as already stated above, Africa is the centre of diversity as well as the origin of the most archaic taxa of Dialium. The ease with which the fruits of D. guianense could have been dispersed by sea currents is attested by its wide distribution pattern, i.e. from S Mexico to the Amazonia which is one of the widest distribution areas covered by a single species of Dialium.

5.5 Evolutionary Trends Within Dialium

It is generally accepted that the Leguminosae can be divided into three major subgroups. It is a matter of opinion (Hutchinson, 1964; Brenan, 1967) whether or not it should be separated into three subfamilies or families. The fact that it can be divided into subgroups means that it has evolved during its current existence.

Evolutionary trends of the legumes have been reviewed by Tutin (1958), and subsequently by Heywood (1971a) who presented some of the questions as to what families show the closest affinities to the legumes, from what group did the legumes have their origin and what is the most satisfactory placing of the Leguminosae in the general system of the dicotyledons (Dickison, 1981). Answers to these questions can now be gleaned from the data accumulated out of the concerted efforts of biologists of various disciplines who had come to the International Legume Conference of 1978, held at the Royal Botanic Gardens, Kew, England. The data resulted in a published updated system of the legumes (Polhill and Raven, 1981) which reasserts the view of Bentham (1865) and Hutchinson (1964) that the Caesalpinioideae precedes and from it diverges the other two subfamilies (Mimosoideae and Papilionoideae). However, the view that the legumes are more related to the Rosaceae via the Chrysobalaneae (Hutchinson, 1964; 1969: p, 67) is abandoned. The evidence indicates the Leguminosae to be close to Sapindales and closer to Sapindaceae than to Connaraceae (Dickison, 1981: p. 50).

According to Polhill, et al. (1981) the most archaic genera of the Leguminosae seem to be the diverse extra tropical woody Caesalpinioideae - represented by the Gleditsia group (Gleditsia and Gymnocladus). In the order of divergence from the Gleditsia group the Dialiinae is placed 6th after the Dimorphandra group, the Sclerolobium group, the Peltophorum and Caesalpinia groups and Ceratoniinae (Polhill, et al. 1981: p. 5, fig. 1).

Among the five subtribes recognised in the Cassieae, the Dialiinae is placed second after Ceratoniinae. Within the Dialiinae, Zenia precedes the rest of the genera with Dialium immediately after it (Irwin and Barneby, 1981).

Evolutionary trends within the angiosperms are generally recognised by taxonomists. The majority of the dicta presented by Bessey (1915), reiterated by Hutchinson (1959) and briefly listed by Davis and Heywood (1973) are accepted by many taxonomists today. Of these dicta, the ones on the general features of the flowers are of particular interest because they can be applied to the evolutionary trends in the Leguminosae in general. The evolutionary trends in the flowers find support from Eames (1961) and Stebbins (1974). Stebbins has listed down the evolutionary trends of the perianth in the angiosperms as follows:

1. reduction - particularly suppression of the corolla and sometimes of the calyx.
2. differentiation of calyx and corolla
3. intercalary concrescence, producing 'fusion' of sepals or petals and 'adnation' of the filaments to the corolla tube
4. change of symmetry, from radial to bilateral, producing zygomorphy or 'irregular' flowers.

The above evolutionary trends of the flower (perianth) are essentially similar to the ones listed down by Eames (1961) and restated by Davis and Heywood (1973).

The morphological evolutionary trends of the Leguminosae have been dealt with by Tutin (1958) and in general terms by Hutchinson (1969). The most recent review of the evolutionary trends of the Leguminosae is given by Polhill, et al. (1981). In agreement with the generally accepted trends in angiosperm evolution put forward by Bessey (1915), Hutchinson (1959) and Stebbins (1974) and also the general trends in the Leguminosae presented by Polhill, et al. (1981), I now present

the evolutionary trends in Dialium. The direction of the evolutionary trends probably could have proceeded as explained below.

The habit, the inflorescence and the fruit of Dialium have stabilised and are not very useful to detect trends.

5.5.1. Leaves

The trends would seem to be from imparipinnate (2 or more pairs) to trifoliolate and finally to unifoliolate, i.e. from subgenus Arouna (except D. angolense) and subgenus Dialium to subgenus Dansera. As noted before, it is only in subgenus Dansera where unifoliolate leaves are found and in D. kunstleri var. trifoliolatum (W Malesian) a single twig sometimes shows together unifoliolate, 2-foliolate and 3-foliolate leaves. The evolution of the leaf in the above variety has not as yet stabilised. In the leaves of Caesalpinioideae the common denominator is reduction in complexity (Cowan, 1981: p. 57).

5.5.2. Flowers

The direction would be from weakly zygomorphic to strongly zygomorphic (e.g. Papilionoideae). Dialium flowers are weakly zygomorphic with a tendency to strong zygomorphy. The trend would seem to be from subgenus Arouna (D. schlechteri) to subgenus Dialium (D. platysepalum). Differences are found in the number of parts in the perianth and the androecium. The perianth and the androecium could have continued to evolve independently after the stabilisation of the basic fruit (Irwin and Barneby, 1981). In this case, the direction would appear to be from numerous to few parts so that 5 sepals would precede 3 sepals, i.e. from subgenera Arouna and Dialium to subgenus Dansera (see Fig. 5.1 for illustration).

The petals are variable in number but the trends would probably be from many to few and stabilised to zero (63% of the species). Subgenus Dansera section Hova has stabilised to 3 petals while subgenus Arouna varies from 5 petals (D. englerianum), to 1 petal (subsection Indumentosa) and without a petal (subsection Pirula, the majority of the species). The subgenus Dialium has stabilised to not having any petal at all. Stamen number could have also evolved in the same way as the petals and culminated in 2 stamens (78% of the species).

The receptacle has probably evolved from one with a disc to one without a disc. The flowers with disc are very weakly zygomorphic (in subgenus Arouna) while the receptacle in subgenus Dialium is rather more recurved (e.g. D. platysepalum). The tendency to strong zygomorphy in leguminous taxa, supposedly to protect the nectar from pollinators (Polhill, et al. 1981: p. 11), could have been the cause of the loss of the disc in Dialium. The loss of the disc could be traced through D. englerianum (section Codarium) and D. hydnocarpoides (subgenus Dialium). In D. englerianum, the disc is not as prominent as in the species in section Arouna and appears similar to the receptacle with narrow but flattish top in D. hydnocarpoides. The shape of the anthers and the sculpturing of the exine (finely reticulate) are almost identical in both species.

5.5.3. Pollen

The evolutionary trends in Dialium pollen are difficult to interpret especially when they are viewed at or above the level of genus. This is because its characters are generally shared by other taxa in the Caesalpinioideae, particularly Dialiinae. A reticulate exine sculpturing, for example, is characteristic not only of Dialium pollen but also of

the majority of the species in Caesalpinioideae. In fact, many taxa in the Leguminosae exhibit reticulate pollen (Erdtman, 1966). Also, striate exine sculpturing, particularly occurring in subgenus Arouna, occurs as well in other rather distantly related taxa in Caesalpinioideae (e.g. Peltogyne, Cynometra, Plagiosiphon, Lysidice, Brownea, etc.) as noted by Fiebner (1959), Erdtman (1966) and recently by Graham and Barker (1981). Ferguson and Skvarla (1981: p. 893) from their study of the pollen of Papilionoideae expressed the view that it is not possible to define the tribes by pollen types and meaningfully compare these with established groups. This is because there is great overlap and parallel in pollen characters between and within groups. Further, Graham and Barker (1981: p. 801) warned of parallelism and convergence in Caesalpinioideae of which similarities of pollen types could be caused by factors such as pollination mechanisms or structural and functional efficiency.

Nevertheless, at the infrageneric level, it is possible to detect evolutionary trends in Dialium pollen if correlated with the trends in the vegetative and floral parts. If subgenus Arouna (Africa) is considered the most primitive (as implied in the previous discussion by virtue of possessing a receptacle with a hypogynous disc) among the three subgenera of Dialium, then its associated striate (excepting section Codarium) exine sculpturing may be considered more primitive than taxa with reticulate exine (subgenera Dansera and Dialium). It is significant to note that the two pollen types (i.e. striate in the majority of species in subgenus Arouna and reticulate in subgenera Dansera and Dialium) are linked together by the striato-reticulate pollen of D. guineense (section Codarium subgenus Arouna) which, together with D. englerianum has floral features which are intermediate between subgenus Arouna section Arouna and subgenus Dialium.

5.5.4. Wood

It is just as difficult to detect evolutionary trends in the structural features of Dialium wood at or above the genus level. In general terms, the wood structure of the Dialiinae is uniform, i.e. all have a strictly storeyed structure, multiseriate rays and banded parenchyma (Reinders-Gouwentak, 1955; Koeppen, 1963, 1976; Koeppen and Iltis, 1962; Baretta-Kuipers, 1981). At the level of genus, the wood structure of Dialium is also uniform (Balan Menon, 1955; Burgess, 1966; Koeppen, 1980; Baretta-Kuipers, 1981) except in the type of inclusion in the axial parenchyma where species either display both silica and oxalate crystals together, silica only or oxalate crystals only. These characteristic features in axial parenchyma of Dialium wood, however, also occur in other genera in the Dialiinae (see Table 3.1, column 14) and in some other genera of the Cassieae (Chattaway, 1956; Baretta-Kuipers, 1981). In other words, the wood of Dialium and of Cassieae, in general, is homogeneous and as a result, evolutionary trends are difficult to detect at their level.

But, as in Dialium pollen, evolutionary trends in Dialium wood structure can be detected at the infrageneric level, i.e. if correlated also with the evolutionary trends in the vegetative and floral parts. Subgenus Arouna (considered more primitive) displays both silica and oxalate crystals together in the wood. Dialium guianense which I consider to have originated from ancestors in W Africa to central and tropical S America (see discussion in section 5.4) retains the same (i.e. silica and oxalate crystals together) inclusions in the wood. The infrageneric taxa which spread towards the east from Africa to Madagascar and Indo-Malesia display or retain only one of either type of inclusion, i.e. silica only (subgenus Dansera, except D. occidentale) and oxalate crystals only (subgenus Dialium). In terms

of inclusions in the axial parenchyma, therefore, subgenus Arouna would precede subgenera Dansera and Dialium. The evolutionary trend in this particular anatomical feature (inclusion in the axial parenchyma) is consistent with the evolutionary trends in the vegetative/floral parts as well as pollen morphology.

The evolutionary trends of vegetative and floral parts discussed above point mostly to the process of reduction, e.g. imparipinnate with many leaflets to unifoliate, 5 sepals to 3 sepals, with disc to without disc etc.. This means that the trends are from many to few parts and then their loss. The trends seem to fit well with some of the general dicta concerning primitive and specialised characters in angiosperms (Bessey, 1915; Hutchinson, 1959) and the general trends in evolution of the Leguminosae (Polhill et al. 1981).

The process of reduction of parts, however, may not have proceeded uniformly as the above assumption would imply. This is because, as generally agreed by biologists, "organs do not evolve at the same rate" and that "rates at which organs evolve are obviously related to the selection pressures affecting them, and to their genetic ability to vary" (Davis and Heywood, 1973; p. 34). An example of this is subgenus Dansera section Hova of Madagascar. In comparison with subgenera Arouna and Dialium, species of this section are advanced in terms of sepals (i.e. 3 instead of 5) but primitive in terms of petals (i.e. 3 instead of apetalous). Obviously, perianth parts in infrageneric taxa of Dialium have not evolved at the same rate. Selection pressures (e.g. pollinators) could have affected them in the past.

Aside from the different rates at which organs have evolved, trends could also have proceeded in reverse direction. This can ideally be checked by comparing them with fossil record, but since in angiosperms (especially in Leguminosae) there are hardly any fossils, interpretations

have to be based on the accepted view of evolutionary relationships of the taxa under discussion (Tutin, 1958; Polhill et al., 1981) using trends in the morphology of the angiosperms such as those listed by Bessey (1915) and Hutchinson (1959) as guide.

5.6. Characters for the Distinction of Species and Varieties

The important taxonomic characters listed in Table 2.1 are not only useful to delimit infrageneric taxa but also to distinguish one species from another. One taxonomic character, e.g. number of leaflets, can sometimes be used to identify a species or variety, although a combination of two or more characters is sometimes needed. These characters are discussed below.

The number of leaflets is useful to distinguish species and varieties within subgenus Dansera but not within subgenus Arouna (except D. angolense) or in subgenus Dialium. The rest of the characters of the leaflets like texture, reticulation and quality of indumentum are only of lesser importance although also useful to distinguish taxa in combination with other taxonomic features.

To consider subgenus Dansera. In section Dansera (W Malesia) D. procerum is unifoliolate; D. kunstleri var. trifoliolatum is partly uni- and trifoliolate; and D. kunstleri var. kunstleri is usually with 2 pairs of leaflets. In section Hova (Madagascar) D. madagascariense and D. unifoliolatum (both species found on the east side of the island) are trifoliolate and unifoliolate, respectively. A species (D. occidentale) on the other side of the island is divided into two varieties based on the number of leaflets, i.e. var. occidentale with trifoliolate leaves and var. septentrionale with unifoliolate ones. These varieties could be confused with the two species on the east side of the island, but other characters, such as shape, would help solve their distinction, i.e. anthers in D. occidentale are humped on the abaxial side while D. madagascariense and D. unifoliolatum have them flattish.

Of the species in Africa (subgenus Arouna) only D. angolense can definitely be identified by leaflet number which is 3. None of the species in subgenus Dialium (Indo-Malesia) can be identified by leaflet number alone.

The characters of the leaflets are uniform in most species but more variable in some others. The most variable of the species in terms of leaflet features is D. platysepalum (subgenus Dialium) of W Malesia. Before the present study, this species was formerly distinguished as five distinct ones. I have reduced them into a single species, i.e. D. platysepalum, and accorded each variant an informal name of 'group' without nomenclatural status. The specific epithet of the former species is applied as the name for each 'group' in order to retain its former identity.

The problem of delimitation of variable species in the tropics (particularly in Malesia) is not new. Since the revision of the flora in the Malesian region started in the 1950s, difficulty of delimiting variable species has been encountered and has been discussed in general terms by Vink (1970), Whitmore (1976) and Mabberley (1979). Particular difficulties were in Pometia (Sapindaceae) (Jacobs, 1962), Lepisanthes (Sapindaceae) (Leenhouts, 1969), Vavaea (Meliaceae) (Pennington, 1969), Drimys (Winteraceae) (Vink, 1970), and Chisocheton (Meliaceae) (Mabberley, 1979). The most extreme of cases is Allophyllus (Sapindaceae) (Leenhouts, 1967) where 255 former species were reduced to synonyms of only one variable species, Allophyllus cobbe (L.) Raeusch. The solution which has evolved amongst taxonomists working on the Malesian flora for naming variable species is the use of the concept 'entity' as has been done on Lepisanthes by Leenhouts (1969) and on Drimys by Vink (1970). Another alternative is to call these informal taxa 'paramorphs' as has been done by Jacobs (1962) on the Pometia pinnata Forst. complex.

In Dialium platysepalum, I prefer to name the variants as 'groups' without nomenclatural status, similar to 'entities'.

In D. platysepalum, variations in characters are in the size of the blades, and in the quality of indumentum and distinctness of the nerves on the under-surface of the blades. Four of these 'groups' I recognise are found in Peninsular Malaysia where the first specimens were collected and described as distinct species. However, the distinctness of these 'species' have been obscured by subsequent collections not only from Peninsular Malaysia itself but also from Sumatra and Borneo. This has resulted in many intermediates which cannot be properly placed exactly within each 'species' such that it is impossible to recognise more than a single polymorphic species. Also, the variation of leaflet characters, mostly in terms of quality of indumentum, seems the only basis for the previous species distinction in the complex. The flowers, although they vary slightly in size, are the same morphologically in all the 'groups'. Therefore, I reduce here the five described species into only one, following previous workers cited above with whose opinions I agree.

The characters of the flowers are also taxonomically important. They are useful not only to delimit infrageneric taxa but also to some extent identify one species from another. Of the parts of the flowers, the anther gives reliable taxonomic features which includes the shape (i.e. especially on the abaxial side) and the presence or absence of hairs. For example, in W Malesia D. hydnocarpoides and D. platysepalum are difficult to identify using leaflet characters. They can be definitely distinguished from each other by the shape of their anthers, i.e. the former is flattish on the abaxial side and the latter is v-channelled. The same is true of the species in Madagascar, i.e. if identification by means of leaflet number cannot be definitely established, then the identification has to be confirmed by the shape of the anthers (see discussion above). Likewise, species in section Arouna subsection Indumentosa are

difficult to identify by leaflet number (except D. angolense which is trifoliolate). Furthermore, the reticulation is areolate in all species and the size of the leaflets is more or less uniform. The shapes of the anthers and the filaments are again the same. But the presence or absence of hairs and the size of the anthers segregates individual species in this subsection. D. pachyphyllum has hairs on the anthers while D. tessmannii and D. polyanthum have them glabrous. Between the latter two species, the former has anthers almost twice as big as the latter.

The number of stamens is also taxonomically important to segregate species in Africa. In section Arouna subsection Pirula, only D. schlechteri and D. pobeguinii can be distinguished outright by means of number of stamens; the former with (8-) 10 and the latter with 5 stamens. The rest of the species in this subsection have 2 stamens. Stamen number is also important in section Arouna subsection Indumentosa and section Codarium: D. pentandrum (subsection Indumentosa) and D. englerianum (section Codarium) have 5 stamens, respectively while the rest of the species in their groups have 2 stamens.

With the exception of the above examples species in the genus cannot be easily recognised by means of the taxonomic characters of the leaflets alone nor also of the flowers alone but rather on the combination of characters of both. The key to the species in the taxonomic part of this study is based mostly on a combination of characters of both the flowers and leaflets.

6. CONCLUSIONS AND SUGGESTIONS FOR FUTURE STUDY

The results of the study give us the following conclusions:

1. The genus Dialium is held together by the conservative characters of the inner bark, the fruit, the testa and partly the flower.

The reddish-brown exudate from the cut inner bark, the drupaceous fruit with crustaceous exocarp and pulpy edible endocarp, the irregularly-cracked testa surface and the generally apetalous flower are taxonomic characters that separate the genus from the rest of the genera in the Dialiinae.

2. The infrageneric taxa (subgenera and sections) are correlated with geographical distribution. Thus subgenus Arouna is mainly confined in Africa; the subgenus Dansera (subdivided into two sections) is found in Madagascar (section Hova) and W Malesia (section Dansera); and the subgenus Dialium is restricted to Indo-Malesia.

3. The characters of wood and pollen provide basic information to test the previous infrageneric delimitations based on gross morphology. On this basis, the sectional and most of the subsectional taxa of Steyaert (1951) cannot be maintained.

4. Species in subgenus Dansera section Dansera and subgenus Dialium could have spread to achieve their present distribution in W Malesia by drifting on the land masses after Gondwanaland broke up. The single species (D. guianense) in the Neotropics could have originated from N Africa and dispersed by sea currents.

5. The evolutionary trends in Dialium probably have proceeded from many to few parts and then their loss. On this basis, most African species are more archaic than their Madagascan and Indo-Malesian counterparts.

6. Most Dialium species had been 'optimistically proposed' (as is generally true in the exploratory phase of any flora) as new to science

and out of about ninety published species, only twenty-seven (four with varieties) are now recognised compared to c. 40 previously estimated by Irwin and Barneby (1981).

7. The genera in subtribe Dialiinae are closely interrelated. Most of the genera, however, are more closely related to each other than they are to Dialium itself. Baudouinia, Eligmocarpus and Mendoravia are taxonomically rather remote from the rest of the Dialiinae and their position needs further evaluation. The subgenus Uittienia (previously reduced to Dialium) does not belong to Dialium, thus it has to be reinstated as a distinct monotypic genus belonging to the Dialiinae.

The present knowledge in Dialium may be aptly classified as within the consolidation phase (Davis and Heywood, 1973: p. 3). With the more or less stable nomenclature of the genus as a result of this study, it is suggested if possible to go to the next phase, i.e. the biosystematic phase. The following studies should be able to provide further information on Dialium although I believe that future results of these studies would not necessarily change the taxonomy of the genus as it is herewith presented.

1. Cytological studies. To date, only four species have chromosome counts and all come from African species. The rest of the species must also be studied especially Madagascan and Indo-Malesian ones.

2. Breeding systems. The breeding systems of Dialium are not known. First hand information on pollinators and pollination are similarly not known.

3. Phytochemical studies. So far, only fruit and seed of one or two species had been studied for chemical constituents or chemical reaction. Other parts of the plant should also be examined.

4. Ecological studies. Interaction of Dialium to type of soil, local climatic condition, competition, defence mechanisms, etc., has to be investigated.

PART IV. TAXONOMY

7. TAXONOMIC TREATMENT

7.1. Notes on the Presentation

This study is presented as a taxonomic revision. It is based on as many specimens (c. 1,965 numbers, excluding duplicates) as possible of the species published under Dialium of which there have been about ninety names. As far as they are extant, almost, if not all, the types were seen by me. These are indicated by the standard abbreviation (Holmgren and Keuken, 1974) of the herbaria where they are extant and an exclamation mark (!). Types of a number of African species described by Harms (1915) and recognised by Steyaert (1952) but which are now placed under doubtful species, have not been seen. This is because their holotypes had been destroyed in Berlin (B) and there are no isotypes extant in major herbaria of W Europe. Interestingly enough, no African specimens in European herbaria happened to be identified under them (see doubtful species) and I believe they could possibly belong to some species presently recognised to which Harms himself indicated they are close.

The descriptions are long but they are drawn as such while they are still in manuscript form. For purposes of publication they can be condensed, i.e. if the publishing journal wishes them to be shortened.

The literature references are a selection of what seem to be important for the knowledge of a particular species in a particular region or country. The standard abbreviations adopted largely follow the style of the Flora Malesiana. Abbreviations of authors follow those listed in "Draft Index of Author Abbreviations" (Meikle, Halliday, Story and Wilkinson, 1980), published by the Royal Botanic Gardens, Kew. Authors not found in the said index are spelt in full.

Under the nomenclature for each species, the names that were based on one type specimen have been listed in the same paragraph, and all in chronological order. A number of lectotypes are selected by me, especially if the original authors failed to designate a particular specimen as the type among the cited syntypes. Some names (series and subseries) now under synonymy are not individually provided with lectotypes. Any other lectotypes are so indicated as not my own selection. Synonyms indicated as syn. nov. are new reductions by me. Other synonyms are those already listed in the Index Kewensis as long as consistent with my findings or in other publication to which I fully agree with. All the names I could find are listed in the Index of Names found in the Appendix.

The distribution of species is documented with citation of specimens which are deemed important to the knowledge of the area. If the specimens from a country or island are more than three, only the number of specimens are indicated, otherwise the collectors and their numbers are cited in full.

The ecological data are extracted from literature and from the field notes in so far as they are consistent.

Remarks should be taken as an important part of the taxonomy of the species. These are sometimes lengthy, i.e. obviously to point out the closeness of one species to another as well as to indicate their variability. It is also in the Remarks that questions of typification are discussed, if any.

7.2. Enumeration and Description of Taxa

The taxa in Dialium as presently recognised are enumerated and described below.

DIALIUM

L., Mant. Pl. 1 (1767) 3; DC., Prod. 2 (1825) 520; Benth. & Hook., Gen. Pl. 1 (1865) 574; Oliver, Fl. Trop. Afr. 2 (1871) 282; Baker, Fl. Br. Ind. 2 (1878) 269; Taubert in Engl. & Prantl, Pfl. Fam. iii 3 (1892) 155; Gagnepain, Fl. Gen. I.-C. 2 (1913) 204; Harms in Engl., Pfl. Welt. Afr. 3, 1 (1915) 489; Baker f., Leg. Trop. Afr. (1930) 643; Ridley, Fl. Mal. Pen. 1 (1922) 621; Corner, Wayside Trees (1940) 393; Pellegrin, Légum. Gabon (1949) 122; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 29; Reinwardtia 2 (1953) 351; Keay in Hutch. & Dalziel, Fl. W. Trop. Afr. 1, 2 (1958) 448; Backer & Bakh. f., Fl. Java 1 (1963) 535; Hutch., Gen. Fl. Pl. 1 (1964) 231; Gomes e Sousa, Dendr. Moçambique (1966) 258; Capuron, Mat. Fl. For. Madagascar Fiche 'Zana' (1966) 1; Adansonia sér. 2, 8 (1968) 211; Brenan in Fl. Trop. E. Afr., Caesalp (1967) 103; Penn. & Sarukhan, Arb. Trop. Mexico (1968) 196; Aubrév., Fl. Cameroun 9 (1970) 33; Palmer & Pitman, Trees S. Afr. 1 (1972) 875; Whitm., Tree Fl. Mal. 1 (1972) 255; Larsen & Vidal, Fl. Camb., Laos & Vietn. 18 (1980) 109; H. Irwin & Barneby in Polh. & Raven, Adv. Leg. Syst. 2, part 1 (1981) 101. - Type species: Dialium indum L.

Arouna Aublet, Hist. Pl. Guian. Franc. 1 (1775) 16. - Type species:

Arouna guianensis Aublet = Dialium guianense (Aublet) Sandw.

Codarium Sol. ex Vahl, Enum. Pl. 1 (1804) 302. - Type species: Coda-

rium nitidum Sol. ex Vahl = Dialium guineense Willd.

Andradia T. Sim, For. Fl. Port. E. Afr. (1909) 46. - Type species:

Andradia arborea T. Sim = Dialium schlechteri Harms

Dansera Steenis, Bull. Jard. Bot. Buitenz. sér. 3, 17 (1949) 413. -

Type species: Dansera procera Steenis = Dialium procerum (Steenis) Stey.

Tree, small to large-sized, occasionally shrubby, evergreen or rarely bare for brief period, unarmed; bark surface generally smooth, inner bark when cut producing red sap. Indumentum simple, patent or adpressed, brown when dry. Twigs (on herbarium specimens) terete, lenticellate, glabrous in the older parts, generally hairy in the young parts; buds small, distinct, with roundish or pointed apex. Stipules small, linear-triangular, slightly falcate, very early caducous and usually absent in the herbarium; stipels wanting. Leaves unifoliolate or simply imparipinnate, alternate; petiole and rachis without conspicuous glands; leaflets generally alternate or sometimes partly subopposite or opposite; blades entire, greyish to dark brown when dry. generally subcoriaceous, hairy above when very young, hairs beneath usually persistent. Inflorescences in many-branched panicles, terminal (usually with lower primary side-axes subtended by normal or reduced leaves) or sometimes axillary in the axils of fallen leaves and often in fascicles or rarely solitary, many-flowered; bracts not seen, bracteoles very early caducous and usually absent in herbarium materials, small, deeply concave; buds pedicellate, ⁺ ellipsoid-ovoid or trulloid, small, usually not more than 6 mm long and 4 mm wide. Flowers hermaphrodite, zygomorphic, with well-developed patent-hairy disc wider than the ovary (African and American species) or disc absent (Madagascar and Indo-Malesian species); sepals generally 5, or 3 (subgenus Dansera) or aberrantly 6; petals generally wanting, sometimes 1 or 3, rarely 5 (D. englerianum), not showy, clawed and rather thick at the base; stamens generally 2 or sometimes 5, 6 or 8-10 (D. schlechteri) with filaments straight or geniculate (subsection Indumentosa); anthers basifixed, sagittate and symmetrical or asymmetrical at the base, variously shaped at the apex, dehiscing by longitudinal slits, either basipetally or evenly, generally hairy along

the margins of the slits and on both sides of the connective; pistil generally eccentric or $\pm$ central (some species in subgenera Dansera and Dialium), ovary generally sessile or sometimes shortly stipitate, densely adpressed hairy, style $\pm$ as long as the ovary, glabrous, either slightly curved at the top or strongly recurved over the ovary (most African species), stigma punctiform to slightly swollen; ovules (1-) 2. Fruit pods indehiscent, $\pm$ ellipsoid or ovoid to subglobose or sometimes (slightly) compressed (some African species); exocarp crustaceous, mostly brittle or sometimes firm (some species in subgenus Dansera), smooth except for the hairs; mesocarp pulpy, mealy, sometimes brownish to reddish when dry, entirely embedding the seed(s). Seeds generally 1, sometimes 2, usually reniform; testa smooth except for irregular cracks seen only microscopically, usually dark brown when dry; areoles absent; endosperm present.

Distribution. Pantropical, except absent from Malesia E of Borneo and Java and from Australia and the Pacific Islands. In tropical America, S of c. 18°N from Mexico (Isthmus of Tehuantepec) to Belize and southeastward (excluding the Caribbean Islands) down to the Amazonia at c. 12°S . In Africa, S of c. 13°N from southern Senegal, southeastward to NW Uganda at Bunyoro-Toro districts (c. equator and $29^{\circ} - 30^{\circ}\text{E}$), then slightly southwestward to Zaire and then straight S along western side of Lake Kivu and Lake Tanganyika to N Zambia and to Wankie district (c. $27^{\circ}\text{E } 18^{\circ}\text{S}$) in Zimbabwe; the southern limit towards the W from Wankie district to Caprivi Strip, the Okavango and Grootfontein, N Namibia and to the coast of Angola at c. 18°S ; also E Africa, coastal region from Kenya at c. 2°S to Natal at c. 29°S . In W and E Madagascar but not as yet found below the line at c. 23°S . In Asia, India (Kerala) and Sri Lanka, then disjunctly in lower Burma, Thailand, S Laos, Cambodia and

S. Vietnam, and W Malesia. - Figs. 4.1 - 4.3.

Ecology. In primary forests or as relicts in old secondary forests at low and medium altitude up to 1,150 m. Of scattered occurrence in mostly tropical rain forests along river banks and hillsides, in low lying swampy areas, sometimes in heath and peat swamp forests, and also in savanna woodlands of which one species is sometimes bare of leaves during flowering. For further discussion on distribution and ecology, see Part II, Chapter 4.

Remarks. As previously discussed, the genus can be subdivided into three subgenera which are distinct, both systematically and geographically. The outline of the proposed subdivision of the genus is shown in Table 5.1 and illustrated in Fig. 5.1. In the taxonomic part, the species are enumerated under each subgenus, section and/or subsection.

The genera Cleyria Necker, Elem. 2 (1790) 183 and Aruna Sprenger in L., Am. Acad. Gen. 1 (1789) 26 have been reduced to synonymy by Hutchinson (loc. cit.). Both genera cited Arouna Aublet as basis for their circumscription. I follow Hutchinson's authority.

KEY TO THE SPECIES

(Based mainly on the characters of the flower and arranged according to their supposed relationship; See Table 7.1)

1. Receptacle with a disc much wider than the ovary (Africa-Neotropics)
..... I. Subgenus Arouna
2. Anthers with pointed apex on the adaxial side, usually humped on the abaxial side, and with basipetally dehiscent slits
..... A. Section Arouna

3. Filaments straight to slightly curved; fruits $\pm$ globose;
petals 0 or sometimes 1 a. Subsection Pirula
4. Stamens 4-10; petals 0-1
5. Stamens 6-10; petal 0; flower buds $\pm$ ellipsoid with
thick sepals; leaflets elliptic to lanceolate with
 $\pm$ distinct nerves 1. D. schlechteri
5. Stamens (4-) 5; petals 0-1; flower buds trulloid-
ovoid with thin sepals; leaflets widely ovate to
subcordate with prominent secondary nerves
..... 2. D. pobeguinii
4. Stamens 2; petals 0 or rarely 1
6. Flower buds to 2.5 mm long; anthers to 1 mm long with
margin outline near the base of the adaxial side not
exceeding that of the abaxial side ... 3. D. bipindense
6. Flower buds 3-3.5 mm long; anthers 1-1.5 mm long with
margin outline near the base of the adaxial side
usually exceeding that of the abaxial side
7. Anthers usually not exceeding 1 mm long; petal 0
(- aberrantly 1) 4. D. guianense
7. Anthers usually exceeding 1.5 mm long; petal 0
8. Leaflets usually more than 7 pairs; blades
throughout the length of the rachis usually
narrowly oblong 5. D. dinklagei

8. Leaflets usually less than 7 pairs; blades at middle part of rachis $\pm$ elliptic-ovate to lanceolate
9. Blades at middle part of rachis elliptic-ovate, apex usually obtuse to roundish and tip often emarginate, base rounded to sometimes subcordate 6. D. orientale
9. Blades at middle part of rachis usually lanceolate, apex usually acuminate, base rounded to cuneate
10. Pedicels c. 0.8-1 (-rarely 3); leaflets 11-15 7. D. holtzii
10. Pedicels c. (1.5-) 3-5 mm long; leaflets 5-9
11. Leaflets small, not exceeding 5 cm long x 2 cm wide, greenish when dry 8. D. reygaertii
11. Leaflets larger, to 10 cm long x 3 cm wide, greyish to dark brown when dry 9. D. excelsum
3. Filaments geniculate, fruits $\pm$ compressed; petals 1
 b. Subsection Indumentosa
12. Anthers glabrous or sometimes hairy along slits, 1-1.5 mm long

13. Flower buds $\pm$ roundish-ovoid, brownish hairy;
 stamens 5 (- rarely 6); sepals thin
10. D. pentandrum
13. Flower buds $\pm$ ellipsoid to sometimes slightly
 trulloid, whitish hairy; stamens 2; sepals rather
 thick 11. D. polyanthum
12. Anthers distinctly hairy all over or glabrous, usually
 more than 2 mm long
14. Anthers glabrous; filaments also glabrous, gradually
 narrowed towards the top; receptacle rather thin ..
 12. D. tessmannii
14. Anthers hairy all over; filaments glabrous or sometimes
 hairy, swollen or flattish at the base and abruptly
 narrowed towards the top; receptacle rather thick
15. Leaflets 3, a few also 2 or 4; blade apex
 generally obtuse to acutish .. 13. D. angolense
15. Leaflets usually 5; blade apex generally long
 acuminate or sometimes acute .. 14. D. pachyphyllum
2. Anthers with retuse apex, $\pm$ flattish on both abaxial and adaxial
 sides, and with evenly dehiscing slits B. Section Codarium
16. Flower buds $\pm$ oblong-ellipsoid; stamens 5; petals 5 or sometimes
 less and often rudimentary 15. D. englerianum
16. Flower buds $\pm$ trulloid-ovoid; stamens 2; petals 1 or sometimes 0

17. Leaflets usually 2-3 pairs; blades oblong-elliptic,
apex obtuse to acutish, sometimes roundish or abruptly
acuminate; petal 1 16. D. guineense
17. Leaflets usually 4-5 pairs; blades variable in shape,
broadly elliptic, lanceolate, sometimes narrowly oblong
or ovate, apex usually long acuminate; petal 1 (-0) ...
..... 17. D. zenkeri
1. Receptacle without a disc, narrow or about as wide as the ovary
18. Sepals 5; petal 0; stamens 2 II. Subgenus Dialium
19. Ovary inserted on flattish patent-hairy receptacle
..... 18. D. hydnocarpoides
19. Ovary inserted on narrow or concave receptacle
20. Receptacle concave; anthers v-channeled on the abaxial
side of the connective; filaments flattish
..... 19. D. platysepalum
20. Receptacle narrow; anthers shallow or at least not
v-channeled on the abaxial side of the connective;
filaments $\pm$ subulate
21. Flower buds narrowly lanceoloid, usually 2.5 times
longer than broad 20. D. ovoideum
21. Flower buds ellipsoid-ovoid, usually 2 times longer
than broad

22. Flower buds usually to 4 mm long; leaflets
 † uniform in size, usually c. 4-6 cm long x
 2-3 cm wide, subcoriaceous to chartaceous;
 fruits usually 1.5 - 1.8 mm long
 21. D. cochinchinense
22. Flower buds usually more than 4 mm long;
 leaflets variable in size, usually c. 6-10
 (-15) cm long x 3-5 (-7.5) cm wide, and shape,
 stiff coriaceous to subcoriaceous; fruits
 usually 2-2.3 cm long 22. D. indum
18. Sepals 3; petals 3 or 0; stamens 2 or 6
 III. Subgenus Dansera
23. Petals 3, stamens 2; anther apex deeply cleft
 C. Section Hova
24. Anthers to 2 mm long, humped on the abaxial side;
 leaflets trifoliolate or unifoliolate
 23. D. occidentale
24. Anthers 2-4 mm long, † flattish on both the abaxial
 and adaxial sides
25. Leaves trifoliolate; flower buds 4-6 mm long;
 fruits to c. 2.5 cm long; pericarp rather thin
 and brittle 24. D. madagascariense
25. Leaves unifoliolate; flower buds 2.5-3.5 mm long;
 fruits 2.5-3.8 cm long, pericarp thick
 25. D. unifoliolatum

23. Stamens 6; petal 0; anther apex not cleft

..... D. Section Dansera

26. Leaflets (1-) 3-5 (-7); fruits to 4 cm long, apex rounded, obtuse or sometimes acutish, base rounded to sometimes cuneate 26. D. kunstleri

26. Leaves unifoliolate; fruits (4-) 4.5-5.5 cm long, apex beaked or $\pm$ acuminate, base usually acute to cuneate 27. D. procerum

I. Subgen. AROUNA (Aublet) Stey.

Subgen. Arouna (Aublet) Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 36; Reinwardtia 2 (1953) 355; Irwin & Barneby in Polh. & Raven, Adv. Leg. Syst. 2, part 1 (1981) 101. - Arouna Aublet - Cleyria Necker - Codarium Soland. ex Vahl - Andradia Sim. - For other full references see under the genus. - Type species: Arouna guianensis Aublet = Dialium guianense (Aublet) Sandw.

Receptacle with well-developed disc much wider than the ovary. Flower buds trulloid-ovoid (except D. englerianum, D. pentandrum and D. schlechteri). Sculpturing of the exine finely striate (section Arouna) or finely (and striato-) reticulate (section Codarium). Secondary xylem axial parenchyma cells predominantly containing silica inclusions and often together with few oxalate crystals in short chambered strands.

Distribution. Tropical America from Mexico (Isthmus of Tehuantepec to the Amazonia and tropical Africa, but extending to Natal at c. 29°S (see Fig. 4.2).

Table 7.1. Inter-relationships of Dialium species.

RECEPTACLE	WITH DISC ⁺			WITHOUT DISC ^o		
SEPAL	5			5	3	
PETAL	0	1	5	0	0	3
STAMENS 2	bipindense dinklagei excelsum guianense holtzii orientale reyaertii	angolense kasaïense <u>guineense</u> pachyphyllum polyanthum tessmannii <u>zenkeri</u> *		cochinchinense hydnocarpoides indum bursa platysepalum ovoidum		madagascariense occidentale septentrionale unifolium
STAMENS 5		pentandrum pobeguini*	<u>englerianum</u>			
STAMENS 6					kunstleri trifoliolatum procerum	
STAMENS 8-10	schlechteri					

+ - pollen finely striate (except underlined species which is reticulate)

o - pollen reticulate

* - petals sometimes absent

Ecology. See genus.

Remarks. Subgenus Arouna can be divided into two sections based on the characters of the anthers and the sculpturing of the exine. The sections are not distinctly geographically separated.

A. Sect. ARCUNA (Aublet) Taubert, ampl. Rojo

Sect. Arouna (Aublet) Taubert in Engl. & Prantl, Pfl. Fam. iii 3 (1892) 155, pro parte, excl. Indo-Malesian species. - sect. Recta Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 36, pro parte, excl. subsect. Discoidea Stey. and D. densiflorum Harms.

Sect. Neodialium Harms in Engl., Pfl. Welt. Afr. 3 (1915) 491. -
Lectotype species: Dialium schlechteri Harms.

Sect. Geniculata Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41. -
Type species: Dialium angolense Welw. ex Oliver.

Anthers with pointed apex on the adaxial side, usually humped on the abaxial side and with basipetally dehiscent slits. Sculpturing of the exine finely striate. Filaments more or less straight or geniculate. Fruits (sub)globose to compressed.

Lectotype species: Dialium guianense (Aublet) Sandw.

Distribution. The same as the subgenus. In the New World (Mexico in the Tehuantepec gulf region, Belize, Guatemala, Nicaragua, Costa Rica, Panama, Venezuela, Guyana, Surinam, French Guiana, Brazilian Amazon, Bolivia, and Peruvian Amazon) and Africa (West of the Lake Districts) from S Senegal to NW Uganda in the north and from Angola through N Namibia, N Botswana to SW Zimbabwe in the south. Also in the coastal regions of Kenya, Tanzania, Mozambique and S Africa (Natal). See map of the subgenus (Fig. 4.2).

Ecology. See genus.

Remarks. All species under this section are characterised by anthers with pointed (acute) apex on the adaxial side as well as with basipetally dehiscent slits (see Figs. 2.15, A-D and 5.1).

Steyaert (1951) attributed this section to Bentham (1865) but actually under Bentham had it as a synonym / Dialium only. Taubert (1892) was the first to recognize Arouna Aublet as a section in which he included both the Indo-Malesian and the Neotropical species (known to him at that time) under it. In the present amplified form, I have excluded from the section all the Indo-Malesian species which now belong to subgenus Dialium. Sections Recta and Geniculata of Steyaert (1951) are found by me to be unnatural mainly because the species under them display different anther characters; furthermore, their pollen grains exhibit different sculpturing of the exine. For practical as well as for taxonomic reasons, the present amplified section can still be divided into subsections based on the shape of the filaments and fruits which more or less coincide with Steyaert's previous sections.

a. Subsect. PIRULA Stey.

Subsect. Pirula Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 36. - ser.

Ramosissima Stey., idem p. 36.

Ser. Anastomosantia Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 37. -

subser. Sessilia Stey. idem p. 37. - subser. Obliqua Stey., idem p. 37.

- subser. Stipitata Stey., idem p. 38. - Type species: Dialium dinklagei Harms.

Filaments straight to slightly recurved at the top. Fruits ellipsoid-al to (sub)globose. Petals 0 or 0-1.

Type species: Dialium guianense (Aublet) Sandw.

Distribution. As the section, see there.

Ecology. Refer under the genus and individual species.

Remarks. The argument as to the retention of this subsection under the newly amplified section is presented in Chapt. 5, sect. 5.3. This subsection is composed of all the species in Steyaert's (1951) section Recta but excluding the species in subsection Discoidea which now belong to the amplified section Codarium (see there). The species under this subsection are characterised by more or less straight filaments and (sub)globose fruits. This subsection is represented by D. guianense (see Fig. 7.1).

1. DIALIUM SCHLECHTERI HARMS, Engl. Bot. Jahrb. 26 (1899) 276; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 37; Gomes e Sousa, Dendr. Moçambique (1966) 258; Palmer & Pitman, Trees S. Afr. 2 (1972) 875; Palgrave, Trees S. Afr. (1977) 286. - Type: Schlechter 11603 (B holotype destroyed, iso at BM! BR! K! P!), from Africa, Moçambique, Lourenço Marquês (Maputo), fl. XII. 1897.

Andradia arborea Sim, For. Fl. Port. E. Afr. (1909) 46, fig. 30. - Type: Sim 6141 (non vidi), from Africa, Moçambique, fl., no precise locality and date stated.

Tree, deciduous, generally small-sized; bole attaining c. 30 cm in diameter at breast height or many-stemmed. Twigs brown to dark brown when dry, lenticellate, the young parts glabrescent. Leaves

with petiole and rachis c. (4-) 5-8 (-12) cm long, rather thin, late glabrescent; leaflets 9-13, petiolules generally 1.5 mm long; blade elliptic, sometimes oblong or ovate, c. 2-3 (-4) cm long x 0.8-1.5 (-2) cm wide, apex obtuse or sometimes acutish, base rounded to obtuse, often asymmetric, surfaces $\pm$ concolorous, above slightly shiny, beneath dull, subcoriaceous to chartaceous; nerves c. 3-6 pairs, $\pm$ distinct; reticulations indistinct. Panicles terminal, sometimes the lower primary side-axes subtended by normal or reduced leaves or sometimes in fascicles axillary to old or fallen leaves; rachis c. 8-12 (-17) cm long, brownish hairy; buds usually broadly ellipsoid, c. 3.5-4 mm long x 2.5-3 mm wide, pedicles short, c. 1.5-2 mm long. Flowers: sepals 5, elliptic-ovate, c. 3-3.5 mm long x 2.5-3 mm wide; petal 0; stamens 8-10, filaments rather thin, c. 0.8-1.5 mm long, glabrous; anthers slightly humped on the abaxial side, c. 1.5 mm long, glabrous; ovary c. 1.5-2 mm long, brownish hairy; style 2 mm long, slightly recurved at the top, stigma rather distinctly swollen. Fruits obovoid to subglobose, exocarp thin, brittle, glabrescent with age. Seeds reniform, c. 1-1.3 cm long x 0.5-0.8 cm wide, testa brown, shiny.

Distribution. SE Africa, restricted in the area from S of river Ave, Moçambique at c. 22°S down to Natal, South Africa at c. 29°S; mainly coastal. Reported to occur in Transvaal, (Gomes e Sousa, loc. cit.), probably near boundary with Moçambique, but I have not seen material from there. Distribution map see Palgrave (loc. cit.).

Collections seen. Moçambique: 16. South Africa, Natal: 15.

Ecology. Frequent in dense maritime dune forest. Observed to flower in Oct.-Dec., fruits in March, sometimes persisting till next flowering season. Trees are bare in winter and fruits are relished by big animals, e.g. elephants (Palmer & Pitman, loc. cit.).

Remarks. A very distinct species characterized by small leaflets with usually asymmetric base and indistinct reticulation. This also has the highest number of stamens, i.e. (8-) 10, among Dialium species.

2. DIALIUM POBEGUINII PELLEGRIN, Bull, Soc. Bot. France 88 (1941) 499; Aubrév., Fl. For. Soud.-guin. (1950) 217, pl. 46, fig. 7-8. - Type: Pobéguin 1629 (P holo!), from W Africa, Guinea, river Koumi, fl. VI. 1907.

Dialium ovatum Hutch. & Dalziel, Dalziel Usef. P. W. Trop. Afr. (1937) 190, nom. nud., description in English.

Tree, medium-sized up to c. 20 m high. Twigs generally chocolate brown when dry, the older parts greyish brown, lenticellate, glabrous, the young parts patent hairy, glabrescent; buds small, apex roundish to acutish, hairy. Leaves with petiole and rachis c. 3-5 cm long, patent hairy, glabrescent; leaflets 5, petiolules c. 2-3 mm long; blade widely ovate to sometimes subcordate, terminal leaflets usually elliptic, c. 3-5 (-6.6) cm long x (2.5-) 3-4 cm wide, apex usually acute or abruptly acuminate, base rounded to obtuse or cordate, surfaces † concolorous, dull on both sides, light to chocolate brown, above sparsely patent hairy, late glabrescent, beneath rather persistent; nerves distinct, beneath prominent, c. (3-) 4-5 (-6) pairs; reticulation faint on both surfaces. Panicles terminal; rachis c. (6-) 8-16 (-20) cm long; buds ovoid-trulloid, c. 3-3.5 mm long x 2.5 mm wide with acute apex, pedicels (1-) 2-3 (-4) mm long, patent hairy, persistent. Flowers: sepals 5, ovate, generally thin, c. 3 mm long x 2 mm wide, sparsely minutely hairy inside; petals 0-1, c. 1.5 mm long, clawed,

hairy on both surfaces especially on the margins; stamens (4-) 5, filaments c. 0.5-1 mm long, straight or slightly recurved at the top. Fruits generally globose, c. 1.5 cm long x 1.2 cm wide, sessile or stipitate to c. 1 mm long, sepal remains somewhat persistent, exocarp thin, brittle, finely hairy. Seeds small, orbicular, c. 5-6 mm in diameter, testa dark brown, dull to slightly shiny.

Distribution. W Africa, so far found only in Sierra Leone and Guinea.

Collections seen. Sierra Leone: Deighton 1752, 1823, 2849, all near Njala; Morton & Jarr 1571, Makeni. Guinea: Pobéguin 1629 (type); Chevalier 12383, Labé.

Ecology. A species growing along rivers, near the water. Rare, as judged from the collections so far seen. Flowers in June-July, fruits in March.

Remarks. A very distinct species characterized by generally ovate leaflets with distinct nerves and patent hairs. The flowers have 5 stamens and thin sepals. It could be confused with D. pentandrum by having the same number of stamens but there the flower buds are roundish-ovoid instead of ovoid-trulloid and the filaments are geniculate instead of straight. Moreover, the fruits of D. pentandrum are compressed instead of globose as here.

3. DIALIUM BIPINDENSE HARMS, Engl. Bot. Jahrb. 53 (1915) 470; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 38; Aubrév., Fl. Gabon 15 (1968) 40; Fl. Cameroun 9 (1970) 39. - Type: Zenker 2695 (B holo destroyed, iso at BM! P!), from W Africa, Cameroon, Bipindi, Mafia, fl. VI. 1903.

Dialium connaroides Harms ex De Wild., Bull. Jard. Bot. État Brux. 7 (1920) 263, nom. nud., enumerated only; Baker f., Leg. Trop. Afr. (1932) 649, in key, description in English. No type indicated.

Dialium fleuryi Pellegrin, Légum. Gabon (1948) 125, nom. nud., name only.

Dialium eurysepalum Harms, Engl. Bot. Jahrb. 53 (1915) 472; Aubrév., Fl. Gabon 15 (1968) 40.- Type: Klaine 754 (B holo destroyed, iso at K! P!), from W Africa, Gabon, fl. XI. 1897. syn. nov.

Tree, small to medium-sized up to c. 35 m high. Twigs greyish brown to dark brown when dry, lenticellate, sparsely hairy, glabrescent, the young parts hairy; buds small, roundish to pointed, glabrescent. Leaves with petiole and rachis c. (3-) 5-8 (-10) cm long, late glabrescent; leaflets (5-) 7-9, petiolules c. 2-3 mm long, glabrescent; blade elliptic to oblongish, c. (3-) 5-7 (-8.5) cm long x (1.5-) 2-3 (-3.5) cm wide, apex usually long acuminate, base acute to cuneate, sometimes rounded especially at lower leaflets, surfaces discoloured, above greyish brown to blackish, glabrous, beneath chocolate brown, dull, hairy, generally charataceous to sometimes subcoriaceous; nerves [†] faint on both surfaces, c. 5-7 pairs; reticulation indistinct on both surfaces. Panicles terminal; rachis (7-) 10-15 (-18) cm long, sometimes laxly branched; buds slightly trulloid to ovoid, c. 2-2.5 mm long x 1.5-2 mm wide, pedicels c. 1.5-2 (-2.5) mm long. Flowers: sepals 5, ovate, c. 2.3 mm long x 1.5-2 mm wide, rather thin, minutely hairy inside; petal 0; stamens 2, filaments c. 1.5 mm long, slightly recurved at the top, glabrous; anthers rather small, c. 1 mm long, the margin outline near the base of the adaxial thecae not exceeding the abaxial one, hairy along slits; ovary c. 1 mm long, light brownish hairy; style c. 2 mm long, sharply recurved down the disc, glabrous at upper

half. Fruits ± globose, c. 14-16 mm long x 10-14 mm wide, exocarp brittle, brown hairy, glabrescent with age. Seeds orbicular, c. 8 mm long x 6 mm wide, testa dark brown, rather shiny.

Distribution. A species presently confined only to Cameroun and Gabon. It could most likely be found in W and SW part of Zaire.

Collections seen. Cameroon: 14. Gabon 9.

Ecology. Found along river banks, also on dry land at low altitudes. Flowers in June-Jan., fruits ripe after 6 months.

Remarks. The fruits can be confused with D. dinklagei and D. pobeguinii. Most of the specimens seen (excepting the type of D. eurysepalum) have small flowers. The anther is the smallest in the genus. Another distinguishing character is the more or less flattish abaxial side of the anther. Its close relatives (i.e. the above mentioned species) have anthers which are more or less humped on the abaxial side.

I reduce D. eurysepalum to synonymy because it differs from this species solely in its slightly larger flowers.

4. DIALIUM GUIANENSE (AUBLET) SANDW., Lloydia 2 (1939) 184; Ducke, Bol. Tech. Inst. Agron. Norte 18 (1949) 112; Woodson & Schery, Ann. Miss. Bot. Gard. 38 (1951) 38; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 37; Lemeé, Fl. Guyane Fr. 2 (1952) 87; Penn. & Sarukhan, Arb. Trop. Mexico (1968) 196; Schnee, Pl. Com. Venezuela (1973) 199. - Arouna guianensis Aublet, Hist. Pl. Guian. 1 (1775) 16, pl. 5. - Dialium guianense (Aublet) Steudel, Nom. ed. 2, 1 (1840) 497; Britton & Killip, Ann. New York Acad. Sc. 35 (1936) 169. - Arouna (Aruma) divaricata Willd. Sp. Pl. 1 (1798) 156. - Dialium divaricatum (Willd.) Vahl, Enum. Pl.

1 (1801) 303. - Type: Aublet cites only 'habitat in sylvis desertis remotis, praecipuè propre fluvium Sinemari'.

- Fig. 7.1.

Tree, small to medium-sized up to c. 30 m high; bole with smooth bark and low buttresses, attaining c. 40 cm in diameter at breast height. Twigs dark greyish brown when dry, lenticellate, the young parts usually dark brown, glabrescent; buds small, apex acute, hairy. Leaves with petiole and rachis c. (2-) 3-6 (-10) cm long, late glabrescent; leaflets (3-) 5-7 (-9), petiolules c. (2-) 3 (-4) mm long; blade generally lanceolate or sometimes broadly elliptic, c. (2-) 3-6 (-9) cm long x (1-) 1.5-2.5 (-4) cm wide, apex usually long acuminate to sometimes cuspidate, base obtuse, rounded or sometimes cordate, generally concolorous, greyish brown with greenish tinge when dry, sometimes rusty brown beneath, subcoriaceous; nerves faint above, rather distinct beneath, c. (5-) 6-8 (-10) pairs; reticulation above indistinct. beneath faint to slightly distinct. Panicles terminal and usually the lower primary branches subtended by leaves; rachis c. 6-15 (-25) cm long, dark chocolate brown when dry; buds ovoid to sometimes $\pm$ trulloid, c. 3-3.5 mm long x 2-2.5 mm wide, pedicels generally 2 mm long. Flowers: sepals 5, ovate to sometimes triangular; petals 0 (- rarely 1 and often rudimentary); stamens 2, usually glabrous with filaments straight to slightly recurved at the top, dark brown when dry; anthers c. 0.8 (-1) mm long, more flattish than humped on the abaxial side, usually glabrous; ovary sessile, style c. 1 mm long, glabrous, sometimes strongly recurved down the disc. Fruits generally subglobose, c. 1-1.5 cm in diameter, the exocarp brittle, dark-brown hairy. Seeds reniform, c. 7 mm long, testa dark brown, shiny.

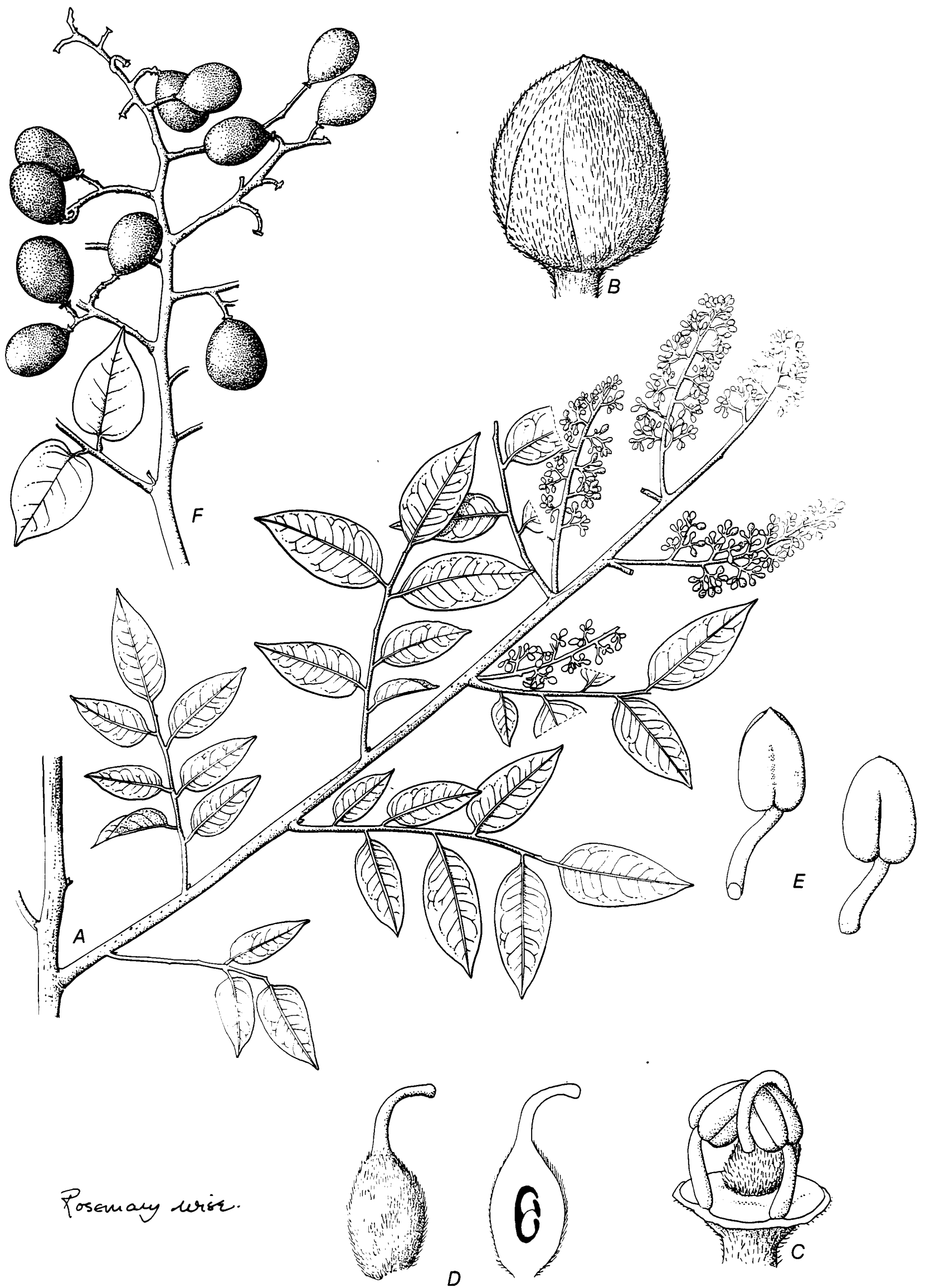


Fig. 7.1. Dialium guianense (Aublet) Sandw. A. habit, x 2/3 (Archer 3069, Belem, Brazil); B. flower bud, C. flower bud with sepals removed, D. ovary with lengthwise section, E. stamen in adaxial and abaxial sides (B-E all x 20, Irwin, et al. 55368, Lucie river, Surinam); F. fruits, x 2/3 (Steyermark and Gibson 95730, Bolivar, Venezuela).

Distribution. Central America (from Isthmus of Tehuantepec, Mexico) to the Brazilian Amazon. - Fig. 4.2.

Collections seen. Mexico: 8. Belize: 8. Guatemala: 4. Nicaragua: Englesing 276 (no precise locality). Panama: Pittier 5486, no precise locality. Colombia: Philipson, et al 1469, Rio Guejar. Venezuela: 4. Guyana: 5. Surinam: 5. French Guiana: 8. Brazil: 63. Bolivia (Amazon): Prance, et al. 5700, 6099, 8650, all S of Pando. Peru (Amazon): Ruiz 135, 213, Maynas prov.

Ecology: In rainforests, usually riverine but also terra firme, on sandy soil, from low altitude to c. 750 m elev. Flowers throughout the year with peaks in Sept.-Jan., fruits also throughout the year with peak in July.

Remarks. The drawing (Aublet, loc. cit., plate 5) is not accurate by modern standards. Except for the leaflets (actually leaves with stipules at each base), the plate definitely represents a Dialium. This is a very widespread species which displays more or less uniform floral and vegetative characters. Collectors noted some individuals to be shrubs, i.e. Archer 8069 or liana, i.e. Prance, et al, 10662, both collected in the Amazon. I doubt whether it really attains a liana habit.

5. DIALIUM DINKLAGEI HARMS, Eng. Bot. Jahrb. 26 (1899) 275; Baker f., Leg. Trop. Afr. (1930); Pellegrin, Légum. Gabon (1948) 126; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 37; Fl. Congo Belge 3 (1952) 544; Exell & Mendonça, Consp. Fl. Angol. 2 (1956) 187; Aubrév., Fl. For. C. d'Ivoire 1 (1959) 258; Fl. Gabon 15 (1968) 42; Fl. Cameroun 9 (1970) 40. - Type: Dinklage 1709 (B holo destroyed), from W Africa, Liberia, Grand Bassa, Fishtown, fl. VIII. 1896. - Fig. 2.7.

Dialium staudtii Harms, Eng. Bot. Jahrb. 26 (1899) 275; Baker f., J. Bot. 66 (1928) 138, suppl. Polyp. - Type: Staudt 492 (B holo destroyed, iso at K!), from W Africa, Cameroon, 'Johann Albrechtshöhe, Stationsberg,' fl. XII. 1895(6).

Dialium klainei Pierre ex Harms, Engl. Bot. Jahrb. 53 (1915) 472. - Type: Klaine 417 (B holo destroyed, iso at K! P!), from W Africa, Gabon, Libreville, fl. III, 1896.

Dialium klainei Pierre ex De Wild., Bull. Jard. Bot. Brux. 7 (1920) 263, nom. inval., a redescription based on the same type of Harms (loc. cit.). syn. nov.

Tree, medium-sized up to c. 25 m high; bole attaining c. 50 cm in diameter at breast height; bark smooth; buttresses slightly prominent. Twigs greyish brown to sometimes blackish when dry, lenticellate, glabrous, the young parts glabrescent; buds rather prominent, c. 3 mm in diameter, roundish to actuish, hairy. Leaves with petiole and rachis c. (5-) 6-12 (-14) cm long, patent hairy; leaflets (13-) 15-17 (-21), petiolules c. 1-2 mm long, patent hairy, glabrescent; blade generally narrowly oblong, c. 3-5 (-6) cm long x 1.5-2 (-2.5) cm wide, apex caudate-acuminate or sometimes abruptly acuminate or acute to obtuse in terminal leaflets, base rounded to broadly cuneate, usually cuneate in terminal leaflets, surfaces discolorous, above greyish brown to dark brown, $\pm$ shiny, beneath greyish brown with greenish tinge, dull, glabrescent, generally chartaceous, nerves $\pm$ distinct on both surfaces, c. (6-) 7-9 (-12) pairs, reticulations generally indistinct. Panicles terminal, sometimes the lower primary side-axis subtended by leaves; rachis c. (5-) 7-17 (-22) cm long, branches sometimes densely set; buds shortly trulloid-ovoid, c. 3 mm long x 2.5-3 mm

wide, pedicels short, c. 1-2 mm long. Flowers: sepals 5, angular to ovate, c. 2-2.5 mm long x 2 mm wide; petal 0; stamens 2, filaments c. 1.5 mm long rather thick, up to c. 0.5 mm wide, glabrous; anthers c. 1.5 mm long x 0.8-1.2 mm wide, slightly humped to $\pm$ flattish on the abaxial side, glabrous; ovary obliquely inserted, c. 1.5 mm long; style c. 2 mm long, strongly recurved over the side of the ovary; disc rather thick. Fruits subglobose to sometimes obovoid, c. (1-) 1.5-2 cm long x 1.8 cm wide, sessile to sometimes substipitate, up to c. 1 mm long, mucro sometimes persistent, exocarp thin and brittle, valvety but rather easily detached. Seeds $\pm$ orbicular, flattish, c. 5-8 mm in diameter, testa brown, shiny.

Distribution. W Africa. coastal countries from Sierra Leone at c. 10° N, down to Zaire (Mayumbe-Leopoldville region) at c. 6° S 16° C.

Collections seen. Sierra Leone: 7. Guinea: Chevalier 20709, Kissidougou: Jacque-Felix 1026, no exact locality. Liberia: 13. Ivory Coast: 11. Ghana: 12. S Nigeria: Espley 11, Afikpo; Kennedy 766 (no exact locality). Cameroon: 9. Gabon: 20. Angola (Cabinda): Gossweiler 6757, Maiombe, Buco Zau. Zaire (Mayumbe-Leopoldville region): 6.

Ecology. A widespread species sometimes found along rivers and lagoons but also scattered in other types of forests. The seeds are probably dehiscent by birds (Aubréville), from low to c. 500 m elev. Flowers in March-Oct. with peaks in June-Aug., fruits in Oct. - April.

Remarks. A very distinct species characterized by its numerous, i.e. 15-17 (-21) small and narrowly-oblong leaflets. In flower characters, this species is closely related to the transatlantic D. guianense.

I have not been able to see existing isotypes of Dinklage 1709.
 However, Dinklage 1743 & 1813 (both ^{of them} in flowers and collected in the same locality as the type) were noted in the collection labels (presumably by Dinklage himself) as similar (i.e. idem) to Dinklage 1709, the type.

6. DIALIUM ORIENTALE BAKER F., J. Bot. 67 (1929) 195; Leg. Trop. Afr. (1930) 648; Trees & Sh. Kenya (1936) 62; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 38; Dale & Greenway, Kenya Trees & Sh. (1961) 104; Brenan, Fl. Trop. E. Afr., Caesalp. (1967) 106. - Type: Webber 613 (K holo!, iso at EA), from E Africa, Kenya, Coast District, fl. undated.

Dialium reticulatum Burtt Davy & MacGregor, Kew Bull. (1932) 261. - Type: Elliot 1489 (K holo!, iso at EA), from E Africa, Kenya, Kilifi District, Mida, fl. IX.

A small tree up to c. 18 m high or sometimes attaining shrubby habit; bark smooth, greyish. Twigs greyish brown when dry, lenticellate, the young parts hairy; buds small, hairy, apex pointed. Leaves with petiole and rachis c. 2.5-4 (-5) cm long, late glabrescent; leaflets (5-) 7-9, petiolules c. (1-) 2 (-2.5) mm long, hairy, $\pm$ persistent; blade generally elliptic or sometimes the lower leaflets ovate, c. (2-) 3-4.5 (-5) cm long x (1.5) 2-2.5 (-3.5) cm wide, apex generally obtuse, sometimes acutish or rounded, often with slightly retuse tip, base rounded to obtuse, sometimes subcordate, surfaces concolorous to slightly lighter beneath, above glabrous, beneath glabrescent, subcoriaceous to chartaceous; midrib above often depressed; nerves on both surfaces distinct, c. 5-7 pairs; reticulation rather

indistinct on both surfaces. Panicles terminal, sometimes with lower side-axes subtended by leaves; rachis c. 6-12 (-14) cm long, rather whitish-hairy; buds trulloid to slightly ovoid, c. 3-3.5 mm long x 2 (-2.5) mm wide, pedicels c. 1.5-2.5 mm long, whitish-hairy as the buds. Flowers greenish white, white or creamy white in life; sepals 5, $\mp$ angular, c. 2-2.5 mm long x 0.5-2 mm wide; petal 0; stamens 2, filaments straight to slightly recurved at the top, short, up to 1.5 mm long, glabrous; anthers c. 1.5 mm long and 1 mm wide or less, humped but not strongly asymmetrical in shape, slits sometimes hairy on the margins; ovary c. 1.5 mm long; style c. 1 mm long, slightly recurved at the top. Fruits obovoid-ellipsoid to subglobose, c. 1.5-1.5 cm long x 1-1.3 cm wide, exocarp thin, brittle, finely hairy. Seeds $\mp$ ellipsoid to reniform, c. 7-9 mm long x 5-7 mm wide, testa dark brown, shiny.

Distribution. E Africa, Kenya, c. 2°S at Lamu district down to N of Tanzania at c. 5°S at Tanga district, occupying mainly the lowland coastal region.

Collections seen. Kenya 28. Tanzania: Semsei 2394, Tanga, Kisosora.

Ecology. Lowland dry evergreen forest, coastal evergreen bushland, grouped-tree grassland; near sea level to c. 60 m (Brenan, loc. cit.). Flowers in Aug.-Dec. and extending to Feb., fruits Jan.-March.

Remarks. This species is closely related to D. holtzii in neighbouring Tanzania. They differ in number, size and shape of the leaflets. In this species the leaflets are only up to 9, consistently smaller and ovate-elliptic, while in the latter, they are bigger and oblong-lanceolate and from 11-15 leaflets. Moreover, the anthers here are smaller and not strongly humped as well as less asymmetrical in shape.

7. DIALIUM HOLTZII HARMS, Engl. Bot. Jahrb. 49 (1913) 427; Baker f., Leg. Trop. Afr. (1930) 647; Stey., Bull. Soc. Roy. Bot. Belg 84 (1951) 37; Brenan, Fl. Trop. E. Afr., Caesalp. (1967) 104. - Lecto-type: Holtz 1182 (B lecto Brenan's choice, destroyed), from E Africa, Tanzania, Livule river near Mhondo (Morogoro district, Liwale river near Mhonda), fl. IV. 1904.

Dialium mossambicense Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 39. - Type: Gomes e Sousa 2302 (BR holo!, iso at MISS, K photo!), from E Africa, Moçambique, Niassa prov., forest of Mecrussine, fl. undated. syn. nov.

Tree up to c. 12-25 m high, bark smooth, grey or creamy grey brown. Twigs greyish brown to dark brown, lenticellate, the young parts hairy, glabrescent; buds small, apex acutish, hairy. Leaves with petiole and rachis c. (4-) 7-15 (-18) cm long, late glabrescent; leaflets (9-) 11-15, petiolules c. (1.5-) 2-3 (-4) mm long, hairy; blade oblong-lanceolate, the lower ones $\pm$ ovate, terminal ones $\pm$ elliptic, apex abruptly acuminate or sometimes subacuminate, base rounded to broadly cuneate, surfaces concolorous to slightly lighter-coloured beneath, subcoriaceous to chartaceous; nerves rather distinct on both surfaces, c. 5-9 pairs; reticulation indistinct to the unaided eye. Panicles terminal, sometimes the lower primary side-axes subtended by leaves; rachis up to c. 20 cm long, rather laxly branched; buds trulloid to slightly ovoid, c. 3-3.5 mm long x 2-2.5 mm wide, pedicels up to c. 1 mm long. Flowers: sepals 5, angular-ovate, c. 2.5-3 mm long x 2.5 mm wide; petal 0; stamens 2 with filaments c. 1-1.5 mm long, glabrous; anthers c. 1.5-2 mm long x 1-1.5 mm wide, sometimes hairy along slit margins or on the adaxial side of the connective;

ovary c. 1.5 mm long; style c. 1.5 mm long, strongly recurved down the disc. Fruits obovoid-ellipsoid to subglobose, c. 1.3-1.8 cm long x 1-1.3 cm wide, exocarp thin, easily crushed in the herbarium. Seeds orbicular, c. 7.5-8 mm long x 7 mm wide, testa brown, rather shiny.

Distribution. E Africa, Kenya (Kilifi district and Tanzania (S of Usambara mountain, Lushoto district at c. 4°40'S) to Moçambique (between Diaca and Moçimboa at c. 11°S).

Collections seen. Kenya: Ede 32, Irinuga; Faden 14/1267, Kilifi. Tanzania: 13. Moçambique: 7.

Ecology. Lowland dry evergreen forest, riverine and swamp forest, woodland; perhaps also lowland rain forest at c. 10-460 m elev. (Brenan). Mainly coastal.

Remarks. This species is very closely related to D. orientale in Kenya where both seem to merge in the Tanga-Lushoto districts in Tanzania. There is a wide gap of uncollected area between this species and D. schlechteri in Moçambique approximately between 11° and 22°S. For differences between this species and D. orientale, see remarks there. The flowers and fruits of this species and D. orientale are very much alike. However, this species is found to be medium to large-sized trees while D. orientale is a small tree to many-stemmed shrub (Brenan).

8. DIALIUM REYGAERTII DE WILD., Bull. Jard. Bot. État Brux. 7 (1920) 265; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 38; Fl. Congo Belge 3 (1952) 535. - Type: Reygaert 646 (BR holo!), from Africa, Zaire, Mandungu, fl., no month, 1918.

Tree up to c. 15 m high, bole $\pm$ straight, without buttresses, attaining c. 45 cm in diameter at breast height. Twigs somewhat thin and crooked, sparsely lenticellate. Leaves with petiole and rachis c. 1.5-3 cm long, sparsely hairy to glabrous; leaflets usually 5, petiolules c. 1.5-3 mm long, glabrous; blade elliptic, sometimes ovate-elliptic, small, c. 1-3 cm long x 0.5-1.5 cm wide, apex usually long acuminate, base broadly cuneate to sometimes obtuse to rounded, surfaces concolorous, grey with greenish tinge, generally chartaceous to sometimes subcoriaceous; nerves c. 4-6 pairs, distinct above, slightly distinct beneath; reticulation indistinct to the naked eye, irregularly set with transparent gland dots. Panicles terminal, sometimes the lower primary side-apex subtended by normal or reduced leaves; rachis c. 6-13 cm long, densely to laxly branched; buds ovoid-ellipsoid to slightly trulloid, pedicels c. 1.5-3 cm long, hairy as the buds. Flowers: sepals 5, $\pm$ lanceolate, c. 2-3 mm long x 1-1.5 mm wide; petal 0; stamens 2, filaments straight, c. 3 mm long; anthers sub lanceolate-elliptic, c. 1-1.5 mm long, apex on the adaxial side acute; ovary sessile; style slightly recurved at the top. Fruits usually globose or subglobose, c. 1.5 cm long x 1 cm wide, exocarp densely brown velvety. Seeds reniform, c. 7 mm long x 6 mm wide, testa brown and shiny.

Distribution. Zaire, Central forest, Mandungu and Yangambi.

Collections seen. 14.

Ecology. Forest formation along rivers; in primary liana forest, at times inundated or in marshy areas up to c. 470 m elev. Flowers in March-Aug., fruits in Nov.-Jan.

Remarks. This species is very closely related to D. excelsum. However, the leaflets are decidedly smaller and fewer, and greyish

with greenish tinge when dry. I refrained from combining this species with D. excelsum because there are only few collections for study. I think that, later, when more materials are available, this species could be merged with D. excelsum giving them infra-specific ranks. Guillardin 143, collected in Sanghaie, which I regard as belonging to this species, has bigger leaflets which more or less approach that of D. excelsum.

9. DIALIUM EXCELSUM LOUIS **ex** STEY., Bull. Soc. Roy. Bot. Belg. 84 (1951) 38; Fl. Congo Belge 3 (1952) 540, fig. 46 A,B; Brenan, Fl. Trop. E. Afr., Caesalp. (1967) 104. - Type: Louis 2881 (BR holo!, iso at B! BM! FHO! K! L!), from Africa, Zaire, Yangambi, fl. XI. 1936.

Tree, medium to large-sized up to c. 50 m high; bole attaining up to c. 30 m high and from 60-100 cm in diameter at breast height; buttresses narrow and up to c. 2 m from the ground. Twigs lenticellate, greyish to dark brown when dry; buds small with usually acute apex. Leaves with petiole and rachis c. (3-) 5-8 (-9) cm long, subglabrous to glabrous; leaflets 5-9 (-11), petiolules c. 1.5-3 mm long; blade lanceolate or ovate-elliptic, c. 2-7 (-10) cm long x 1.5-2.5 (-3) cm wide, apex acuminate, sometimes acute on the lower leaflets, base rounded to slightly cuneate, surfaces concolorous or slightly lighter-coloured beneath, generally subcoriaceous to chartaceous, glabrescent beneath; nerves indistinct above, $\pm$ distinct beneath, c. 5-8 pairs; reticulation fine and usually indistinct. Panicles terminal, usually with the lower primary side-axes subtended by normal or reduced leaves; rachis c. (6-) 12 (-20) cm long, laxly to sometimes

densely-branched, many-flowered; buds generally ovoid to narrowly trulloid, pedicels c. (1.5-) 3 (-5) mm long. Flowers: sepals 5, long triangular, minutely hairy inside; petal 0; stamens 2, filaments c. 1.5-2 mm long, usually straight; anthers c. 1.5-2 mm long. Apex on the adaxial side acute, slightly humped on the abaxial side, sparsely hairy along slit margins; ovary sessile, c. 1.5 mm long; style as long as the ovary and recurved at the top. Fruits $\pm$ subglobose, c. 1-1.5 cm long and about as wide, substipitate to c. 1-2 mm long. Seeds reniform, c. 7-8 mm long x 6-7.5 mm wide, testa dark brown, shiny.

Distribution. Zaire, SW Sudan (near Maridi), Uganda and doubtfully in Angola (Lunda).

Collections seen. Zaire: 57. Uganda: 4.

Ecology. Dominant in dense forest in dryland or along river banks, up to c. 470 m elev. Flowers in Aug.-Sept., fruits in Jan.-May.

Remarks. This species is closely related to D. reygaertii, and also to D. holtzii and D. orientale of Tanzania and Kenya, respectively. Their flowers and fruits are very closely similar. This species, however, is found in rain forests. Hoyle 452, collected in SW Sudan near Maridi belong to this species. Another collection with detached fruits, i.e. Gossweiler 13703, collected in Angola (Lunda, Dundo) is doubtfully referred here.

b. Subsect. INDUMENTOSA Stey.

Subsect. Indumentosa Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 42. - ser. Velutina Stey., idem p. 42. - ser. Hirsuta Stey., idem p. 43.

Subsect. Glabra Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41. - ser. Cylindrica Stey., idem p. 41. - ser. Triangularia Stey., idem p. 41. - Type species: Dialium polyanthum Harms.

Filaments geniculate. Fruits $\pm$ compressed. Petals 1.

Type species: Dialium angolense Welw. ex Oliver.

Distribution. As the section but excluding the Neotropics and E Africa (see Fig. 7.2).

Ecology. The species under this subsection are mostly rain forest species excepting D. angolense which occurs in savanna woodlands.

Remarks. The appropriate name for this subsection should have been 'Geniculata' because all species belonging to it have geniculate filaments. But since there are two existing subsections in Steyaert's (1951) section Geniculata (i.e. subsect. Glabra and subsect. Indumentosa), one of them must be chosen even if the name may not sound taxonomically appropriate for the species under it. Subsect. Glabra is as good as subsect. Indumentosa to represent this group but the latter is chosen because Steyaert indicated that it is the typical subsection in his section Geniculata.

10. DIALIUM PENTANDRUM LOUIS ex STEY., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41; Fl. Congo Belg. 3 (1952) 539, pl. 39. - Type: Louis 4017 (BR holo!, iso at B! FHO! K! L! P!), from Africa, Zaire, Yangambi, fl. V. 1937.

Tree, medium to large-sized to c. 40 m high; clear bole attaining from 10-20 m high and to c. 1 m in diameter at breast height;

crown dome-like, sometimes spreading. Twigs rather rusty brown, lenticellate, the young parts covered with rusty-brown hairs.

Leaves with petiole and rachis c. (2-) 3-6 (-8) cm long, rather thin, early glabrescent; leaflets (3-) 5, petiolules c. (4-) 6-7 mm long, glabrescent; blade elliptic to sometimes ovate-lanceolate, c. (3-) 4-7 (-11) cm long x (2-) 3-6 cm wide, apex acuminate, sometimes obtuse, base generally cuneate, sometimes roundish, surfaces rather concolorous, greyish-brown, above sometimes shiny, glabrous on both surfaces, generally subcoriaceous; nerves $\pm$ distinct on both surfaces, c. (6-) 8-10 (-12) pairs; reticulation rather distinct on both surfaces, areoles $\pm$ quadrangular. Panicles terminal or sometimes in fascicles axillary to fallen leaves or older nodes; rachis (5-) 10-20 cm long, the branches rather densely set, rusty brown; buds roundish-ovoid, c. 3 mm long x 2.5 mm wide, pedicels subsessile to c. 1.5 mm long. Flowers: sepals 5, roundish-ovate, c. 2.5-3 mm long x 2 mm wide, rusty brown-hairy outside; petals 1 (-rarely 2), tongue-shaped, unguiculate, yellowish in life; stamens 5 (-rarely 6), the filaments geniculate, green in life, gradually narrowed from the base to the top; anthers up to c. 1 mm long with acute apex on the adaxial side, humped on the abaxial side, the base rather slightly asymmetric, glabrous or sometimes sparsely hairy on the adaxial side of the connective; ovary generally sessile, dark brown hairy when dry; style short, sharply recurved over the ovary.

Fruits subrhombic, compressed, the margin rather sharp, obtuse at the base, obtuse or sometimes grooved at the apex, with persistent mucro, c. 2 cm long x 1.5-1.8 cm wide, exocarp generally with distinct veins, thin, brittle, sparsely hairy, glabrescent. Seeds $\pm$ reniform, flat-tish, testa dark brown, shiny.

Distribution. Zaire, central forest area, Yangambi.

Collections seen. 20

Ecology. Primary forest on firm ground, up to c. 470 m elev.

Flowers in May-Aug., ripe fruits observed in Sept.

Remarks. In terms of vegetative (especially leaflets) and fruit characters, this species is closely similar to D. polyanthum (see there), but stands out because of its small roundish-ovoid rusty-brown flowers and 5 stamens. It would be rather difficult to separate both species without available flowers to base identification on. As to its differences from D. pobeguinii (also with 5 stamens), see there.

11. DIALIUM POLYANTHUM HARMS, Eng. Bot. Jahrb. 53 (1915) 469; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41. - Type: Zenker 950 (B holo destroyed, iso at K! P!), from W Africa, Cameroon, Bipindi, fl. V. 1896.

Dialium corbisieri Staner, Rev. Zool. Bot. Afr. 22 (1932) 242; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41; Fl. Congo Belge 3 (1952) 538. - Lectotype: Corbisier-Baland 1078 (T holo*, iso* at BR! K! P!), from Africa, Zaire, Eala, fl. IV. 1931. syn. nov.

Dialium aubrevillei Pellegrin, Bull. Soc. Bot. France 80 (1933) 463; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 41; Aubrév., Fl. For. C. d'Ivoire, ed. 2, 1 (1959) 260. - Lectotype: Aubréville 191 (P holo!, iso at K!), from W Africa, Ivory Coast, Abidjan, fl. 1. 1930. syn. nov.

Tree, medium to large-sized up to c. 35 m high; bole attaining a meter or more in diameter at breast height. Twigs lenticellate, glabrous, the young parts glabrescent except upper part of the

* Holo and iso in this case mean the lectotype and duplicate (isolectotype), respectively.

inflorescences; buds small, roundish top, glabrescent. Leaves with petiole and rachis c. (3-) 4-7 (-10) cm long, glabrous; leaflets (3-) 5 (-7), petioles^{u/} c. (3-) 4-7 mm long, early glabrescent; blade elliptic to oblong-elliptic, sometimes lanceolate, c. (4-) 5-9 (-12) cm long x (2-) 3-4 (-5.5) cm wide, apex abruptly to long acuminate or sometimes almost caudate, base rounded to cuneate, surfaces slightly discolorous, glabrous, subcoriaceous to sometimes chartaceous; nerves distinct on both surfaces, c. (5-) 6-10 (-12) pairs; reticulation distinct on both surfaces, areoles rather $\pm$ quadrangular. Panicles terminal, sometimes with lower primary side-branches subtended by leaves or in fascicles axillary to fallen leaves or old nodes; rachis c. (6-) 10-12 (-35) cm long, branches rather laxly set, whitish-hairy; buds rather ellipsoid-ovoid or sometimes slightly trulloid, c. 3-4 mm long x 2-3 mm wide, pedicels c. 0.5-1 (-2) mm long, whitish to brownish hairy as the buds. Flowers: sepals 5, $\pm$ ovate, c. 2.5-4 mm long x (1.5-) 2-3 mm wide, rather thick at the base, minutely hairy inside; petals 1, rather thick, clawed, sparsely hairy at adaxial side; stamens 2, filaments geniculate, c. 1.5 mm long, glabrous; anthers rather short, c. 1.5 mm long and c. 1 mm wide, slightly asymmetrical at the base, glabrous except the sparsely hairy adaxial side of the connective; ovary c. 1.5-2 mm long, whitish to brownish hairy when dry; style c. 1-2 mm long, sparsely hairy towards the base, sharply recurved at the upper half. Fruits compressed, $\pm$ discoid, c. 1.5-2 cm in its narrowest diameter, the flat faces usually with distinct nerves, apex sometimes with persistent mucro, exocarp glabrous or very early glabrescent. Seeds orbicular, flattish, c. 10 mm long x 8 mm wide, testa brown, shiny.

Distribution. In its present circumscription, a widely distributed species extending from Sierra Leone at c. $10^{\circ}\text{N } 13^{\circ}\text{W}$ to Ghana, then farther eastward through SE Nigeria and Central African Republic (Oubangui area) down to its easternmost limit in Zaire at Mayumbe, c $5^{\circ}\text{S } 13^{\circ}\text{E}$ to Kasai region at c. $4^{\circ}30'\text{S } 21^{\circ}\text{E}$. Not as yet reported to occur in NW Angola. - Fig. 7.2.

Collections seen. Sierra Leone: 4. Liberia: 5. Ivory Coast: 7. Ghana: 5. SE Nigeria: FH 18791, Ogoja province. Cameroon: 12. Central African Republic (Oubangui region): Le Testu 52, 1856; Tisserant 52. Gabon: 5. Zaire: 76.

Ecology. A rain forest species, inundated to dry forests, along marshes and river banks, from low altitude to c. 500 m elev. Flowers in June-Jan., extending to April, fruits in Nov.-April.

Remarks. In his account of the forest flora of the Ivory Coast, Aubréville (loc. cit.) already noted that D. aubrevillei is very close to D. corbisieri. On the other hand, Steyaert (loc. cit.) maintained D. corbisieri as a separate species occurring only in Zaire. However, the isotypes of D. polyanthum available at K, L and P match very well with the types of the former two 'species'. Again in writing the flora of Cameroon, Aubréville (loc. cit.) went further by reducing this species to D. pachyphyllum (an entirely different species). The flowers of D. pachyphyllum, especially in some specimens with whitish hairy buds, could be confused with this species, but the flower buds here are smaller and roundish-ovoid, the anthers are also smaller and glabrous (except on the adaxial side of the connective), and the receptacle is narrower but thick.

12. DIALIUM TESSMANNII HARMS, Eng. Bot. Jahrb. 45 (1910) 303; Staner, Ann. Soc. Scient. Brux. 57, 3 (1937) 25; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 43; Fl. Congo Belge (1952) 534; Torre & Hillcoat, Consp. Fl. Angol. 2 (1956) 191; Aubrév., Fl. Gabon 15 (1968) 34, pl. III; Fl. Cameroun 9 (1970) 35, pl. 3. - Type: Tessmann 730 (3 holo destroyed, iso at K! P!), W Africa, Equatorial Guinea, "Bebao, Campogebeit" (Aubréville, loc. cit., attributed this to Campo, Cameroon), fl. XII. 1908.

Dialium mayumbense Baker f., J. Bot 66 (1928) 137, Suppl. 1; Leg. Trop. Afr. (1930) 647. - Type: Gossweiler 6089 (BM holo!, iso at K! BR photo!) from W Africa, Angola, Cabinda, Mayumbe, Pango Munga, fl. I. 1919.

Tree, medium-sized up to c. 20 m high with bole attaining c. 65 cm in diameter at breast height. Twigs with prominent lenticels, dark brown when dry, hirsute; buds very small, pointed, hairy. Leaves with petiole and rachis c. (2-) 3-7 (-9.5) cm long, hirsute; leaflets 5-7 (- rarely 9), petiolules c. 2-4 mm long, hirsute; blade elliptic-oblong, sometimes ovate-lanceolate or obovate, c. (3.5-) 5-8 (-9.5) cm long x (1.5-) 2-3 (-4) cm wide, apex usually long acuminate to sometimes abruptly acuminate, base cuneate to rounded or sometimes attenuate, surfaces $\pm$ concolorous, dark brown, above glabrous except the midrib, beneath slightly lighter-coloured, dull, hairy on the nerves, veins and veinlets, generally subcoriaceous; nerves $\pm$ distinct, c. 6-10 (-12) pairs; reticulation rather slightly prominent on both surfaces. Panicles terminal or in fascicles axillary to fallen leaves or old nodes; rachis c. (10-) 15-25 (-30) cm long, hirsute; buds distinctly trulloid, c. (4-) 5-5.5 (-6) mm

long x (2.5-) 3.5 (-4.5) mm wide, pedicels c. (2-) 3-4 (-5) mm long, hirsute. Flowers: sepals 5, triangular, c. 4.5-5.5 mm long x 3-4 mm wide, minutely hairy inside; petals 1, c. 2-4 mm long x 1-2.5 mm wide, shortly clawed, glabrous except sometimes along midvein; stamens 2, filaments sometimes not sharply geniculate at the mid point of its length, gradually thickened from the base towards the top, c. 3 mm long when stretched; anthers rather big, c. 2.3-2.8 mm long, humped on the abaxial side, glabrous except the sparsely hairy adaxial side of the connective; ovary c. 2-2.5 mm long, sometimes substipitate to 1 mm long, brownish hairy when dry; style c. 3 mm long, glabrous, sharply to slightly recurved at the top, sometimes with light-coloured glandular hairs at the base; receptacle rather thin, disc wide. Fruits somewhat ellipsoidal-compressed, the flat faces with distinct nerves, c. 2-2.5 cm long x 1.2-1.5 cm wide, mucro sometimes persistent, substipitate to c. 1 mm long, old sepals persistent, exocarp very finely short-hairy, glabrescent with age. Seeds slightly flattish, roundish, c. 6-9 mm long x 5-7 mm wide, testa chocolate to dark brown, $\pm$ shiny.

Distribution. W Africa, mainly coastal countries from S Cameroon at c. 3°N to Zaire at c. 6°S (but extending to the E region at c. 21°E, at Boende, once collected). - Fig. 7.2.

Collections seen. Cameroun (pro Aubréville): Tessmann 730 (type). Gabon: 6. Angola (Cabinda): Gossweiler 6089 (type). Zaire: 18 (mainly at Equator province).

Ecology. In swampy areas and remnants of forest on hillsides.

Remarks. A very distinct species characterized by hirsute twigs and big (i.e. c. 5-6 mm long x 3.5-4.5 mm wide) trulloid flowers.

13. DIALIUM ANGOLENSE WELW. ex OLIVER - Dialium angolense Welw. ex Oliver - Dialium kasaiense Louis ex Stey. - Dialium evrardii Stey. For full references, see under the varieties.

Tree, small to medium-sized up to c. 20 m high with wide-spreading branches. Twigs brownish hairy in the young parts. Leaves with petioles and rachis c. (1.5-) 2.5-3 (-3.5) cm long, hairy; leaflets trifoliolate, very rarely together with 2 or 4 in a twig, petiolules c. (1-) 2-3 mm long, patent-hairy, glabrescent; blade ovate, elliptic or elliptic-oblong, c. (2.5-) 3-8 (-11) cm long x (1.5-) 2-4 (-5) cm wide, apex obtuse, acute, or abruptly to long acuminate, base rounded, obtuse to cuneate, surfaces generally concolorous or slightly darker above, glabrescent beneath, subcoriaceous to chartaceous; nerves above faint, $\pm$ distinct beneath; reticulation fine, distinct, raised on both surfaces, areoles $\pm$ lax. Panicles terminal, sometimes with the lower primary side-branches subtended by leaves or in fascicles axillary to fallen leaves or older nodes; rachis c. (5-) 7-11 (-15) cm long; buds generally trulloid, c. 4-5 mm long x 3.5-4 mm wide with pedicels c. 1-2 mm long. Flowers: sepals 5, angular, whitish to light-brown hairy outside, minutely hairy inside; petals 1, white in life, blackish when dry, unguiculate, c. 2-2.5 mm long x 1-1.5 mm wide; stamens 2, filaments geniculate, flattish to sometimes swollen at the base, glabrous or rarely hairy; anthers usually humped on the abaxial side, incurved at the adaxial side, asymmetric at the base, hairy all over; ovary chocolate-brown hairy, blackish when dry; style sharply recurved at the top. Fruits compressed, $\pm$ discoid, sometimes shortly stipitate, c. 2 cm long x 1.5 cm wide, exocarp dark-brown velvety, remnant of sepals usually persistent. Seeds $\pm$ reniform, c. 1 cm long x 0.5-0.7 cm wide, testa shiny.

Distribution. Africa, mainly S of the equator, i.e. Angola and Zaire (Kasai-Katanga and NE) from c. 4° - 15° S; the eastern limit at c. 31° E in N Zambia, with a curious disjunction (4 collections) in Bangui-Libenge area bordering Central African Republic and Zaire at c. $4^{\circ}20'$ N and $18^{\circ}35'$ E. - Fig. 7.2.

Ecology. See under the varieties.

KEY TO THE VARIETIES

1. Flower buds 4-5 mm long by 3.5-4 mm wide; blades (sub)coriaceous, apex generally obtuse to acutish .. 13 a. D. angolense var. angolense
1. Flower buds 3.5 mm long by 2 mm wide; blades chartaceous, apex long acuminate 13 b. D. angolense var. kasaiense

13 a. DIALIUM ANGOLENSE WELW. ex OLIVER var. ANGOLENSE. - Dialium angolense Welw. ex Oliver, Fl. Trop. Afr. 2 (1871) 283; Baker f., Leg. Trop. Afr. (1930) 648; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 42; Fl. Congo Belge 3 (1952) 533; Torre & Hillcoat, Consp. Fl. Angol. 2 (1956) 188; F. White, For. Fl. N. Rhodesia (1962) 122.
- Type: Welwitsch 602 (BM holo!, iso at K! BR photo!), from Africa, Angola, Pungo Adongo, fl. III.

Dialium evrardii Stey., Bull. Jard. Bot. Brux. 30 (1960) 279.
- Type: Evrard 2575 (BR holo!, iso at K!), from Africa, Zaire, Ubanguï-Uele, y. fr. VII. 1957. syn. nov.

The blades are generally subcoriaceous and the apex obtuse to acutish. Flower buds 4-5 mm long by 3.5-4 mm wide.

Distribution. Angola, Zaire, Central African Republic (Bangui area) and Zambia.

Collections seen. Angola: 8. Zaire: 12. Central African Republic (Bangui area): Chevalier 10876, Bangui; Guisgouis 1860, 2287, Oubangui. Zambia: 19.

Ecology. In gallery forests (Steyaert), "muteshi" forest and thickets (White), usually near water (Fanshawe), on sandy or quartzitic soils, from low altitude to c. 1,140 m elev. Flowers in Aug.-May, fruits in March-Oct.

Remarks. I consider D. evrardii as a synonym of D. angolense for the following reasons:

1. Both Evrard 2575 (the type of D. evrardii) and Gossweiler 13895 (collected in NE Lunda, Angola, here identified as D. angolense) are identical by having bracteoles in the inflorescences and also with abnormally small flower parts which indicate that their flowers are still young.

2. I observed petals in Evrard 2575 (although Steyaert, loc. cit. said there were none) which correspond to D. angolense.

13 b. DIALIUM ANGOLENSE WELW. ex OLIVER var. KASAIENSE (LOUIS ex Stey.) ROJO, stat. & var. nov. - Dialium kasaiense Louis ex Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 43; Fl. Congo Belge 3 (1952) 533. - Type: Gillardin 383 (BR holo!, iso at K!), from Africa, Zaire, Port Francqui, fr. V.

Differs from the typical variety in its chartaceous and long acuminate leaflets and slightly smaller flower buds with thinner sepals. Measurement of flowers recorded for the first time follows:

Buds trulloid-ovoid, c. 3.5 mm long by 2 mm wide; sepals rather thin, finely hairy and sparsely intermixed with rather coarser hairs; petal 1, clawed, distinctly veined, c. 2.5 mm long by 1.5 mm wide, apex acute; stamens 2, filaments geniculate, swollen at the base, c. 1 mm long when stretched, glabrous; anthers hairy all over, c. 2 mm long.

Distribution. Africa, Zaire, Kasai. - Fig. 7.2.

Collection seen. 5.

Ecology. In gallery forest? Flowers Oct.-Dec., fruits in May.

Remarks. Flowers are similar to the typical variety but dimensions are apparently smaller. The leaflets (c. 4.5-10 mm long by 2-4 mm wide) which are also trifoliolate are chartaceous and long acuminate instead of (sub)coriaceous and acutish in the typical variety.

Steyaert (Fl. Congo Belge 3 (1952) 533) observed only the flowers at anthesis of Flamigni 7043 and Dechamps 93 but I have dissected a few unopened buds on the same specimens which form the basis of the above measurement. The rather lax reticulation of this variety approaches that of D. pachyphyllum but there, the blades are decidedly thicker and bigger, and moreover, the leaflets are usually 5-foliolate.

The more or less depauperate vegetative parts (slender twigs and small leaves), the trifoliolate leaflets, and the more southern distributional pattern make this variety more close to the typical variety than to D. pachyphyllum. However, more materials are needed to find out whether or not the present circumscription holds good. It could stand as a good species as first envisioned by the original author.

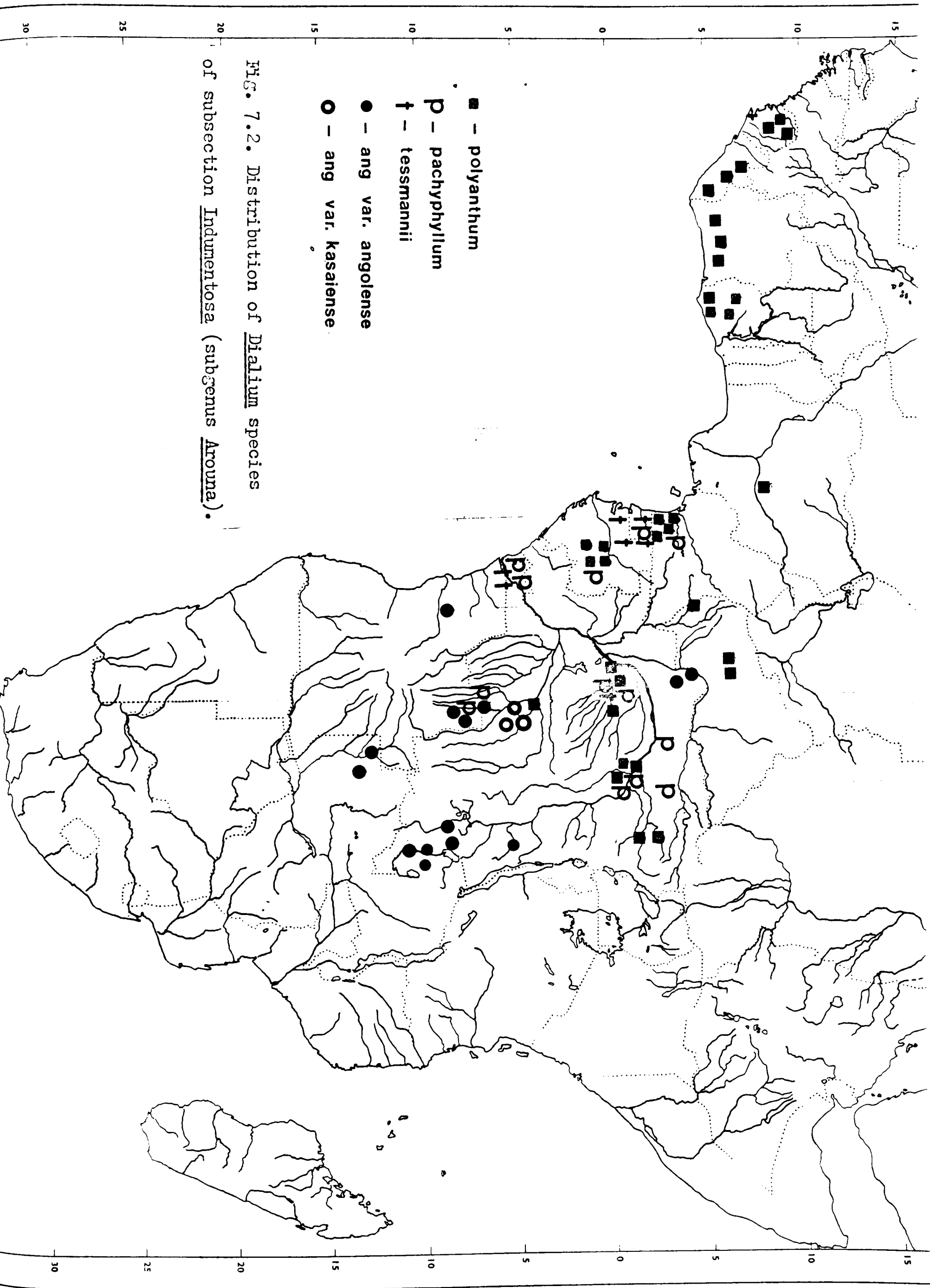


FIG. 7.2. Distribution of Dialium species
of subsection Indumentosa (subgenus Arouma).

14. DIALIUM PACHYPHYLLUM HARMS, Engl. Bot. Jahrb. 53 (1915) 468; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 42; Fl. Congo Belge 3 (1952) 539; Torre & Hillcoat, Consp. Fl. Angol. 2 (1956) 191; Aubrév., Fl. Gabon 15 (1968) 36; Fl. Cameroun 9 (1970) 36. - Lectotype: Zenker 2360 (B holo destroyed, iso at BM! BR! K! L! P!), from W Africa, Cameroon, Bipindi, fl. V. 1901.

Dialium macranthum A. Chev., Bois Gabon (1916) 175, tab. 17; Veg. Ut. Afr. Trop. Franc. 9 (1917) 176. - Type: Le Testu 1491 (P holo!, iso at BM! BR!), from W Africa, Gabon, Mayombe, Tchibanga, fl. XI.

Dialium yambataense Vermoesen, Man. Ess. For. Congo Belge (1923) 101, pl. p. 102. Lectotype: Vermoesen 2241 (BR holo!, iso at BM! K! P!), from Africa, Zaire, Eala, fl. IV. 1919.

Dialium gossweileri Baker f., J. Bot. 66 (1928) 137, Suppl. 1; Leg. Trop. Afr. (1930) 645; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951); Fl. Congo Belge 3 (1952) 537, fig. 46D; Torre & Hillcoat, Consp. Fl. Angol. 2 (1956) 188. - Lectotype: Gossweiler 6001b (BM holo!, iso at K! BR photo!), from W Africa, Angola, Mayumbe, Pango Munga, fl. XII. syn.nov.

Tree, small to medium-sized up to c. 30 m high with straight bole and regular rounded crown. Twigs lush, rather distinctly lenticellate, brown to blackish when dry, the young parts early glabrescent. Leaves with petiole and rachis c. (4-) 7-14 (-18) cm long, early glabrescent; leaflets (3-) 5 (-6), petiolule c. 4-7 (-10) mm long, slightly canaliculate, glabrescent; blade oblong-elliptic, sometimes obovate, c. (5-) 8-15 (-21) cm long x (3-) 4-6 (-9.5) cm wide, apex usually long acuminate, sometimes acute, base cuneate, obtuse or sometimes rounded, surfaces generally concolorous, above shiny, beneath rather dull, chocolate or dark brown, glabrous,

coriaceous to subcoriaceous; nerves prominent, c. (-7) 8-12 (-14) pairs with secondary ones in-between rather distinct; reticulation very distinct on both surfaces, areoles rather lax, $\pm$ quadrangular. Panicles terminal, sometimes with the lower primary side-axes subtended by leaves or sometimes axillary either few-fascicles, or rarely solitary; rachis c. (4-) 8-14 (-20) cm long; buds generally trulloid to sometimes ovate-lanceolate, c. 3-5 mm long x 2.5-3 (-4.5) mm wide, pedicels c. 2-4 mm long. Flowers yellow in life; sepals 5, triangular, minutely hairy inside; petals 1, c. 2.5-3 mm long x 1-1.5 mm wide, sparsely hairy along midvein on both sides, unguiculate; stamens 2 (- rarely 3) with filaments geniculate, glabrous to rarely hairy; anthers c. 1.5-2 mm long, the apical adaxial side acute, adaxial side incurved, the abaxial side humped, the base asymmetrical; ovary sessile to slightly substipitate; style recurved, glabrous on upper half. Fruits slightly compressed, discoid to sometimes slightly ovoid, c. 2.5 cm long x 1.5 cm wide, exocarp dark-brown velvety, substipitate, remnant of sepals rather persistent. Seeds reniform, c. 12-15 mm long x 6-8 mm wide, testa brown, shiny.

Distribution. SE Nigeria, Cameroon, Equatorial Guinea, Gabon, Angola, Central African Republic, Zaire, - Fig. 7.2.

Collections seen. SE Nigeria: Cathwall: 15. Cron river; Olorunfemi et al. 76399, SE Obura. Cameroon: 19. Equatorial Guinea: Tessmann 43, no precise locality. Gabon: 2. Angola (Cabinda & Dundo): 8. Central African Republic: 8. Zaire: 179.

Ecology. Mostly codominant in rain forests, in swampy areas or on firm ground, from low altitude to c. 700 m elev. Flowers in April-Dec. with peaks in May and Nov.-Dec.; fruits in Aug.-July.

Remarks. This species is very closely related to D. angolense. Both their flowers are similar and very difficult to distinguish

one from the other. They differ in their vegetative characters, i.e., lush in this species and rather depauperate in the other. The leaflets here are usually 5 while they are trifoliolate in the other.

The type of D. gossweileri (Gossweiler 6001b) has roundish-swollen and hairy filaments. Excepting the type and one or two specimens, the rest of the specimens attributed to it display glabrous filaments. I think that hairs on the filaments (the only character that separates this taxon from D. pachyphyllum) occur only aberrantly. I have, therefore, reduced D. gossweileri here.

This species has one of the biggest leaflets among African Dialium.

B. Sect. CODARIUM (Sol. ex Vahl) Benth., ampl. Rojo

Sect. Codarium (Sol. ex Vahl) Benth. in Benth. & Hook., Gen. Fl. 1 (1865) 574; Taubert in Engl. & Prantl, Pfl. Fam. iii 3 (1892) 155. - sect. Eudialium Harms in Engl. Pfl. Welt. Afr. 3, 1 (1915) 489. - sect. Recta subsect. Discoidea Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 39. - ser. Codaria (Sol. ex Vahl) Stey., idem p. 39.

Sect. Mesodialium Harms in Engl. Pfl. Welt. Afr. 3, 1 (1915) 490. - ser. Engleriana Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 40. - Lectotype species: Dialium englerianum Henriq.

Anthers with retuse apex, the abaxial side more or less flattish, and with evenly dehiscent slits. Sculpturing of the exine finely (and striato-) reticulate. Filaments more or less straight. Fruits ellipsoid-ovoid to sometimes more or less discoid.

Lectotype species: Dialium guineense Willd.

Distribution. As subsection Indumentosa (see there) but extending to the south and southeast from Grootfontein to the Okavango, across Caprivi Strip at c. 21°E and Zimbabwe (Wankie district) to SE Zambia in Mpangwe at c. 16°S, 32°E (see Fig. 7.3).

Ecology. Rain forest (D. guineense and D. zenkeri) and savanna (D. englerianum).

Remarks. All species in this section have anthers with retuse apex (see Fig. 2.15, E-F and Fig. 5.1) and with finely (and striato-) reticulate pollen. It is for this fact that this section is kept separate from section Arouna.

15. DIALIUM ENGLERIANUM HENRIQ., Bol. Soc. Brot. 16 (1899) 48; Baker f., Leg. Trop. Afr. (1930) 650; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 40; Fl. Congo Belge 3 (1952) 542; Torre & Hillcoat, Consp. Fl. Angol. 2 (1956) 187; F. White, For. Fl. N. Rhodesia (1962) 122. - Type: Sissenando Marquès 176 (Coi holo, non vidi, BR photo!), from W Africa, Angola, Ma-Chinge & Ma-Lunda terr., fl. undated.

Dialium simii Phillips, Kew Bull. (1922) 194; Baker f., J. Bot. 66 (1928) 138, suppl. 1 - Lectotype: Sim 19004 (K holo!) from Africa, Zimbabwe, Victoria Falls, near railway station, fl. VII. 1920.

Dialium lacourtianum De Wild, ex Vermeesen, Man. Ess. For. Congo Belge (1923) 98, in the key. Type: No specimen indicated.

Dialium quinquepetalum Pellegrin in Humbert Not. Syst. 14 (1950) 56. Type: No specimen indicated. "Moyen Congo: Service Forestier de Pointe-Noire (Lau)".

Tree, small to medium-sized up to c. 25 m high; bole usually short and irregular; crown rounded or spreading; bark smooth to sometimes furrowed and in young branches peeling off in thin flakes. Twigs greyish to dark brown when dry, lenticels - prominent, young parts brown hairy, glabrescent; buds small, apex rounded to sometimes pointed, glabrescent. Leaves with petiole and rachis c. (6-) 8-10 (-12) cm long, glabrescent; leaflets 5-9 (-11), petiolules

c. (1-) 1.5-2 (-3) mm long, glabrescent; blade ovate-lanceolate or narrowly elliptic, c. (3-) 3.5-6 (-8) cm long x (1.5-) 2-3 (-5) cm wide, apex acute to abruptly acuminate, base usually rounded to obtuse, surfaces discolorous, above greyish brown, $\pm$ shiny, beneath lighter brown, generally subcoriaceous; nerves $\pm$ distinct on both surfaces, c. (5-) 6-9 (-10) pairs; reticulation very fine but $\pm$ distinct beneath. Panicles terminal, usually with lower primary side-axes subtended by reduced leaves; rachis c. 10-25 (-35) cm long; buds broadly ellipsoid to oblongish, c. (4-) 5-6 mm long x 3-4 mm wide, pedicels c. (1.5-) 2-3 mm long. Flowers: sepals 5, elliptic, c. 4-5 mm long x 2.5-3.5 mm wide, minutely hairy inside; petals usually 5, small, c. 1.5 mm long x 0.5 mm wide, usually smaller than the filaments, clawed; stamens 5, filaments thick, c. 1-1.5 mm long, reddish to dark brown when dry; anthers somewhat lanceolate, apex retuse, c. 2.5 (-3) mm long, connective hairy on both abaxial and adaxial sides; ovary c. 2 mm long, dark brown hairy; style c. 2-2.5 mm long, slightly recurved at the top. Fruits ellipsoid to ovoid, sometimes slightly compressed, mucro sometimes persistent, exocarp thin, brittle, brown hairy. Seeds reniform to roundish, c. 1-1.2 mm long x 0.8-1 mm wide, testa chocolate brown, shiny.

Distribution. Africa, from Zaire at c. 3°S (from the W to Haut-Katanga at c. 29°E) in the north to Angola (at Benguela to Bie and Moxico), eastward down to Namibia (Grootfontein), Botswana (in the Okavango), Zimbabwe (Wankie district) and to Zambia at Mpangwe, c. 16°S, 32°E in the south. - Fig. 7.3.

Collections seen. Zaire: 59. Angola: 21. Zambia: 24. Namibia (Grootfontein-Omuramba-Caprivi Strip): 4. Botswana: 5. Zimbabwe: 8.

Ecology. Savannah woodlands on Kalahari sands associated with Baikiaea (White), Brachystegia, Julbernardia (Lawton), Burkea-Erythrophloeum (White) and Copaifera (Brenan), up to 1000 m elev. (Robyns). Flowers in March-July, fruits in June-Oct.

Remarks. A very distinct species characterized by its 5 petals and 5 stamens. The flowers are more or less ellipsoid and rather big for an African Dialium, i.e. 5-6 mm long x 4 mm wide.

16. DIALIUM GUINEENSE WILLD., Roemer Archief. 1, 1 (1796) 31, t. 6; Sp. Pl. 1 (1797) 49; Hook. f., Hook. Niger Fl. (1849) 329; Oliver, Fl. Trop. Afr. 2 (1871) 283; Hutch. & Dalziel, Fl. W. Trop. Afr. 1 (1928) 336; Usef. Pl. W. Trop. Afr. (1937) 190; Baker f., Leg. Trop. Afr. (1930) 646; Exell, Cat. Vasc. Pl. S. Tomé (1944) 167; Pellegrin, Legum. Gabon (1949) 124; Keay in Hutch. & Dalziel, Fl. W. Trop. Afr. 1, 2 (1958) 449; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 39; Aubrév., Fl. For. C. d'Ivoire 1 (1959) 260. - Type: Willdenow (loc. cit.) cites that this plant was discovered by 'Herr Kapitain Isert in Guinea.' (see remarks).

Codarium nitidum Sol. ex Vahl, Enum. Pl. 1 (1804) 302. -

Dialium nitidum (Sol. ex Vahl) Guillemin & Perrottet, Fl. Senegamb. 1 (1832) 267, t. 59. - Type: "Isert" & "Thonning" (non vidi), from Africa, Guinea.

Codarium acutifolium Afzel. in Schrader Neu. Journ. 2 (1807) 237; DC., Prod. 2 (1828) 520. Type in Herb. DC, not seen. Plant from Guinea.

Codarium obtusifolium Afzel. in Schrader Neu. Journ. 2 (1807) 238; DC., Prod. 2 (1828) 520. - Dialium guineense Willd. var. obtusifolium (Afzel.) Baker f., Leg. Trop. Afr. (1930) 646. Type probably in Herb. DC., not seen. Plant from Guinea.

Codarium discolor DC., Prod. 2 (1828) 520. - Dialium discolor (DC) Hook. f., Hook. Niger Fl. (1849) 329. - Type: "Smeathman".

In Herb. DC, not seen. A sheet labelled "Smeathman" is available at BM but is not marked as a type.

Tree, small to medium-sized up to c. 25 m high with usually spreading branches. Twigs lenticellate, dark brown when dry, the young parts glabrescent; buds usually with rounded apex. Leaves with petiole and rachis c. (3-) 4-8 (-11) cm long, leaflets (3-) 5-7 (-9), petiolules c. (2-) 3-4 (-5) mm long; blade generally oblong-elliptic, c. 6-9 (-13) cm long x (1.5-) 3-6 (-7) cm wide, apex rounded or obtuse or sometimes shortly acuminate or acute, base rounded to obtuse or sometimes broadly cuneate, surfaces discolorous, above darker brown, beneath lighter, glabrescent, generally coriaceous; nerves rather prominent beneath, c. (6-) 8-11 (-12) pairs; reticulation fine, generally indistinct to the unaided eye or sometimes distinct. Panicles terminal, sometimes with lower primary side-branches subtended by leaves; rachis † densely branched, c. (8-) 11-25 (-30) cm long, dark brown; buds generally ovoid to slightly trulloid, c. 3.5-4.5 mm long x 2.5 mm wide, pedicels c. (1-) 1.5 (-2) mm long. Flowers: sepals 5, triangular, finely hairy inside; petals 1, c. 2 x 0.5 mm, clawed, blackish when dry; stamens 2 (- rarely 3), filaments c. 1.4 mm long x 0.5 mm wide at the base; anthers c. 1.5 mm long x 1.2 (-1.5) mm wide, retuse at the apex, connective rather flattish on both abaxial and adaxial sides, hairy on both sides; ovary sessile to subsessile, rarely aberrantly double, dark-brown hairy when dry; style strongly recurved at the top. Fruits compressed, † discoid, c. 1.5-2 cm at its widest, sometimes substipitate to c. 1 mm long. Seeds reniform, c. 8-12 mm long x 7-9 mm wide, testa brown, shiny.

Distribution. W Africa from 14°N eastward down to N Cameroun (including St. Tomé and Príncipe islands). - Fig. 7.3.

Collections seen. Senegal-Gambia: 26. Guinea Bisau: 7. Guinea: 21. Sierra Leone: 32. Liberia: 4. Ivory Coast: 14. Ghana: 24. Togo: Milbraed 7473, 7494, Warnecke 211, all from Lomé, Dahomey: 4. Nigeria: 59. Cameroun: 6. St. Tomé: Espiriru Santo 207. San Vicente: Ribeiro s.n., no particular locality; Welwitsch 4127, no particular locality. Príncipe: Mann 1112, no particular locality.

Ecology. A species growing along big rivers where it is dominant; also in dense and semi-deciduous forest; in S Mali and upper Ivory Coast, it is found in gallery forest and savannah (Aubréville, loc. cit.), from low altitude to c. 1500 (Chapman 4288) m elev. Flowers in Aug.-Jan. with peaks in Oct.-Dec., fruits in Nov.-June with peaks in Jan.-April.

Remarks. The drawing (Willdenow, loc. cit. tab. 6) is more or less an accurate representation of the species except for the flower buds which should have been rather trulloid-ovoid instead of ellipsoid. This drawing was criticized by Guillemin & Perrottet (loc. cit.) as 'mala' and they then made another illustration (more accurately) of the species (tab. 59) in their work.

This species is very closely related to D. zenkeri and perhaps it is logical to merge the two under one species. But I maintain them as separate species because of the following differences:

	<u>D. guineense</u>	<u>D. zenkeri</u>
Flower bud	Ovoid to slightly trulloid	More sharply trulloid
Filaments	0.5 mm thick at base	Generally less
Pollen	Striato-reticulate	Finely reticulate
Leaflets	Generally 5-7	Generally 8-9

	<u>D. guineense</u>	<u>D. zenkeri</u>
Blade	Shortly oblong-elliptic	Generally lanceolate
Blade apex	Generally obtuse to acutish	Generally long acuminate
Distribution	N Cameroun westward to southern Senegal-Gambia	S Cameroun, Gabon and Zaire

17. DIALIUM ZENKERI HARMS, Engl. Bot. Jahrb. 30 (1901) 86; Pellegrin, Légum. Gabon (1948) 125; Stey., Bull. Soc. Roy. Bot. Belg. 84 (1951) 40; Fl. Congo Belge 3 (1952) 543, fig. 46 C; Aubrév., Fl. Cameroun 9 (1970) 42. - Type: Zenker 1913 (B holo destroyed, iso at BM! BR! K! L! P!), from W Africa, Cameroon, Bipindi, fr. XI. 1898.

Dialium laurentii De Wild., Miss. Laurent (1905) 100. - Type: Em. et M. Laurent s.n. (BR holo!), from Africa, Zaire, Lulonga, fl. I. 1904.

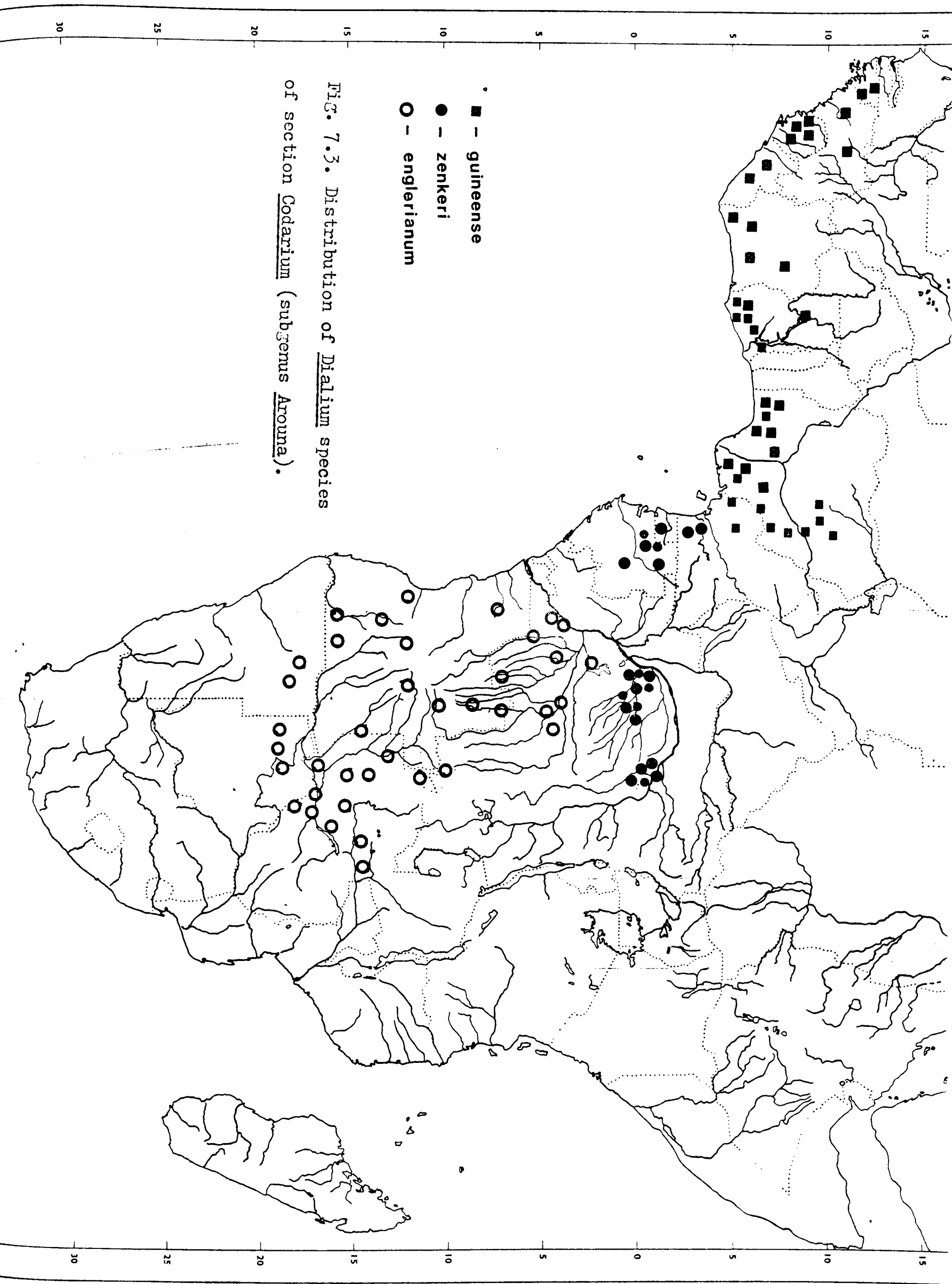
Dialium acuminatum De Wild., Ann. Mus. Congo Belge sér. 5, 2 (1907) 139. - Type: Laurent 797 (BR holo!), from Africa, Zaire, Eala, fl. VI. 1905.

Dialium densiflorum Harms, Engl. Bot. Jahrb. 53 (1915) 471; Pellegrin, Légum. Gabon (1948) 126; Aubrév., Fl. Gabon 15 (1968) 37; Fl. Cameroun 9 (1970) 38. - Type: Zenker 3770 (B holo destroyed, iso at BR! K! L!), from W Africa, Cameroon, Bipindi, fl. III (X in field label), 1908. syn. nov.

Dialium soyauxii Harms, Engl. Bot. Jahrb. 53 (1915) 471; Aubrév., Fl. Gabon 15 (1968) 38. - Type: Soyaux 303 (B holo destroyed, iso at K! P!), from W Africa, Gabon, Munda, fl. X. 1881. syn. nov.

Dialium pierrei De Wild., Bull. Jard. Bot. Etat Brux. 7 (1920) 264. - Type: Klaine 37 (BR holo!, iso at K! P!), from W Africa, Gabon, fl. XII. 1894.

Tree, medium to large-sized attaining c. 40 m high; bole usually cylindrical with up to c. 1 m in diameter at breast height; generally without buttresses; crown rounded. Twigs generally dark brown when dry, usually densely lenticellate. Leaves with petiole and rachis c. (6-) 10-16 (-24) cm long; leaflets (5-) 7-11 (-15), petiolule, c. (2-) 3-6 (-7) mm long; blade oblong-elliptic, sometimes ovate-lanceolate, c. (5-) 6-9 (-14) cm long x (2-) 3-4 (-6) cm wide, apex generally long acuminate, base rounded, obtuse to slightly cuneate, sometimes subcordate, surfaces concolorous to only slightly discolorous, beneath dull, sometimes rusty brown, glabrescent, generally subcoriaceous; nerves c. (6-) 8-12 (-15) pairs, beneath rather prominent; reticulation indistinct above, - distinct beneath. Panicles terminal, usually with lower primary side-branches subtended by leaves; rachis c. (5-) 10-16 (-20) cm long, sometimes rather laxly branched; buds generally trulloid, c. 2.5-4 (-4.5) mm long and about as wide, pedicels c. (1-) 2 (-3) mm long. Flowers: sepals 5, triangular, c. (2.5-) 3 (-4) mm long x 2-3 mm wide, finely hairy inside; petals 0-1 or very rarely 3, filaments c. 1-15. mm long and less than 0.5 mm thick at the base, usually straight; anthers c. 1-1.5 mm long, retuse at the apex, hairy especially on the adaxial side of the connective; ovary sessile or sometimes substipitate up to 1.5 mm long, dark-brown hairy; style usually strongly recurved at the top. Fruits compressed, ± discoid, sometimes obliquely stipitate, c. 2 cm long x 1.5 cm wide, exocarp dark-brown velvety. Seeds c. 7-10 mm long x 5-6 mm wide, testa brown, shiny.



Distribution. S Cameroun, Gabon, Zaire, Equatorial Guinea.

Collections seen. S Cameroun: 11. Gabon: 19. Equatorial Guinea: Tessmann 355, no particular locality. Central African Rep.: Tisserant 978, 2096, Oubangui. Zaire: 40. - Fig. 7.3.

Ecology. Riverine, periodically inundated forests, sometimes in firm ground, at low altitude to c. 470 m elev. Flowers in Feb.-June, lasting to Nov., fruits in March-Nov., lasting to June.

Remarks. This species is very closely related to D. guineense (see there) and the two species seem to merge in Cameroon (see Fig. 7.3.)

In its present circumscription, this species is rather polymorphic. At first it would appear that D. densiflorum and D. soyauxii are distinct from this species but they all represent variations within the species complex. It must be noted that there are no other collections that could **nearly** match the vegetative characters of the types of D. densiflorum and D. soyauxii. But the types have anthers with retuse apex and are **referable** to this species. Therefore, I reduce them to this species for the first time.

II. Subgen. DIALIUM

Dialium L. (See under the genus for full references). - Type species: Dialium indum L.

Receptacle with disc absent, narrow or as wide as the ovary. Sepals 5. Petal 0. Stamens 2. Sculpturing of the exine finely reticulate. Secondary xylem axial parenchyma cells exclusively containing oxalate crystals in long chambered strand. Leaves imparipinnate, usually more than 2 pairs.

Distribution. Indo-Malesia (see Fig. 4.3.)

Ecology. See genus and individual species.

Remarks. Subgenus Dialium has already been recognized as such by Stey. (loc. cit., 1951) and Irwin & Barneby (loc. cit.). The finely reticulate exine and oxalate crystal deposits in secondary xylem axial parenchyma cells of the member-species confirm the subgenus as a natural group. The subgenus is represented by D. indum (see Fig. 7.4)

18. DIALIUM HYDNOCARPOIDES DE WIT, Blumea 7 (1953) 320. - Type: 185T.3P.541 (L holo!, iso at BO!), from W Malesia, Sumatra, Palembang, prope Lematang Ilir, fl. I.

Dialium praetermissum de Wit, Blumea 7 (1953) 321. - Type: bb. 13951 (BO holo!, iso at L!), from W Malesia, Borneo, Kalimantan, SE Division, Tanjung, prope Pangelak, fl. undated. syn. nov.

Tree, medium to large-sized up to c. 30 m high; bole attaining c. 45 cm in diameter at breast height; buttresses relatively high, up to c. 5 m high from the ground. Twigs greyish brown to dark brown when dry, lenticellate, the young parts brownish hairy, glabrescent; buds small, apex pointed, hairy. Leaves with petiole and rachis c. (5-) 7-20 (-24) cm long, patent brownish hairy; leaflets (11-) 15-17 (-19), petiolules c. 2-4 mm long; blade elliptic-oblong on leaflets at middle parts of rachis, ovate on leaflets near the petiole, c. (2.5-) 3.5-6 (-8.5) cm long x (1.5-) 2-3 (-3.5) cm wide, apex rounded, obtuse or abruptly acuminate, base generally rounded, sometimes cuneate, surfaces $\pm$ concolorous but rather dull on both sides, beneath brownish hairy, glabrescent, generally subcoriaceous; nerves rather fine, $\pm$ distinct on both

surfaces, c. (5-) 6-9 pairs; reticulation on both surfaces indistinct to the unaided eye. Panicles terminal, usually with the lower primary side-branches subtended by reduced or normal leaves; rachis c. (6-) 9-15 (-20) cm long, densely brownish hairy; buds ovoid to lanceoloid, c. 4-5 mm long x 2.5-3 mm wide, pedicels c. 1-2 mm long. Flowers white in life; sepals 5, ovate-lanceolate, c. 3.5-4 mm long x 1.5-2.5 mm wide, minutely hairy inside; stamens 2 (- rarely 3), filaments c. 1-1.5 mm long, glabrous; anthers c. 2.5-3 mm long, rather flattish on both abaxial and adaxial sides, connective hairy on both sides; ovary inserted on a narrow, flattish and patent-hairy receptacle, c. 1.5-2 mm long; style c. 1-1.5 mm long, glabrous, slightly recurved at the top. Fruits subglobose, sometimes slightly compressed, c. 1.5-2 cm in diameter, exocarp brittle, densely brownish hairy, rather persistent. Seeds orbicular, c. 9 mm long x 8 mm wide, tests chocolate brown, shiny. part
○

Distribution. W Malesia, S Sumatra and Borneo (Kalimantan and Sabah).

Collections seen. S Sumatra: 185T.3P.541 (type); 185T.3P.540 (fl); T.540 (fr.), all from Palembang. Kalimantan: 7. Sabah: 5.

Ecology. In primary forest at low altitudes, 20-60 m elev. on yellow sandy loam soils (Kostermans). Rather rare and scattered. Flowers in Jan.-July, fruits in April-June.

Remarks. In terms of quality of indumentum, this species is close to some 'groups' of D. platysepalum. The flattish, narrow and patent-hairy receptacle more or less links this species with the African ones. At a glance, its flowers could indeed be mistaken for D. platysepalum, but dissections will show that aside from

the receptacle with narrow and flattish top, it has also anthers with flattish abaxial side (not v-channelled as in D. platysepalum). D. praetermissum clearly belongs to this species although its type has fewer leaflets.

The receptacle of D. turbinatum conforms to this species but is reduced to synonymy under D. indum (see there) because the vegetative parts of the former match that. Furthermore, there has not been any other collection that could closely match the type of D. turbinatum.

19. DIALIUM PLATYSEPALUM BAKER, Fl. Br. Ind. 2 (1878) 270; Prain, J. As. Soc. Beng. 66 (1897) 172; Ridley, Fl. Mal. Pen. 1 (1922) 623; Whitm., Tree Fl. Mal. 1 (1972) 261, fig. 7. - Lectotype: Griffith 1847 (K holo!), from W Malesia, Peninsular Malaysia, Malacca, fr. undated.

Dialium platysepalum Baker var. wallichii Baker, Fl. Br. Ind. 2 (1878) 270. - Dialium wallichii (Baker) Prain, J. As. Soc. Beng. 66 (1897) 174; Ridley, Fl. Mal. Pen. 1 (1922) 623; Whitm., Tree, Fl. Mal. 1 (1972) 261; Cockburn, Trees Sabah (1976) 169, fig. 35. - Lectotype: Wallich 8534 (excl. a connaraceous element on the same sheet) (K holo!), from W Malesia, Singapore, fl. X. 1822 syn. nov.

Dialium platysepalum Baker var. papan Prain, J. As. Soc. Beng. 66 (1897) 173. - Lectotype: Goodenough 1553 (SING holo!), from W Malesia, Peninsular Malaysia, Malacca, Ayer Panas, fr. X. 1893 syn. nov.

Dialium platysepalum Baker var. burong Prain, J. As. Soc. Beng. 66 (1897) 173. - Lectotype: Holmberg 855 (SING holo!), from W Malesia, Peninsular Malaysia, Malacca, Selandan, fr. VIII. 1891. syn. nov.

Dialium maingayi Baker, Fl. Br. Ind. 2 (1878) 269; Prain, J. As. Soc. Beng. 66 (1897) 171; Ridley, Fl. Mal. Pen. 1 (1922) 622; Burkill, Dict. Ec. Prod. Mal. Pen. 1 (1935) 800; Whitm., Tree Fl. Mal. 1 (1972) 260. - Lectotype: Maingay 1398 (excl. the specimen with fruits) (K holo!), from W Malesia, Singapore, fl. VII?.
1865-66. syn. nov.

Dialium ambiguum Prain, J. As. Soc. Beng. 66 (1897) 172; - Dialium platysepalum Baker var. ambiguum (Prain) Ridley, Fl. Mal. Pen. 1 (1922) 623. - Lectotype: Kunstler 6142 (K holo, iso at SING!), from W Malesia, Peninsular Malaysia, Perak, Goping, fl. V.

Dialium kingii Prain, J. As. Soc. Beng. 66 (1897) 175; Ridley, Fl. Mal. Pen. 1 (1922) 624; Whitm., Tree Fl. Mal. 1 (1972) 259. - Lectotype: Kunstler 8187 (K holo!), from W Malesia, Peninsular Malaysia, Perak, Goping, fl. IX. 1885. syn nov.

Dialium havilandii Ridley, Kew Bull. (1929) 255. - Type: Haviland 1700 (K holo!), from W Malesia, Sarawak, Kuching, fl. IX. 1892. syn. nov.

Dialium triste de Wit, Blumea & (1953) 321. - Type: Daud & Tachun SING Field No. 35743 (SING holo!), from W Malesia, Borneo, Sarawak, fr. VIII. syn. nov.

Tree, medium to large-sized up to c. 45 m high and attaining from 90-120 cm in diameter at breast height. Twigs greyish-brown to rusty-brown when dry, the young parts generally brownish hairy, lenticels sometimes light-coloured, distinct; buds small, roundish to acutish top, hairy. Leaves with petiole and rachis c. (10-) 15-24 (-28) cm long, hairy, sometimes late glabrescent; leaflets (5-) 7-11 (-15) pairs, petiolules c. 2-4.5 mm long; blades oblong-elliptic to oblong-lanceolate, (5-) 6-8 (-15) cm long x (1.5-) 2-4 (-7) cm wide, apex abruptly to long acuminate, the acumen sometimes up to c. 2 cm long, base rounded to cuneate, surfaces generally discolorous, above

dark brown, beneath chocolate brown to rusty brown, sometimes rather long persistent, generally coriaceous to sometimes subcoriaceous; nerves distinct on both surfaces, sometimes nerves beneath obscured by thick golden hairs, c. 10-12 (-15) pairs; reticulation sometimes distinct, veinlets usually squarish. Panicles terminal, usually with the lower primary side-branches subtended by leaves; rachis c. 10-15 (-30) cm long, usually rusty brown; buds generally ovoid, usually slightly incurved at the base, c. (5-) 5.5-7 (-7.5) mm long x 3.5-4.5 mm wide, pedicels c. (2-) 2.5-4 (-7) mm long. Flowers: sepals 5, $\pm$ triangular, up to 6 mm long x 4 mm wide, minutely hairy inside; petal 0; stamens 2; the filaments short and generally flat-tish, c. 1-2.5 mm long x 1-1.5 mm wide; anthers with both slits drawn towards the abaxial side forming a v-channel on the abaxial side of the connective, hairy except marginal area along slits, c. 3-4 (-5) mm long; ovary dark brown when dry, c. 2-3.5 mm long; style sharply recurved at the top, usually sparsely hairy on the lower half, glabrous towards the top, up to c. 3 mm long when stretched. Fruits subglobose to obovoid, sometimes rather slightly compressed, c. (1.5-) 2-2.5 (-3) cm long, sometimes with up to c. 2 mm stipe, pericarp firm and usually intact in the herbarium, exocarp densely brown velvety, persistent. Seeds 1 (-2), roundish to reniform, c. 9-13 mm long x 9 mm wide, testa light brown to blackish, shiny.

Distribution. W Malesia.

Collections seen. Peninsular Malaysia and Singapore: 180. Sumatra: 50. Borneo (Sarawak): 16. (Brunei): 4. (Sabah): 5. (Kalimantan): 35.

Ecology. Usually in low-lying areas and hills at very low and up to c. 500 m elev.; also freshwater swamp forests (Corner), usually on yellow clay-sandy soils. Flowers throughout the year with peaks in Dec.-March and May-Sept., fruits also throughout the year but quite heavy in July-Oct.

Remarks. This is distinct from the rest of Dialium species by the following characters:

1. Mature flower buds are c. 5.5-7 (-7.5) mm long, i.e. the longest in the genus.
2. The anthers are from 4-5 mm long, also the longest in the genus, and v-channelled on the abaxial side of the connective (see Fig. 2.16, C).
3. The base of the flower bud is usually incurved appearing distinctly zygomorphic.
4. The receptacle is deeply concave with the filaments and ovary inserted eccentrically on opposite sides.

Excepting the continuous variability in size of the flower buds, the characters of the flower are uniform. However, the size of the leaflets as well as the colour and the quality of indumentum on the undersurface of the blades (which have provided some taxonomic characters in the delimitation of previous 'species' now placed under synonymy) tends to segregate into more or less discrete 'groups' especially if the materials from the whole distributional range of the species are compared. These 'groups', here listed without nomenclatural status, are the following:

- a. 'maingayi' group - This has a rather whitish to slightly golden indumentum underneath; the nerves not very distinct.

b. 'platysepalum' group - Often tinged golden underneath and the most common among the groups. Not easily separable from 'maingay' group.

c. 'wallichii' group - Slightly golden or light yellow beneath but blades are smaller, not bigger than 7 cm x 2 cm (Whitmore, loc. cit.).

d. 'kingii' group - Golden to chocolate brown beneath; nerves prominent, blades slightly bigger than the 'wallichii' group.

e. 'triste' group - Dark chocolate brown beneath; nerves much more prominent and blades much bigger than 'kingii' group.

As can be seen from the informal 'groups' above, the differences are slight and form a gradient. There are other collections which do not necessarily fit within the above groups. It is for this reason that I refrained from giving them formal names. Local botanists and foresters who are familiar with the previously named 'species' in their respective flora could surely discriminate the various groups above in the herbarium. By tradition, they may even insist on giving these groups the same formal names they previously had. However, as soon as all the materials they have (including those from the neighbouring areas outside of the area of their flora) are spread on the table, as I did with over 200 specimens available to me from the whole of its range, it then becomes apparent that any specimen of one group can easily be merged with the other group next to it or even to the group farthest from it. I have personally presented the problem of delimiting this species and shown the specimens to Dr. T.C. Whitmore, who has written an account of Dialium of Peninsular Malaysia (Whitmore, loc. cit.). Dr Whitmore agreed with me that it is impossible to separate the groups without overlaps.

The 'platysepalum' group is the most common of the groups in the whole distributional range of this variable species, and, therefore, the name (platysepalum) is chosen as the correct one for it.

20. DIALIUM OVOIDEUM THWAITES, Enum. Pl. Zeylan. 1 (1859) 97; Beddome, Fl. Sylv. S. Ind. (1872) 181, pl. 181; Baker, Fl. Br. Ind. 2 (1878) 269; Trimen, Handb. Fl. Ceylon 2 (1894) 112; Lewis, Veg. Prod. Ceylon (1934) 155; Worthington, Ceylon Trees (1959) 194, photo. - Type: C.P. 3149 (BM holo!, iso at BR! K! L! P!), from Sri Lanka, "districts N of Kandy, at no great elevation," fl. undated.

Tree, moderately large with pale brown or light reddish grey bark. Twigs rather thin, lenticellate, dark brown to blackish when dry, glabrous; buds small, apex somewhat roundish, brownish hairy. Leaves with petiole and rachis c. 5-8 cm long, glabrescent, petioles rather long, c. (3-) 4-5 (-7) mm long; blade elliptic, lanceolate or sometimes ovate, c. (2.5-) 4-6 (-7) cm long x (1.5-) 2-4 (-5) cm wide, apex abruptly acuminate, base rounded, subobtuse or cuneate, surfaces concolorous or slightly darker above, beneath glabrescent, subcoriaceous to chartaceous; nerves rather faint above, distinct beneath, c. (5-) 6-8 (-9) pairs; reticulation rather indistinct. Panicles terminal, usually with lower primary side-axes subtended by leaves; rachis c. (5-) 8-12 (-16) cm long, laxly branched, usually dark brown when dry; buds lanceoloid, c. (4.5-) 5.5-6.5 mm long x 2-2.5 mm wide, pedicels c. (2-) 3-4 (-5) mm long, hairy as

the buds. Flowers white in life; sepals lanceolate, c. 4.5-5.5 mm long x 1.5-2 (-2.5) mm wide, adpressed hairy outside, minutely hairy inside; petal 0; stamens 2, filaments short, c. 0.8-1 mm long, glabrous; anthers linear, c. 3.5-4 mm long, connective hairy on both abaxial and adaxial sides; ovary c. 1-1.5 mm long; style c. 2.5-3.5 mm long, slightly recurved at the top, glabrous. Fruits ovoid, $\pm$ slightly compressed, c. 1-2 cm long, exocarp thin, very brittle, hairy. Seeds reniform, c. 8 mm long x 7 mm wide, testa dark brown to blackish, shiny.

Distribution. Sri Lanka (seems to be found only in and around Kandy towards the east, Scattered.

Collections seen. 8.

Ecology. On hills from 100-450 m elev. Flowers in April-May, fruits mature from 4-6 months later.

Remarks. A rather distinct species characterized by lanceoloid flower buds which sometimes measure to 6.5 mm long. The size of the leaflets vary very little which then compares with those of D. cochinchinense, and without flowers, both could be mistaken for the other.

21. DIALIUM COCHINCHINENSE PIERRE, Fl. For. Coch. 5 (1898) t. 384 A; Gagnepain, Fl. Gen. I.-C. 2 (1913) 205; Craib, Fl. Siam. Enum. 1 (1928) 515; Whitn., Tree Fl. Mal. 1 (1972) 259; K. & S. Larsen & J. Vidal, Fl. Camb. Laos & Vietn. 18 (1980) 109, pl. 19 (1-6). -
Lectotype (Vidal's choice): Pierre 1814 (F holo!, iso at BM! K! L!), from Indochina, Vietnam, Bien Hoa, Bao Chang, fl. VII. 1877?.

Tree, medium to large-sized up to c. 30 m high and attaining c. 50 cm in diameter at breast height. Twigs blackish when dry, lenticellate, the young parts hairy, glabrescent except inflorescences; buds small, apex acute, glabrescent. Leaves with petiole and rachis c. (3-) 4-10 (-12) cm long; leaflets (3-) 5-7 (-9), petiolules c. 2-4 (-6) mm long, late glabrescent; blade ovate-lanceolate, sometimes elliptic or ovate, c. (2.5-) 4-6 (-8) cm long x (0.5-) 2-3.5 (-5) cm wide, apex abruptly acuminate, sometimes acute, base cuneate, rounded or rarely cordate, surfaces concolorous to slightly discolorous, dark greyish brown, sometimes with greenish tinge, generally chartaceous; nerves $\pm$ distinct on both surfaces, c. 6-8 (-9) pairs; reticulation indistinct to the naked eye on both surfaces. Panicles terminal, rachis generally laxly-branched, c. (6-) 9-15 (-24) cm long; buds ovoid-ellipsoid, c. 3.5-4 (-4.5) mm long x (1.5-) 2-2.5 mm wide, pedicels c. (1-) 2-3 (-4) mm long. Flowers white or yellowish in life; sepals 5, generally ovate, c. 3-4.5 mm long x (1.5-) 2-2.5 (-3) mm wide, glabrous to minutely hairy inside; petal 0; stamens 2, with filaments short, c. 0.8-1.5 mm long, blackish when dry; anthers c. 2.5-3.5 mm long, connective hairy especially on the adaxial side; ovary sessile; style with slightly recurved top. Fruits $\pm$ ellipsoid to rather ovoid, sometimes slightly compressed, c. 1.5-1.8 cm long x 0.8-1 cm wide, exocarp thin, brittle, finely hairy, glabrescent with age. Seeds small, c. 8 mm long x 6 mm wide, slightly compressed, testa chocolate brown, rather shiny.

Distribution. Lower Burma, Thailand, Cambodia, Laos and S Vietnam.

Collections seen. Burma: Mg Po Khant 13275, Mergui, Theindawya. Thailand: 26. Cambodia: 17. Laos: 4. S Vietnam: 14.

Ecology. In evergreen as well as deciduous dipterocarp forest (Thailand), in dense, semi-dense and open forest, very ^{low} ~~low~~ level low altitude to c. 300 m ele. Flowers in Feb.-Aug., with peaks in May-July, fruits in May-Jan., quite heavy in June-Dec.

Remarks. This species is very closely related to D. indum var. indum but differs in the smaller leaflets which are more or less uniform in size, generally smaller flowers, smaller fruits, and very thin and more brittle exocarp. The smaller leaflets, however, seem to overlap with the smaller-leaflet forms of D. indum especially those in Peninsular Malaysia, which make identification rather difficult. For the time being and for practical purposes, I would consider the southern limit of this species to be at c. 11°N in southern Thailand. There are no other collections belonging to this species below this line (see remarks in D. indum).

This species is said to be cultivated in certain villages in Peninsular Malaysia especially in N Kedah and Perlis but D. indum also occurs there naturally.

22. DIALIUM INDUM L. - D. javanicum Burm. f. - D. coromandelianum Houtt. - D. laurinum Baker - D. patens Baker - D. angustisepalum Ridley - D. marginatum de Wit - D. turbinatum de Wit - D. laurinum var. bursa de Wit. For full references, see under the varieties.

Tree, medium to large-sized, up to c. 40 m high with wide-spreading branches; bole usually columnar reaching c. 6-12 m high to the first branch and up to c. 1 m in diameter at breast height. Twigs rather slender, lenticellate, grey to dark brown when dry, the young parts hairy, glabrescent; buds small, usually rarely present in the herbarium. Leaves with petiole and rachis c. (7-) 10-15 (-20) cm long, glabrescent; leaflets (5-) 7-9 (-11), petiolules c. (3-) 4-6 (-10) mm long, sometimes slightly canaliculate, late glabrescent; blade ovate-oblong to ovate-lanceolate or ovate-elliptic to generally broadly elliptic, sometimes roundish c. (4-) 6-10 (-11) cm long by (2.5-) 3-5 (-7) cm wide, apex abruptly acuminate to long acuminate, sometimes distinctly cuspidate or obtuse to rounded, base rounded or broadly to sometimes narrowly cuneate, surfaces $\pm$ concolorous or sometimes discolorous, greyish brown to dark brown when dry, above slightly light-coloured, sometimes shiny, glabrous, beneath glabrous to late glabrescent, generally subcoriaceous or sometimes stiff coriaceous nerves fine but distinct especially beneath, c. 8-10 (-14) pairs; reticulation generally distinct beneath, not areolate but veinlets mostly squarish. Panicles terminal, usually with lower primary side-branches subtended by leaves or in fascicles axillary to fallen leaves or old nodes; rachis c. 10-20 cm long, branches rather laxly set; buds ellipsoid-oblongish to sometimes - lanceoloid, c. 4-5 (-5.5) mm long by 2-2.5 (-3) mm wide, pedicels c. 2-6 mm long. Flowers at anthesis $\pm$ white in life; sepals 5, ovate-oblong to sometimes elliptic, up to c. 5 mm long x 2.5 mm wide, minutely hairy inside; petal 0; stamens 2, filaments short even at anthesis but up to c. 1.5 mm long; anthers

rather oblongish, c. 3.5-4.5 (-5) mm long, connective sparsely hairy on both sides, the slits usually dehiscing even before anthesis; ovary sessile, up to c. 2 mm long, white hairy in life; style short and before anthesis generally not exceeding the anther, usually straight to only slightly recurved at the top. Fruits orbicular or ovoid, sometimes very slightly compressed, c. 1.5-2 (-2.5) cm long x 1-1.5 cm wide, exocarp brittle, hairy but not velvety. Seeds squarish to reniform, c. 7-12 mm long x 5 mm thick, testa light brown to dark brown, shiny.

Distribution. W Malesia and southernmost Thailand, near the border with Peninsular Malaysia.

Ecology. Low well-drained flat country and hills; sometimes in low lying swampy areas including peat swamps to c. 1200 m elev. (Mt. Kinabalu). For details, see under the varieties.

Remarks. D. indum can be distinctly divided into two varieties by the shape, texture and to a lesser extent by reticulation of the blades. See individual remarks under the varieties.

KEY TO THE VARIETIES

1. Blade generally subcoriaceous, ovate-oblong to ovate-lanceolate; apex usually long acuminate to sometimes cuspidate
..... 22a. D. indum var. indum
1. Blade stiff coriaceous, generally broadly elliptic, sometimes roundish or broadly lanceolate; apex obtuse to sometimes roundish or abruptly acuminate 22b. D. indum var. bursa

22a. DIALIUM INDUM L. var. INDUM. - Dialium indum L., Mant. Pl. 1 (1767) 24; Willd., Sp. Pl. 1 (1797) 49; Miq., Fl. Ind. Bat. I, 1 (1855) 79; Baker, Fl. Br. Ind. 2 (1878) 269; Prain, J. As. Soc. Beng. 66 (1897) 168; Ridley, Fl. Mal. Pen. 1 (1922) 622; Burkill, Dict. Ec. Prod. Mal. 1 (1935) 799; Backer & Bakh. f., Fl. Java 1 (1963) 535; Whitm., Tree Fl. Mal. 1 (1972) 259; Meijer, Field G. Trees W. Mal. (1974) 183; Cockburn, Trees Sabah (1976) 167, fig. 35. - Type: LINN 23.1 Dialium indum (LINN holo!), from W Malesia, no exact locality (see remarks), fl. undated. - Figs. 2.7, 7.4 & 7.5.

Dialium javanicum Burm. f., Fl. Ind. (1768) 12 (reduced by Miquel, loc. cit. to this species). Type specimen not indicated.

Dialium coromandelianum Houtt., Handleid. 2 (1773) 39, t. V, fig. 2. The drawing seems to be a Dialium sp.; no type specimen cited.

Dialium patens Baker, Fl. Br. Ind. 2 (1878) 270; Prain, J. As. Soc. Beng. 66 (1897) 169; Ridley, Fl. Mal. Pen. 1 (1922) 622; Whitm., Tree Fl. Mal. 1 (1972) 260. - Lectotype: Griffith 1846 (K holo!, iso at L!), from W Malesia, Peninsular Malaysia, Malacca, fl. undated. syn nov.

Dialium angustisepalum Ridley, Kew Bull. (1929) 255. - Type: Yusop C.F. No. 4123 (K holo!, iso at L! SING!), from W Malesia, Peninsular Malaysia, Pahang, Kuantan, Gunong Lesang, fl. III. 1919.

Dialium marginatum de Wit, Blumea 7 (1953) 320. - Type: Beccari, Piante Bornensi 3381 (K holo!, iso at L!), from W Malesia, Borneo, Sarawak, fl. XI?. 1871. syn. nov.

Dialium turbinatum de Wit, Blumea 7 (1953) 321. - Type: For. Dept. Herb. (SAN) 3782 (K holo!, iso at L! P!), from W Malesia, Borneo, Tambunan, prope Kampung Tambata, fl. undated. syn. nov.

Blade subcoriaceous, ovate-oblong to ovate-lanceolate, apex usually long acuminate to sometimes cuspidate. Leaflets variable in size; nerves and reticulation distinct but apparently slightly raised.

Distribution. Thailand (Naratiwat, Pattani and Ranaung), Peninsular Malaysia, Borneo, Sumatra and Java.

Collections seen. Thailand (Naratiwat, Pattani & Ranaung):

4. Peninsular Malaysia: 52. Borneo, Sarawak: 10; Brunei: 5; Sabah: 50; Kalimantan: 30. Java: 13; Sumatra: 9.

Ecology. Low well-drained flat country and hills; sometimes in low lying swampy areas including peat swamp (Whitmore, 1972) up to c. 1150 m elev. (Clemens 40440, Mt. Kinabalu). Flowers throughout the year but with peaks from Feb.-June, fruits also throughout the year with peaks in May, Aug. and Oct.

Remarks. This typical variety is very variable in size and to a lesser extent in the shape of the leaflets. The smaller leaflet forms were before usually attributed to D. patens (now reduced here) and D. cochinchinense. The latter had been recorded to be cultivated in some villages in Peninsular Malaysia (Whitmore 1972). However, I have not come across any material (i.e. previously identified as D. cochinchinense) indicating that they were collected from introduced or cultivated trees. Since D. indum is widespread and naturally growing in the whole of Peninsular Malaysia, I therefore consider all materials previously identified as D. cochinchinense and coming from this region, as belonging to this variety, unless hard evidence (recorded date of introduction, e.g.) proves the contrary.

Occasional field notes on some materials previously identified

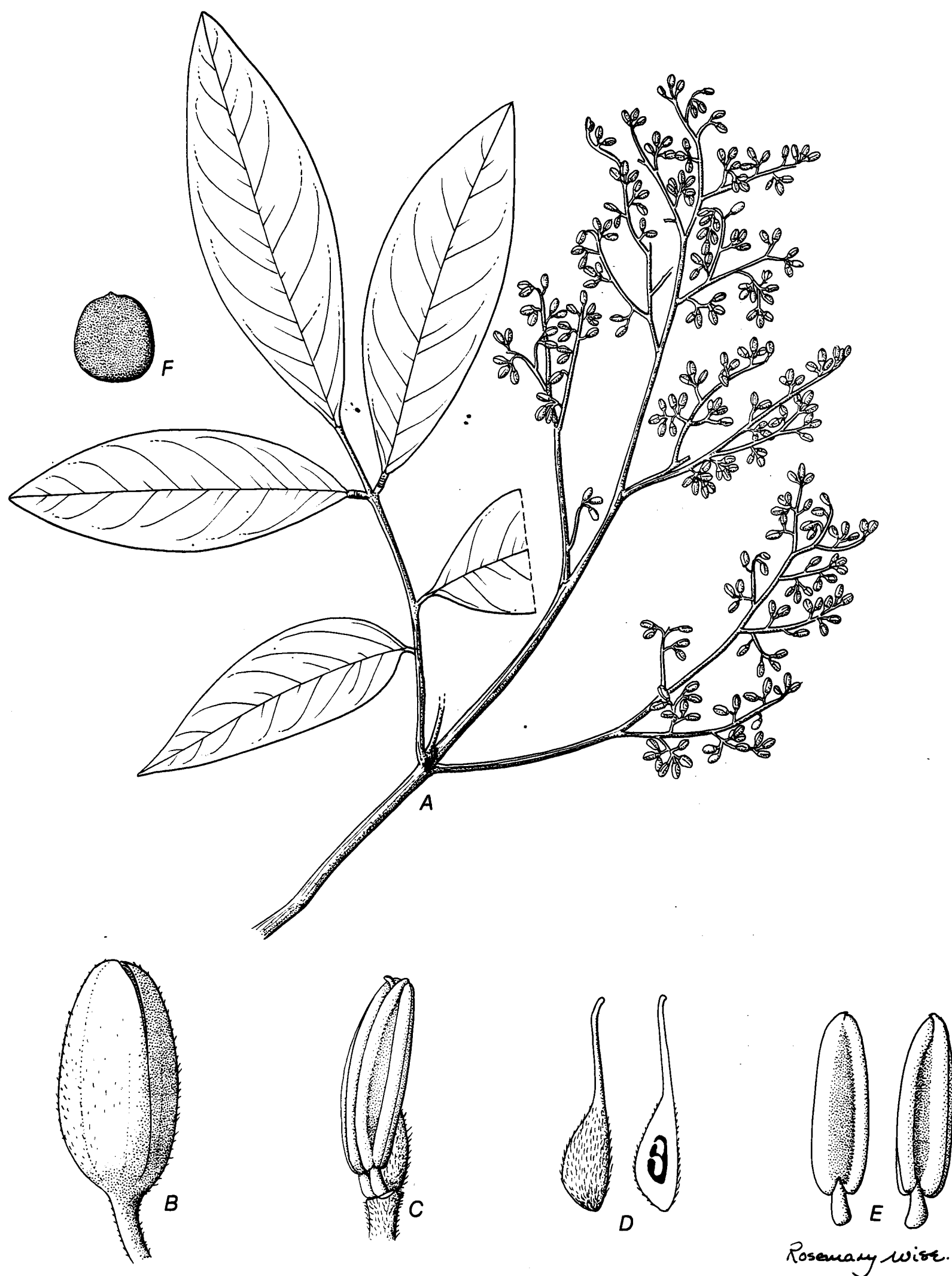


Fig. 7.4 *Dialium indum* L. A. habit, x 2/3 (Ibrahim s.n., anno 1909, Peninsula Malaysia); B. flower bud, C. flower bud with sepals removed, D. ovary with lengthwise section, E. stamen in adaxial and abaxial sides (B-E all x 10, FRI 1617, Selangor, Peninsular Malaysia); F. fruit, x 2/3 (SAR 29688, Sarawak).

as D. patens stated that they were collected in swampy areas. Previously, this type of habitat was sometimes used as the only basis for separating D. patens with D. indum. But other materials collected from firmer grounds match very well with those collected in wetter areas. Examples are so numerous that it is needless to mention them here.

This species (variety) occurs also in the southernmost part of Thailand (Pattani) at c. 7°N near the border with Peninsular Malaysia. There is an uncollected area in Thailand that forms the gap in the distribution pattern between this species and D. cochinchinense at c. latitude 11°N down to 7°N. Pending availability of materials coming from this said uncollected gap, I would consider the northernmost limit of this species at more or less 8°N in S Thailand.

Merrill in his Int. Rumph. (1917: p. 257), interpreted Tamarindus altera Rumph. (Herb. Amb. 2 (1741) 93) as this species. If this interpretation is correct, then Rumphius could have described his plant (introduced and grown in his garden) from Java because D. indum does not occur naturally in Amboina.

22b. DIALIUM INDUM L. var. BURSA (DE WIT) ROJO - Dialium laurinum Baker var. bursa de Wit, Blumea 7 (1953) 320. - Type: 186 T.lP.197 (L'holo!, iso at K!), Sumatra, Palembang, Banjuasin and Kubu Lands, near Banjung Lintjir, fl. undated.

Dialium laurinum Baker, Fl. Br. Ind. 2 (1878) 269; Prain, J. As. Soc. Beng. 66 (1897) 170; Ridley, Fl. Mal. Pen. 1 (1922) 622; Burkill, Dict. Ec. Prod. Mal. 1 (1935) 800; Whitm., Tree Fl. Mal. 1 (1972) 260, - Lectotype: Maingay 1625 (K holo!), Peninsular Malaysia, Malacca, fl. III?, 1865-66. syn. nov.

This variety is characterised by its leaflets which are stiff coriaceous, generally broadly elliptic, with acute to abruptly acuminate apex. The nerves and reticulation underneath are prominently raised.

Distribution. W Malesia.

Collection seen. Peninsular Malaysia and Singapore: 28.

Sumatra: see type (var. bursa). Borneo, Sarawak: 13; Brunei: 4;

Sabah: SAN 49561, 4585 and 58471, all from Keningau; Kalimantan: 10.

Ecology. Same as the typical variety but not as yet reported to occur in low-lying swampy areas and peat swamps.

Remarks. The only putative difference between this variety and the typical one are the shape and texture of the leaflets. Although the generally broadly elliptic and stiff coriaceous leaflets in this variety are sufficient enough to distinguish it from the other, there are many intermediates which obscure definite separation between the two. A good example is Griffith 1846 (lectotype of D. patens), the leaflets of which correspond very well to this variety. The lectotype of D. laurinum (Maingay 1625) is also intermediate between this and the typical variety. It is for this reason that I could not maintain D. laurinum (now under synonymy of this variety) as a separate species from D. indum.

I have identified a number of specimens (especially Kostermans' collection from E Kalimantan) as belonging to this variety on the basis of stiff coriaceous leaflets and bigger fruits although their venation and shape are referable to the typical variety. But other than these particular specimens, the two varieties can be identified fairly accurately.

Note on the type. The protologue of Dialium indum L. in Mant. Pl. (loc. cit.) cites the habitat as India but mentions nothing about type specimens. However, there is an extant specimen in the Linnaean Herbarium (LINN) which consists of a sheet with mounted fragments of two twigs with paniculate inflorescences (see Fig. 7.5). It is labelled by Linnaeus in his own handwriting with the number 23.1 at the top margin of the sheet and Dialium at the bottom margin. The specific epithet indum in pencil is supposedly added later by Sir James Edward Smith (who originally purchased Linnaeus' herbarium). At almost the centre of the sheet, a word "coerand(i)je" (also in Linnaeus' handwriting) is written. This word was obviously misinterpreted or wrongly deciphered by Savage in his catalogue (Catalogue of the Linnaean Herbarium, 1945) as "Coi(m)andel" (probably associating it with India). I think the word "coerand(i)je" is a Dutch spelling of a vernacular name "kranji" or "keranji" used in Java and Malay Peninsula for species belonging to Dialium. I agree with Prof. Dr. H.C.D. de Wit of Agricultural University, Wageningen, Netherlands, who in the 1950s deciphered the word as "coerand(i)je" rather than "Coi(m)andel". From this interpretation, there is no doubt that the habitat or type locality of the plant (or from where the specimen of Linnaeus originated) is W Malesia (most particularly Java). The specimen now designated as LINN 23.1 is therefore the holotype, not only of the species but also of the genus.

It is noted by Stearn in his introduction to the facsimile edition of the Mantissa (Mantissa Plantarum, facsimile edition, repr. J. Cramer, Weinheim, 1961) that the Burmans (father and son) were among Linnaeus' sources of plants described in it. The type in the Linnaean Herbarium (LINN) resembles that of the Burmans'



Fig. 7.5. LINN 23.1, the type of Dialium indum.

specimen now preserved at Leiden (L). It could be possible that the Burmans sent duplicate material of D. indum to Linnaeus and that Linnaeus labelled his specimen as "coeran(i)je" which the Burmans could have communicated to him as the vernacular name of the plant. Following this argument, it is safe to say that Dialium javanicum Burman f. is the same plant as D. indum L. and both described from duplicates of the same material. The specific epithet javanicum could have been the most appropriate name, but unfortunately, D. javanicum was published half a year later (i.e. April 1768) than that of D. indum (i.e. October 1767). However, because of this interpretation, there is good reason to believe that the type locality of D. indum could be Java and not any other locality in W Malesia.

III. Subgen. DANSERA (Steenis) Stey.

Subgen. Dansera (Steenis) Stey., Reinwardtia 2 (1953) 355.

Subgen. Hova Irwin and Barneby in Polh. and Raven, Adv. Leg. Syst. 2, part 1 (1981) 101. Type species: Dialium madagascariense Baillon.

Receptacle with disc absent, as wide as the ovary. Sepals 3. Petals 3 or 0. Stamens 2 or 6. Sculpturing of the exine coarsely reticulate. Secondary xylem axial parenchyma cells containing silica (except D. occidentale which rarely contains oxalate crystals). Leaves unifoliolate or imparipinnate to 2 pairs (rarely 3 pairs).

Type species: Dialium procerum (Steenis) Stey.

Distribution. Madagascar and W Malesia (see Fig. 4.3).

Ecology. See under the genus.

Remarks. Dansera was already treated by Steyaert (1953) as a subgenus while Irwin and Barneby (1981) consolidated all Madagascan species into subgenus Hova. The two subgenera are now combined by me into only one subgenus for the reason I stated in Chapter 3 (section 3.4) and Chapter 5 (section 5.2).

Although the subgenus is homogeneous enough, it can still be subdivided into two sections based on androecial characters which are correlated with geographical distribution.

C. Sect. HOVA (Irwin & Barneby) Rojo, stat. & sect. nov.

Subgen. Hova Irwin & Barneby in Polh. & Raven, Adv. Leg. Syst. 2, part 1 (1981) 101.

Sepals 3. Petals 3. Stamens 2. Anther apex deeply cleft. Leaves unifoliolate or trifoliolate.

Type species: Dialium madagascariense Baillon

Distribution. Madagascar (see Figs. 4.3 and 7.6).

Ecology. See individual species.

Remarks. This section forms a natural group composing species found only in Madagascar. It differs from section Dansera (see there) in having 3 petals and 2 stamens, and in having a deeply-cleft anther apex.

23. DIALIUM OCCIDENTALE (CAPURON) ROJO, stat. nov. - Dialium madagasca-
riense Baillon ssp. occidentale Capuron - Dialium unifoliolatum Capuron
 ssp. septentrionale Capuron. For full references, see the varieties.

Tree, large-sized; bole attaining c. 90 cm in diameter at breast height. Twigs rather thin, light grey to greyish brown when dry, sparsely lenticellate; buds minute, roundish, hairy. Leaves with petiole and rachis c. 1-2.5 cm long, both petiole and rachis $\pm$ equal in length; leaflets trifoliolate or very rarely together with uni- or bifoliolate ones by abortion, petiolules short, c. 1.5-2 mm long, glabrous; blade elliptic to lanceolate, c. (2.5-) 3.5-5 (-6.5) cm long x (1-) 1.5-2 (-2.5) cm wide, apex acute, sometimes abruptly to long acuminate, base cuneate, obtuse or roundish, surfaces concolorous, brown with greenish tinge, above shiny, glabrous, beneath often dull, very early glabrescent, usually subcoriaceous; nerves distinct on both surfaces, c. 4-6 (-7) pairs; reticulation distinct on both surfaces, areoles rather fine. Panicles axillary, in fascicles or sometimes solitary; rachis very short, c. 2-4 cm long, sparsely hairy; buds ellipsoid, c. 3.5-4 (-4.5) mm long x 1.5-2 mm wide, pedicels c. 1.5-3 mm long. Flowers: sepals 3, $\pm$ elliptic, c. 3-3.5 (-4) mm long x 1.5-2.5 mm wide, sparsely hairy outside, $\pm$ glabrous inside; petals 3, as long and as wide as the sepals, clawed, $\pm$ glabrous; stamens 2, filaments rather short, c. 1.5-2 mm long, slightly curved at the top, glabrous; anthers humped on the abaxial side, apex deeply cleft, c. 1.5-2 mm long, sparsely hairy especially on the adaxial side of the connective; ovary sessile to subsessile, c. 1-1.5 mm long, whitish hairy; style c. 1-1.5 mm long, slightly recurved at the top, glabrous. Fruits ovoid or subglobose, c. 1.5-2.5 cm long x 1.5-2 cm wide, exocarp brittle, sparsely hairy, glabrescent with age. Seeds orbicular, 10 mm long x 8 mm wide, testa brown, shiny.

Distribution. W and N Madagascar. - Fig. 7.6.

Ecology. Please see individual variety.

Remarks. Capuron (loc. cit.) recognised this taxon as a subspecies of D. madagascariense on the basis of leaflet size and from the fact that it is trifoliolate. I raised it to a separate species on the basis of its smaller flowers and anthers being humped (see fig. 2.16 F) on the abaxial side (flattish in D. madagascariense). The humped shape of the anther on the abaxial side is used as a sectional character of the African section Arouna (subgenus Arouna); see Fig. 2.15 A-D.

KEY TO THE VARIETIES

1. Leaves trifoliolate or rarely together with unifoliolate ones
in the same twig by abortion

..... 23a. D. occidentale var. occidentale

1. Leaves unifoliolate .. 23b. D. occidentale var. septentrionale

23a. DIALIUM OCCIDENTALE (CAPURON) ROJO var. OCCIDENTALE - Dialium mada-
gascariense Baillon ssp. occidentale Capuron, Adansonia sér. 2, 8 (1968)

213. - Type: 12857 SF (P holo!), from Madagascar, Zombitsy forest near
Sakaraha, Karimbola, fl. XI. 1959.

Leaflets trifoliolate or rarely uni- or bifoliolate by abortion.

Distribution. W and NW Madagascar. - Fig. 7.6.

Collection seen. 14. .

Ecology. In primary forest on calcareous and sandy soils from low
altitude to c. 600 m elev. Flowers in Sept.-Nov. and ripe fruits observed
in Dec.-May.

23b. DIALIUM OCCIDENTALE (CAPURON) ROJO var. SEPTENTRIONALE
(CAPURON) ROJO, stat. and var. nov. - Dialium unifoliolatum
Capuron ssp. septentrionale Capuron, Adansonia sér. 2, 8 (1968)
215. - Type: 24699 SF (P holo!), from NW Madagascar, forest of
Sahafary, Saharenana basin, fl. II. 1966.

Differs from the type variety in its unifoliolate leaves.

Distribution. Restricted to N Madagascar, around Diego
Suarez to NW of Vohemar - Fig. 7.6.

Collections seen. 8.

Ecology. Deciduous forest or remnant of forest from 50-450 m
elev., on sandy soils. Flowers in Feb. and fruits in April-May.

Remarks. On account of its unifoliolate leaves, Capuron
(loc. cit) recognized this present variety as subspecies of his
D. unifoliolatum. However, they differ distinctly in the following:

	var. <u>septentrionale</u>	<u>unifoliolatum</u>
Anther - length	1.5-2 mm long	2-2.5 mm long
- shape	humped on the abaxial side	flattish on both abaxial and adaxial sides
Fruit - size	1.5-2.5 cm long x 1-2 cm wide	2.5-3.8 cm long x 2-2.6 cm wide
- exocarp	brittle	exocarp firm

24. DIALIUM MADAGASCARIENSE BAILLON in Grandidier, Hist. Nat. Pl.
Madag. Atlas 1 (1888) pl. 30 B; Drake in Grandidier, Hist. Nat. Pl.
Madag. (text) 1 (1902) 95; Capuron, Adansonia ser. 2, 8 (1968) 212,
pro parte, excl. ssp. occidentale. - Type: Humblot 426 (P holo!,
Drake's choice), from E Madagascar, no precise locality, fl. undated.

Tree, large to very large-sized up to c. 40 m high; bole attaining over 100 cm in diameter at breast height. Twigs glabrous, rather thick, lenticellate, dark greyish brown to blackish when dry, the young parts glabrous except inflorescences; buds small, roundish, early glabrescent. Leaves with petiole and rachis c. 2-3 (-3.5) cm long, both petiole and rachis $\pm$ of equal length; leaflets trifoliolate or exceptionally together with unifoliolate ones by abortion, petiolules c. (2-) 3-5 (-7) mm long, glabrous; blade ovate to elliptic, c. (3-) 4-7 (-10) cm long x (2-) 3-4 (-5.5) cm wide, apex obtuse to rounded or sometimes acute with the top usually folded in the herbarium, base cuneate to obtuse, sometimes rounded, surfaces concolorous, above usually shiny, beneath sometimes dull, glabrous, stiff coriaceous; nerves distinct on both surfaces, c. 4-6 (-7) pairs; reticulation distinct on both surfaces, areoles rather large and deep. Panicles axillary, usually in fascicles or rarely solitary; rachis c. (4-) 7-9 (-14) cm long, sparsely hairy, very early glabrescent, blackish when dry; buds oblongish-ellipsoid, c. 4-6 mm long x 3-3.5 mm wide, pedicels c. 2-5 mm long, sparsely hairy, glabrescent. Flowers: sepals 3, sparsely hairy outside, glabrous inside, oblong-elliptic, c. 3.5-5.5 mm long x 2.5-3 mm wide; petals 3, obovate, c. 3-5 mm long x 2-2.5 mm wide, clawed and with distinct nerves; stamens 2, filaments c. 1.5-2 mm long, glabrous; anthers $\pm$ linear-oblong, c. (2-) 3-3.5 mm long x 1-1.3 mm wide, apex deeply cleft, flattish on both abaxial and adaxial sides, sparsely hairy all over; ovary $\pm$ eccentric, c. 1.5-2 mm long, densely whitish hairy; style c. 1-2.5 mm long, slightly recurved at the top, glabrous. Fruits $\pm$ ovoid or subglobose, sometimes slightly compressed, c. 2-2.5 cm long x 1.5-2.5 cm wide, exocarp dark brown to blackish when dry, thin,

brittle, sparsely hairy, glabrescent with age. Seeds orbicular, c. 10-12 mm long x 8-9 mm wide, testa dark brown, shiny.

Distribution. NE Madagascar, between c. 15° - 17°30'S latitude. Less widespread than the closely related D. unifoliolatum. - Fig. 7.6.

Collections seen. 13.

Ecology. Forest, sublittoral to c. 500 m elev., on sandy soils. Flowers in Oct.-Dec., fruits in Jan.-Feb.

Remarks. This is distinct from the rest of the species in Madagascar on account of its bigger-sized trifoliolate leaves, stiff coriaceous blades and bigger flowers. It is more related to D. unifoliolatum in characters of the anther (see there) than D. occidentale (see also there). However, the thin exocarp of this species is the same as that of D. occidentale.

The original description (Drake del Castillo, loc. cit.) did not mention number of sepals, petals and stamens. The plate of Baillon (loc. cit.) clearly shows 2 stamens but the number of sepals and petals are not clearly discernible.

25. DIALIUM UNIFOLIOLATUM CAPURON, Adansonia sér. 2, 8 (1968) 214, fig. 3 (1-10), pro parte, excl. ssp. septentrionale. - Lectotype: 1877 SF (P holo!), from E. Madagascar, fl. undated.

Tree, sometimes deciduous, medium-sized up to c. 30 m high; bole attaining c. 100 cm in diameter at breast height; outside bark falling off in thin flakes. Twigs glabrous, greyish brown to sometimes blackish when dry, lenticellate, the young parts also glabrous. Leaves unifoliolate, petioles c. 3-5 mm long, articulate;

blade elliptic, ovate or ovate-elliptic, c. 3-8 cm long x 1.5-5 cm wide, apex attenuate or long acuminate, base rounded or obtuse, surfaces concolorous, light brown with greenish tinge, shiny above, slightly shiny beneath, subcoriaceous; nerves distinct on both surfaces c. (3-) 4-6 pairs; reticulation distinct on both surfaces, the areoles rather fine. Panicles usually axillary or sometimes terminal, usually in few fascicles; rachis rather short, c. (3-) 5-6 (-10) cm long, sparsely hairy, glabrescent; buds ellipsoid-oblongish, c. 2.5-3.5 mm long x c. 1.5 mm wide, pedicels 2-4 mm long. Flowers: sepals 3, elliptic-oblong, c. 2.5-3 mm long x 1-2.5 mm wide, sparsely hairy outside, $\pm$ glabrous inside; petals 3, $\pm$ obovate, c. 3-3.5 mm long x 1-1.5 mm wide, clawed; stamens 2, filaments short, c. 1 mm long, glabrous; anthers $\pm$ linear-oblong, c. 2 (-2.5) mm long, flattish on both abaxial and adaxial sides, sparsely hairy all over but rather denser on both sides of the connective, apex deeply cleft; ovary c. 1 mm long, whitish hairy; style c. 1.5 mm long, slightly recurved at the top. Fruits $\pm$ obovoid, c. 2.6-3.8 cm long x 2-2.6 cm wide, pericarp thick and firm, exocarp dark brown to blackish when dry, not brittle, sparsely adpressed-hairy, glabrescent with age. Seeds $\pm$ orbicular, c. 9 mm long x 7 mm wide, testa light to dark brown, shiny.

Distribution. E Madagascar, at latitude between 15° - 23° S.

- Fig. 7.6.

Collections seen. 31.

Ecology. Common in littoral forest up to 700 m altitude or rarely up to 1000 m elev. Flowers in Jan.-June, fruits in July-Jan. (mostly in July-Sept.).

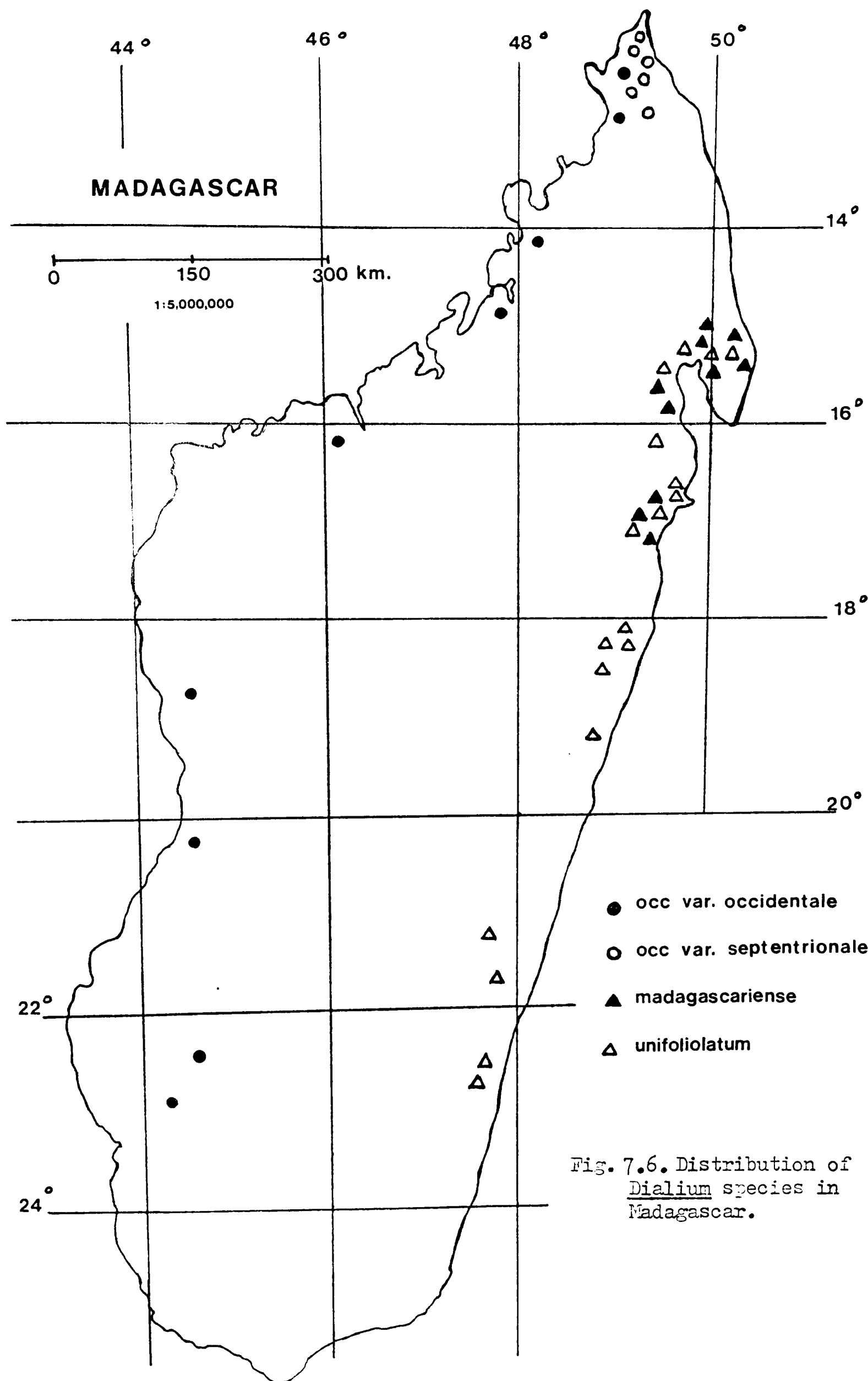


Fig. 7.6. Distribution of Dialium species in Madagascar.

Remarks. This is closely related to D. madagascariense in characters of the anther. These are flattish on both abaxial and adaxial sides. However, this species differs considerably with the other in having small unifoliolate leaves, bigger and firmer (pericarp firm and exocarp not brittle) fruits and smaller flowers.

This seems to be more common and widely distributed in the east than D. madagascariense (see Fig. 7.6).

Capuron (loc. cit.) did not assign any type to represent his subspecies. I have selected 1877 SF which he used in his drawing (fig. 3, 1-10) as the lectotype.

D. Sect. DANSERA

Subgen. Dansera (Steenis) Stey. sect. Dansera.

Sepals 3. Petals 0. Stamens 6. Anther apex not cleft. Leaves unifoliolate or (1-) 3-5 (-rarely 7) leaflets.

Type species: Dialium procerum (Steenis) Stey.

Distribution. W Malesia (see Fig. 4.3).

Ecology. See individual species.

Remarks. Differs from section Hova in being apetalous and having 6 stamens instead of 2.

26. DIALIUM KUNSTLERI PRAIN - Dialium silvestre de Wit - Dialium trifoliolatum de Wit - Dialium dewittei Steenis. For full references, see the varieties.

Tree, large-sized to c. 40 m high; bole attaining c. 90 cm in diameter at breast height; crown with spreading branches. Twigs lenticellate, pale or greyish to dark brown when dry, the young parts patent

hairy, glabrescent; bud small, apex roundish, $\pm$ glabrous. Leaves with petiole and rachis c. (0.5-) 1.5-3.5 (-5) cm long, glabrescent; leaflets (3-) 5 (-rarely 7) or trifoliolate and often with unifoliolate ones in the same twig; petiolules c. 3-4 (-7) mm long, hairy when young, glabrescent; blade elliptic, elliptic-oblong or ovate to lanceolate, c. (4-) 5-15 (-19) cm long x (2-) 3-6 (-7.5) cm wide, apex long acuminate, sometimes acute to abruptly acuminate, base cuneate or rounded, surfaces $\pm$ concolorous, dark brown, sometimes with greenish or yellowish tinge, above shiny, glabrous, beneath dull, glabrescent, generally coriaceous; nerves especially halfway between midrib to margin sharply arcuating towards the apex, c. (5-) 6-8 (-9) pairs; reticulation rather distinct on both surfaces. Panicles generally axillary, sometimes in axils of fallen leaves or old nodes, mostly in few fascicles or rarely terminal; rachis c. (4-) 6-12 (-20) cm long, sparsely hairy; buds ellipsoid-oblongish, c. 4.5-5.5 mm long x 2-2.5 mm wide, pedicels c. (2-) 3-4 mm long. Flowers: sepals 3, elliptic-oblong, c. 3.5 mm long x 2-2.5 mm wide, minutely hairy inside; petal 0; stamens 6, filaments c. 1-1.5 mm long, glabrous; anthers linear, c. 3-3.5 mm long, sometimes hairy along both abaxial and adaxial sides of the connective; ovary c. 1.5 mm long, whitish hairy; style c. 1.5-2 mm long, slightly recurved at the apex. Fruits broadly ellipsoid to sometimes ovoid, c. 3-4 cm long x 2.5-3 cm wide, sometimes mucro persistent, pericarp rather thick and firm, usually intact in the herbarium, hair on the exocarp glabrescent with age. Seeds rather orbicular, flattish, c. 1.5 cm long x 1 cm wide, testa chocolate brown to blackish.

Distribution. W Malesia (Peninsular Malaysia and Borneo).

Ecology. See individual variety.

Remarks. The species is clearly divisible into two varieties by the number of leaflets.

KEY TO THE VARIETIES

1. Leaflets 5, sometimes together with 3 or very rarely 7 in the same twig 26a. D. kunstleri var. kunstleri
1. Leaflets 3 and often together with unifoliate ones in the same twig 26b. D. kunstleri var. trifoliolatum

26a. DIALIUM KUNSTLERI PRAIN var. KUNSTLERI. - Dialium kunstleri Prain, J. As. Soc. Beng. 66 (1897) 168; Ridley, Fl. Mal. Pen. 1 (1922) 621; Whitm., Tree Fl. Mal. 1 (1972) 259. - Type: Kunstler 4415 (K holo! iso at BM!), from W Malesia, Peninsular Malaysia, Perak, Goping, fr. undated.

Dialium silvestre de Wit, Blumea 7 (1953) 321. - Type: bb. 12957 (BO holo!, iso at L!), from W Malesia, Borneo, SE Kalimantan, E Rutau, Pengadan, fl. anthesis, XI. syn. nov.

Leaflets often 5, rarely with 3 or 7 in the same twig, generally c. (4-) 5-12 (-17) cm long x (2-) 2-5 (-6.5) cm wide with nerves prominent but not distinctly raised beneath.

Distribution. W Malesia. Seems to be rare in Peninsular Malaysia but very common in Borneo (SE Kalimantan, Sabah and Sarawak).

Collection seen. Peninsular Malaysia: Kunstler 4415 T, 4416, Perak; KEP 5452, Kelantan. Borneo, Sarawak: 5. Sabah: 6. Kalimantan: 8.

Ecology. In primary forest at c. 30-250 m elev., usually brown to yellowish silt to sandy loam soils; in Sarawak once collected in Kerangas forest. Flowers in May and Nov. (one specimens SAN 23954 with few flowers and old fruits together), fruits in June and Oct.-Nov.

Remarks. This typical variety is related to D. procerum, with var. trifoliolatum intermediate between them (see remarks there).

The type of D. silvestre is not in good condition but it shows that the leaf rachises have 5 leaflets. I have dissected flowers that de Wit (loc. cit.) failed to examine. A few specimens attributed to this variety have more than two pairs of leaflets.

26b. DIALIUM KUNSTLERI PRAIN var. TRIFOLIOLATUM (DE WIT) ROJO
stat. & var. nov. - Dialium trifoliolatum de Wit, Blumea 7 (1953)
321. - Type: bb. 19826 (BO holo!, iso at L! SING!), from W Malesia,
Borneo, Kalimantan, S Martapura, old fr. VI.

Dialium dewittiei Steenis, Bull. Bot. Gard. Buitenz. ser. 3,
17 (1948) 415. nom. nud., name only.

Characterized by trifoliolate leaves but often together with unifoliolate ones in the same twig. The blades are generally larger than the typical variety, i.e. c. (5-) 6-15 (-19) cm long x (2-) 3-6 (-7.5) cm wide, with very distinctly-raised nerves beneath.

Distribution. W Malesia, Borneo (common in Kalimantan and Sabah and collected in the same areas as the typical variety but no collections from Sarawak) and Peninsular Malaysia.

Collections seen. Peninsular Malaysia: FRI 12859, Pahang.
Borneo, Sabah: 12. Kalimantan: 15.

Ecology. The same as the typical variety. Flowers in April-Nov., fruits in May-Dec.

Remarks. This variety stands between the typical variety and D. procerum (see there). Its closeness with D. procerum is attributed to the presence of unifoliolate leaves together with the predominantly trifoliolate ones in the same twig. The fruits, however, conform to the typical variety. All flowers seen were at their anthesis and no stamens were available for description. I believe the stamens of this variety would be similar to the typical one.

27. DIALIUM PROCERUM (STEENIS) STEY., Reinwardtia 2 (1953) 355; Whitm., Tree Fl. Mal. 1 (1972) 261. - Dansera procera Steenis, Bull. Bot. Gard. Buitenz. sér. 3, 17 (1948) 415 /Rhynchocarpa monophylla Backer (nomen nudum) in K. Heyne, De Nutt. Pl. Ned. Ind. (1927) 739⁷. - Type: For Serv. 117T.3P.390 (L holol., iso at L! BO!), from W Malesia, Sumatra, Palembang, Lemantang Ilir, fl (anthesis), XI. - Figs. 2.8 & 7.7.

Tree, large-sized up to c. 45 m high; bole attaining up to c. 90 cm in diameter at breast height; bark smooth, often grey-green with orange patches. Twigs light to greyish brown when dry, lenticellate, the young parts hairy, soon glabrescent except inflorescences. Leaves unifoliolate, petioles short, c. (0.5-) 1-3 mm long, petiolules c. as long as the petioles, glabrescent; blade ovate to ovate-oblong or elliptic, c. 6.5-16 cm long x 3.5-7 cm wide, apex bluntly acuminate, often folded in the herbarium, base usually rounded to cuneate, surfaces concolorous, above often shiny, glabrous, beneath dull, glabrescent, generally coriaceous; nerves distinct on both surfaces, c. (5-) 6-8 (-9) pairs, the ones near the top arcuating sharply towards the apex; reticulation

± distinct but not areolate. Panicles generally axillary or sometimes terminal especially in side-branchlets, sometimes in fascicles; rachis laxly branched, c. (6-) 9-15 (-16) cm long, flower buds rather laxly set; buds ellipsoid-oblongish, c. 3.5-4 mm long x 1.5-2 mm wide, pedicels c. 2-4 mm long, rather sparsely hairy. Flowers: sepals 3, ± elliptic, c. 3-4 mm long, minutely hairy inside; petal 0; stamens 6, filaments c. 0.5-1 mm long, glabrous; anthers linear, c. 2.5 mm long, glabrous or hairy on both sides of the connective; ovary c. 1.5-2 mm long; style short, c. 0.5-1 mm long, slightly recurved at the top. Fruits ± ovoid, c. 4 (-5) cm long x 2.5 cm wide, rather slightly compressed, with distinct sulcate sutures, usually acute to cuneate at base, beaked or apiculate at apex, exocarp blackish, ± shiny when dry, hairs easily detached and glabrescent. Seeds reniform, c. 1.5 cm long x 1 cm wide, testa ± chocolate brown, shiny.

Distribution. W Malesia. Sumatra, Peninsular Malaysia, Borneo (Sarawak and Brunei); not as yet collected in Sabah and Kalimantan but could possibly be found there.

Collections seen. S Sumatra (Palembang, Berkoelen and Indragiri): 20. Peninsular Malaysia (Negri Sembilan, Pahang & Selangor): 7. Sarawak: Jacobs 5221, Kapit district. Brunei: BRUN 856, Tulong, Ulong Supon.

Ecology. Primary and old secondary forests, sometimes inundated, 15-560 m elev., on alluvium with sandstone substratum (Jacobs). Rather scattered. Flowers June-March, old fruits collected Jan.-April.

Remarks. This species is homogeneous except in the size of the leaves where big-sized ones are found in Peninsular Malaysia. It is very close to D. kunstleri var. trifoliolatum which sometimes

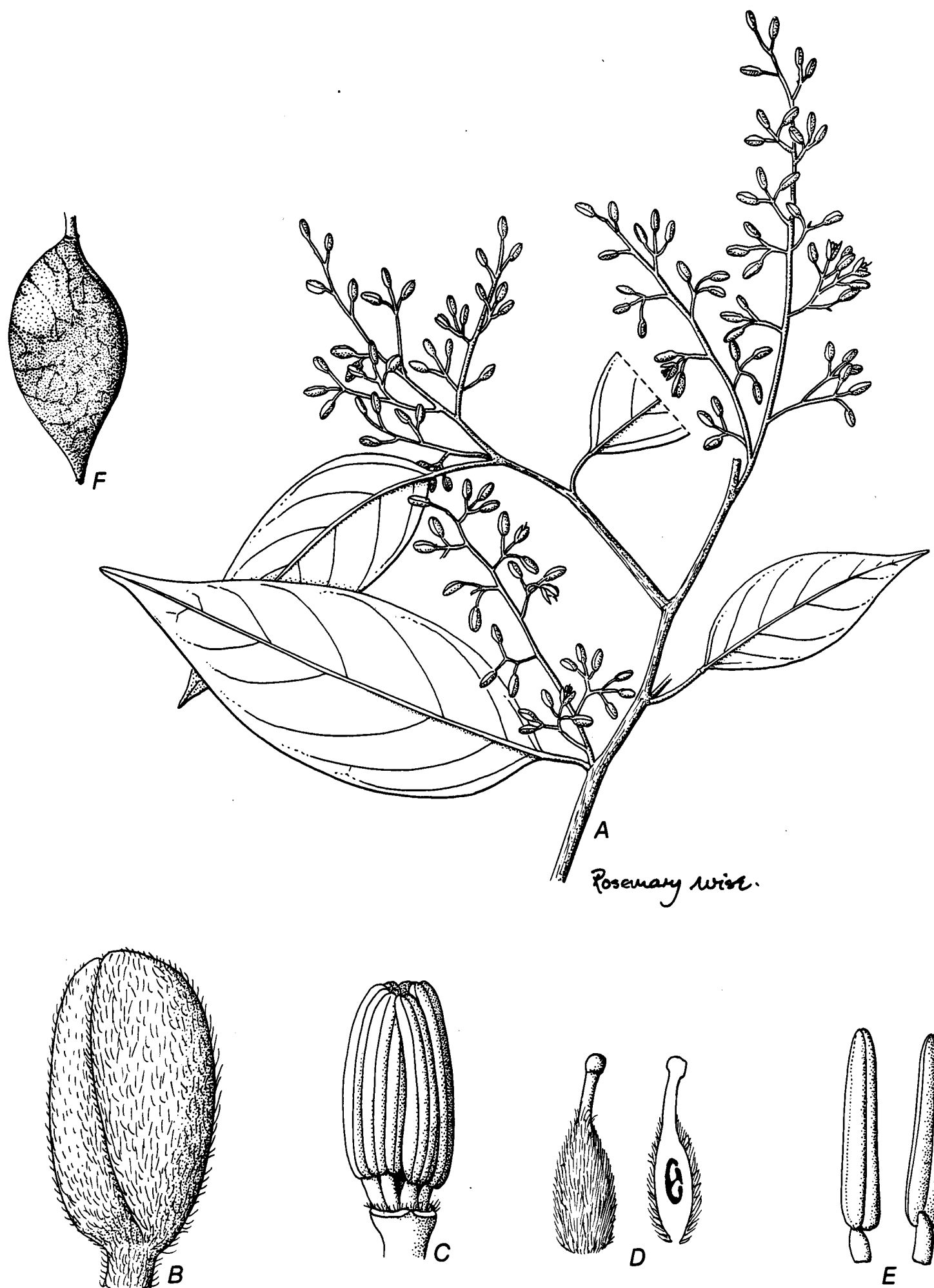


Fig. 7.7. Dialium procerum (Steenis) Stey. A. habit, $\times 2/3$ (117T.3P.390, isotype, Palembang, Sumatra); B. flower bud, C. flower bud with sepals removed, D. ovary with lengthwise section, E. stamen in adaxial and abaxial sides (B-E all $\times 10$, T.579. 16/10, Palembang, Sumatra); F. fruit, $\times 2/3$ (BRUN 856, Brunei).

displays unifoliolate leaves in an otherwise trifoliolate condition. However, the size and shape of the pods differ considerably between each other; this species having the biggest (to c. 5 cm long x 2.5 cm wide; see also Fig. 2.15P) fruit among Dialium species.

I think van Steenis (loc. cit.) was correct in rejecting Rhynchocharpa monophylla as a validly published species because, although Heyne (loc. cit.) technically published the binomial in his book, Heyne himself indicated there that the species had not as yet formally been published. Van Steenis, therefore, merely followed Heyne's suggestion by publishing, but using another name for it. Dr. M. Jacobs (pers. comm.) said Heyne's description is invalidly published. I follow the view of Dr. Jacobs.

INCOMPLETELY KNOWN SPECIES

Dialium travancoricum Bourd., Indian For. 30 (1904) 243 (with unnumbered illustration). There is no type indicated in the publication, but specimens (Bourdillon 1005) marked as type in K and FHO exist. The flowers are very young and therefore inappropriate for description. Obviously, the description by Bourdillon is based on the young flowers. Up to the present, there are no other specimens available for examination.

DOUBTFUL SPECIES

Dialium anomalum Webb, Hook. Kew Journ. 2 (1850) 347. There is no indication of any type specimen. The description seems to indicate a close affinity with D. guineense and the epithet refers likely to the number of ovaries, i.e. 1 or 2. Chakravorthy (1969) found double ovaries in D. guineense.

Dialium graciliflorum Harms, Engl. Bot. Jahrb., 53 (1915) 467. Type: Milbraed 3218, not seen. According to Harms (loc. cit.) it only differs from D. polyanthum by its smaller leaves.

Dialium hexasepalum Harms, Engl. Bot. Jahrb., 53 (1915) 470. Type: Milbraed 3020, not seen. The sepals are (5-) 6 (-7). This number of sepals (i.e. 6) is abnormal in Dialium.

Dialium poggei Harms, Engl. Bot. Jahrb., 53 (1915) 408. Type: Pogge 1375, not seen. Steyaert (1952) indicated that this species is closer to D. corbisieri or D. gossweileri (both are now reduced to D. polyanthum and D. pachyphyllum, respectively).

Dialium latifolium Harms, Engl. Bot. Jahrb. 53 (1915) 470. Type:
Filbraed 5805, not seen. This species was described with fruiting material
only. The fruit is compressed and velutinous. It could be D. pachyphyllum
or D. zenkeri.

EXCLUDED SPECIES

Dialium modestum (Steenis) Stey. = Uittienia modesta Steenis

EXCLUDED GENUS

Uittienia Steenis (A genus previously reduced to Dialium but herewith
rejected as not belonging to Dialium.)

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APPENDIX

Appendix A.

INDEX TO NAMES

The accepted names are not underlined. The synonyms are underlined while the new names are in capitals. The names are referred to the species of Dialium where they belong, or to the incompletely known species (Inc. kn. Sp.), excluded species (Excl. Sp.) and doubtful species (Doubt. Sp.) as the case may be. The accepted names under Dialium are abbreviated with their first three letters, with the first letter of the infraspecific name added as a fourth one, if any. Numbers represent pages in the text.

Andradia Sim - Dialium, 156

arborea Sim : sch, 168

Arouna Aublet - Dialium, 156

divaricata Willd.: gua (guianense), 173

guianensis Aublet : gua, 173

Cleyria Necker - Dialium, 159

Codarium Sol. ex Vahl - Dialium, 156

acutifolium Afzel. : gui (guineense), 203

discolor DC. : gui, 203

nitidum Sol. ex Vahl : gui, 203

obtusifolium Afzel. : gui, 203

Dansera Steenis - Dialium, 230, 239

procera Steenis : pro, 243

Dialium, 156, 209

acuminatum De Wild. : zen, 206

ambiguum Prain : pla, 213

angolense Welw. ex Oliver : ang, 193

var. ANGOLENSE : ang, 124

var. KASAIENSE (Louis ex Stey.) Rojo : angk, 195

angustisepalum Ridley : ind, 223

anomalum Webb : Doubt. Sp., 247

aubrevillei Pellegrin : pol, 188

bipindense Harms : bip, 171

cochinchinense Pierre : coc, 210

connaroides Harms : bip, 172

corbisieri Staner : pol, 188

coromandelianum Houtt. : ind, 223

densiflorum Harms : zen, 206

dewittii Steenis : kunt, 242

dinklagei Harms : din, 176

discolor (DC.) Hook. f. : gui, 203

divaricatum (Necker) Vahl : gua, 173

englerianum Henr. : eng, 201

euryssepalum Harms : bip, 172

evrardii Stey. : ang, 194

excelsum Louis ex Stey. : exc, 184

fleuryi Pellegrin : bip, 172

gossweileri Baker f. : pac, 198

graciliflorum Harms : Doubt. Sp., 247

guianense (Aublet) Sandw. : gua, 173

guineense Willd. : gui, 203

var. obtusifolium (Afzel.) Baker f. : gui, 203

havilandii Ridley : pla, 213

hexasepalum Harms : Doubt. Sp., 247

holtzii Harms : hol, 181

Hova Irwin and Barneby = Subgen. Dansera sect. Hova, 231

hydnocarpoides : hyd, 210

indum L. : ind, 221

var. INDUM : ind, 223

var. BURSA (de Wit) Rojo : indb, 226

javanicum Burm. f. : ind, 223

kasaiense Louis ex Stey. : angk, 195

kingii Prain : pla, 213

klainei Pierre ex Harms : din, 177

klainei Pierre ex De Wild. : din, 177

kunstleri Prain : kun, 239

var. KUNSTLERI : kun, 241

var. TRIFOLIOLATUM (de Wit) Rojo : kunt, 242

lacourtianum De Wild. ex Vermoesen : eng, 201

latifolium Harms : Doubt. Sp., 248

laurentii De Wild. : zen, 206

laurinum Baker : indb, 226

var. bursa de Wit : indb, 226

macranthum A. Chev. : pac, 198

madagascariense Baillon : mad, 234

ssp. occidentale Capuron : occ, 233

maingayi Baker : pla, 213

marginatum de Wit : ind, 223

mayumbense Baker f. : tes, 191

modestum (Steenis) Stey. : Excl. Sp., 247

mossambicense Stey. : hol, 181

nitidum (Sol. ex Vahl) Guillemin & Perrottet : gui, 203

OCCIDENTALE (Capuron) Rojo : occ, 232

var. OCCIDENTALE : occ, 233

var. SEPTENTRIONALE (Capuron) Rojo : occs, 234

orientale Baker f. : ori, 172

ovatum Hutch. & Dalziel : pob, 170

ovoideum Thwaites : ovo, 217
 pachyphyllum Harms : pac, 198
patens Baker : ind, 223
 pentandrum Louis ex Stey. : pen, 186
pierrei De Wild. : zen, 207
 platysepalum Baker : pla, 212
 var. ambiguum (Prain) Ridley : pla, 213
 var. burong Prain : pla, 212
 var. papan Prain : pla, 212
 var. wallichii Baker : pla, 212
 pobeguinii Pellegrin : pob, 170
poggei Harms : Doubt. Sp., 247
 polyanthum Harms : pol, 186
praetermissum de Wit : hyd, 210
 procerum (Steenis) Stey. : pro, 243
quinguepetalum Pellegrin : eng, 201
reticulatum Burt Davy : ori, 179
 reygaertii De Wild. : rey, 182
 schlechteri Harms : sch, 168
sivestre de Wit : kun, 241
simii Phillips : eng, 201
soyauxii Harms : zen, 206
staudtii Harms : din, 177
 tessmannii Harms : tes, 191
travancoricum Bourd. : Inc. kn. Sp., 247
trifoliolatum de Wit : kun, 242
triste de Wit : pla, 213
turbinatum de Wit : ind, 223

unifoliolatum Capuron : uni, 236

ssp. septentrionale Capuron : occs, 232

wallichii (Baker) Prain : pla, 212

yambataense Vermoesen : pac, 198

zenkeri Harms : zen, 206

Uittienia - Excluded genus, 248

Appendix B.

LIST OF SPECIMENS USED FOR POLLEN OBSERVATION

<u>Species</u>	<u>Collector's Number</u>	<u>Origin</u>
schlechteri	Gomes e Sousa	Mocambique
	Borle 63	"
pobeguinii	Deighton 1752	Sierre Leone
bipindense	Zenker 2695 (type)	Cameroon
guianense	Irwin, <u>et al.</u> 55368	Surinam
	Krukoff B6262	Brazil
dinklagei	Klaine 417 (type)	Ghana
orientale	Elliot 754	Kenya
excelsum	Louis 2881	Zaire
polyanthum	Zenker 950 (type)	Cameroon
pentandrum	Louis 4017 (type)	Zaire
tessmannii	Donis 1653	"
angolense	White 3096	Zambia
pachyphyllum	Bates 1832	Cameroon
englerianum	Fanshawe 6911	Zambia
	White 2987	"
	Barros Machada 13911B	Angola
guineense	Hepper 1465	Cameroon
	Moore 165	Ghana
	Smith 10	Nigeria
zenkeri	Louis 3831	Zaire
	Leemont 287	"
	H. Soyaux 303 (type)	Gabon
hydnocarpoides	185 T. 3P. 540	Sumatra

platysepalum	Shouts 8337	Pen. Malaysia
ovoideum	Kostermans 24514	Sri Lanka
cochinchinense	B. S. & K. B. 1665	Thailand
indum	Reinwardt s.n.	Java
occidentale	24499-SF	Madagascar
madagascariense	8625-SF	"
procerum	117T. 3P. 599	Sumatra
kunstleri	SAN 65841	Sabah
Androcalymma	Krukoff 9005 (type)	Brazil
Apuleia	Maguire <u>et al.</u> 56115	"
Baudouinia fluggei	dela Bathie 9903	Madagascar
formis	dela Bathie 5503	"
Dicorynia	Boschbeher 44	Surinam
Distemonanthus	Green & Vigne 9	Ghana
Eligmocarpus	20501-SF	Madagascar
Kalappia	bb. 33693	Celebes
Koompassia grandiflora	Kostermans 492	New Guinea
Martiodendron excelsa	Samuels 243	Surinam
Mendoravia dumaziana	McWhirter 212	Madagascar
Storckiella pancheri	Franc 32	New Caledonia
Uittienia modesta	Kostermans 13413A	E Borneo
Zenia insignis	Poilane 25752	N Vietnam

Appendix C.

LIST OF SPECIMENS OBSERVED FOR PULVINUS VASCULAR PATTERNS

<u>Species</u>	<u>Collector's Number</u>	<u>Origin</u>
schlechteri	Miller N 22	Natal
	White 10458	"
	Gomes e Sousa 1650	Mocambique
	Barbosa & Lemos 8112	"
	" " 7962	"
	Borle 63	"
pobeguinii	Deighton 1752	Sierra Leone
bipindense	Zenker 1922	Cameroon
	Thollon 912	Gabon
	Klaine 222	Zaire
	Corbisier 1689	"
guianense	Pennington & Sarukhan 9530	Mexico
	Irwin <u>et al.</u> 55368	Surinam
	Pires <u>et al.</u> 50744	Brazil
	Prance <u>et al.</u> 10662	"
	Steyermark & Gibson 95730	Venezuela
	Stevenson 84	Belize
dinklagei	Devred 1215	Zaire
	Dubois 325	"
	Klaine 4	"
	Klaine 417	Gabon
	Vigne 194	Ghana
	Le Testu 8994	Gabon
	W. de Wilde 650	Ivory Coast

orientale	Cons. For. 166	Kenya
	Cons. For. A59/39	"
	Dale 3838	"
	Graham 377 & 1783	"
	Elliot 746	"
	MacNaughton 152	"
	Polhill & Paulo 779	"
holtzii	Greenway 4628 & 6692	Tanzania
	Schieben 6125	"
	Gomes e Sousa 466	Mocambique
	Semsei 2412	Tanzania
reygaertii	Louis 8908	Zaire
excelsum	Louis 1159, 2881, 1150, 1158	"
pentandrum	Louis 2528	"
	Louis 4017 (type)	"
	Enti FH 7456	Ghana
polyanthum	Andoh FH 386	"
	Jones & Onochie 18791	Nigeria
	Louis 3824	"
	Dubois 745	"
	Toussaint 88 & 105	"
tessmannii	Donis 1653 & 1914	"
	Clorbisier 1642	"
	Lawton 777	Zambia
angolense	Gossweiler 13987	Angola
	Toussaint 303	"
	Le Testu 7608	Gabon
	Zenker s.n.	Cameroon
	Leemans 348	Zaire
	Robyns 1031	"
	Gossweiler 7562	Cabinda

englerianum	Gossweiler 13911 & 13932	Angola
	White 2987 & 3476	Zambia
	Miller B/645	Bechuanaland
	Brenan & Keay 7711	Zambia
	Barbosa & Moreno 9877	Angola
	Freeman, <u>et al.</u> 5	"
guineense	Aubreville 191 & 559	Ivory Coast
	Vigne 1400 & 2020	Ghana
	Chapman 4288	Nigeria
	Chester 134	"
	Langdale-Brown 2581	Guinea
	Cons. For. Nigeria 70	Nigeria
	MacGregor 337	"
	Smith 10	Nigeria
	White 8303	"
	Cons. For. (Nig) 74 & 316	"
zenkeri	Dubois 8860	Zaire
	Evrard 4039	"
	Leonard 30 & 247	"
	Le Testu 2231 & 8484	Gabon
	Soyaux 303	"
	Louis 8860 & 15041	Zaire
	Leemans 387	"
	Klaine 754	Gabon
hydnocarpoides	T.540. 29/4	Sumatra
	185 T. 3P. 540	"
platysepalum	K.L. 1763, 366	Pen. Malaysia
	FMS 15706, 48876, 11199	" "
	ICEP 105012, 32635, 71922, 72223, 122603	" "

platysepalum	CF 0653, 4523	Pen. Malaysia
	FRI 11601, 18353	" "
	FOR.DEPT. 23662, 23731, 13770	" "
	Henderson 22133	" "
	S. 12749, 23787	Sarawak
	BRUN 3331	Brunei
	SAN 43704, 44225, 44591	Sabah
	SAN 47351, 47360, 66222	"
	SAN 57171, 81862	"
	Kostermans 9700, 9875, 9969, 13606	Kalimantan
ovoideum	Thwaites 3149 (type)	Sri Lanka
cochinchinense	B.S. & K.B. 1665	Thailand
	King 5612	"
	Collins 398	"
	Pierre 123, 1026	S Vietnam
indum	KEP 0019, 35964, 51998, 64565, 105133, 94900, 122604	Pen. Malaysia
	FMS 15709, 48876	
	S. 24410, 10680, 25204, 16962	Sarawak
	SING 1504, 1530, 37721, 37721	Singapore
	SAN 44041, 54335, 58471, 57171	Sabah
	Reinwardt s.n.	Java
	Kostermans 6604	Kalimantan
madagascariense	8444-SF, 8943-SF, 3048-SF	Madagascar
kunstleri	SAN 24979, 25000, 36829, 42689	Sabah
	bb. 16786, 16080, 34379	Kalimantan
	Kostermans 6578	"
	S. 23699	Sarawak

Dicorynia paraensis	Boschbeher 44	Surinam
Distemonanthus	Vigne 1653	Ghana
	Green & Vigne 9/1926	"
Eligmocarpus	McWhirter 204	Madagascar
Kalappia	Reppie 389	Celebes
	bb. 32456, 33693	"
	Cel. 57	"
Koompassia grandiflora	Kostermans 359	W New Guinea
	bb. 33641, 33537	" "
Mendoravia	McWhirter 212	Madagascar
Storckiella pancheri	Vieillard 402	New Caledonia
	Franc 32	" "

Appendix D.

LIST OF SPECIMENS OBSERVED FOR STOMATA TYPES

<u>Species</u>	<u>Collector's Number</u>	<u>Origin</u>
schechteri	Gomes e Sousa 1650	Mocambique
pobeguinii	Deighton 1752	Sierre Leone
bipindense	Zenker 2695 (type)	Cameroon
guianense	Irwin, <u>et al.</u> 55368	Surinam
	Pires, <u>et al.</u> 50744	Brazil
dinklagei	Edwardson 131	Sierra Leone
	Andoh 5028	Ghana
orientale	Polhill & Paulo 779	Kenya
holtzii	Schlieben 6125	Tanzania
	Gillman 1190	"
reygaertii	Louis 8904	Zaire
excelsum	Louis 1159 & 11520	"
pentandrum	Louis 3824	"
polyanthum	De Wilde, c.s. 2726	Cameroon
	Andoh FH 5386	Ghana
	Voorkoeve & de Wilde 3662	Liberia
	Corbisier 1078	Zaire
	Louis 9638	"
tessmannii	Donis 1653	"
	Toussaint 105	"
angolense	White 3507	Zambia
	Gossweiler 13895 & 13987	Angola
pachyphyllum	Louis 3933	Zaire
	Ghesquiere	"
englerianum	Gossweiler 13911	Angola
	Barros Machads 13911B	"
	Robyns 3731	Zaire

guineense	Leemans 287	Zaire
	White 8303	Nigeria
zenkeri	Latilo & Daramula FH 34415	Cameroon
	Louis 8860	Zaire
hydnocarpoides	T.540. 29/4	Sumatra
platysepalum	Ogata 10299	Pen. Malaysia
	KEP 72223	" "
	CF 0653	" "
	FRI 20354	" "
cochinchinense	Collins 389	Thailand
	B.S. & K.B. 1665	"
indum	Reinwardt s.n.	Java
	SAN 43336	Pen. Malaysia
madagascariense	8625-SF, 8444-SF, 9033-SF, 9048-SF	Madagascar
kunstleri	Kostermans 6578	Kalimantan
	bb. 34319	"
procera	Jacobs 5221	Sarawak
Dicorynia paraensis	Boschbeher 44	Surinam
Distemonanthus	Rosevear 23/28	Ghana
Eligmocarpus	McWhirter 204	Madagascar
Kalappia	bb. 33693	Celebes
Koompassia grandiflora	bb. 33537	W New Guinea
Mendoravia	McWhirter 212	Madagascar
Martiodendron	Samuels 243	Surinam
Storckiella pancheri	Vieillard 402	New Caledonia
Uittienia	Kostermans 13231	Kalimantan

Appendix E.

LIST OF MATURE WOOD AND TWIGS ANATOMICALLY STUDIED

<u>Species</u>	<u>Collector's Number</u>	<u>Origin</u>
schlechteri	White 10458	Natal
pobeguinii	Deighton 1752	Sierre Leone
bipindense	Klaine 222	Gabon
	Zenker 2695 (type)	Cameroon
guinanense	Pennington & Sarukhan 9530	Mexico
	Pires, <u>et al.</u> 507441	Brazil
	BAFOG 113 M (CTFT 8050)	French Guiana
	Krukoff B6262	Brazil
dinklagei	W. de Wilde, C.S. 650	Ivory Coast
	FH1 17362 (FPRL 23163)	Nigeria
	Letouzey 11440 (CTFT 20055)	Cameroon
	SFRG 2062 (CTFT 13971)	Gabon
	Chevalier 16206 (CTFT 24200)	Ivory Coast
orientale	Dale 3899	Kenya
	FPRL 13455	"
	CFI 14980	"
holtzii	Greenway 4628 & 5369	Tanzania
	Schlieben 6125	"
reygaertii	Louis 8909	Zaire
	Evrard 1701	"
excelsum	Louis 2881 (type), 1159 & 3820	"
	FPRL 27306 (Herb. no. 2464)	Central Afr. Rep.
pentandrum	Louis 2528, 6224	Zaire
polyanthum	Gilbert 2380	"
	J. de Wilde 3663	Liberia
	Louis 9638	Zaire

polyanthum	Detienne 55 (CTFT 20430)	Ivory Coast
	FPRL 18593 (S.L. 279)	Sierre Leone
	FPRL 28269 (Dechamps 658)	Zaire
	FPRL 27356 (Dechamps 14000)	"
tessmannii	Donis 1653	Zaire
	Corbisier 1642	"
angolense	Stevenson 262/31	Zambia
	Robyns 1886	Zaire
pachyphyllum	Louis 14726	"
	SFRG 1714 (CTFT 10344)	Gabon
	Letouzey 11584 (CTFT 20056)	Cameroon
englerianum	Barbosa & Moreno 9877	Angola
	White 2987	Zambia
	FPRL 21027	Angola
	Milne-Redhead 4598	Zambia
guineense	Aubreville 191, 559 (CTFT 24319)	Ivory Coast
	Chelters 134	Nigeria
	Chevalier 16256 (CTFT 24248)	Ivory Coast
	Sargos 894 (FPRI 15305)	" "
zenkeri	Louis 15041	Zaire
	Leemans 287	"
	Le Testu 7653	Gabon
	Chevalier 26556 (CTFT 24534)	"
	SFRG 2064 (CTFT 13972)	"
hydnocarpoides	SAN 44221	Sabah
	T.540. 29/4	Sumatra
platysepalum	KEP 20354, 6693 (FMS 1161), 26101, 33239	Pen. Malaysia
	King's coll. 6142 (type)	" "

platysepalum	Normand 604	Sumatra
	Corner s.n. (year 1935)	Pen. Malaysia
	KEP 29385, 4624 (FMS 1167)	" "
	FMS 1168, 1169	" "
ovoideum	Holmes 107 (FPRL 22136)	Sri Lanka
cochinchinense	Collins 398	Thailand
	Pierre 1026	S. Vietnam
	Phengkhlai 422	Thailand
	Kerr 9009	"
	Chevalier 30040 (CTFT 10926)	Cambodia
	FPRL 22788 (Thai. No. 7)	Thailand
	CFI 6342	"
	SAN 63886	Sabah
	KEP 94900, 15772 (FMS 1170)	Pen. Malaysia
indum	FRI 14273	" "
	S. 193, 23803	Sarawak
	KEP 32365 (FMS 1931), 15664	Pen. Malaysia
	FMS 161	" "
	8444-SF, 24699-SF	Madagascar
occidentale	11916-SF (CTFT 13585)	"
	17149-SF (CTFT 13587)	"
	8943-SF, 8625-SF, 9048-SF	"
madagascariense	8664 (CTFT 9018)	"
	9033-SF, 51R77 (CTFT 13597)	"
unifoliolatum	bb. 16080, 16039	Kalimantan
	S 23699	Sarawak
	SAN 24979, 43905	Sabah
	Kostermans 6729, 13576	Kalimantan
kunstleri		

procerum	T. 588	Sumatra
	BRUN 856	Brunei
	FRI 16234 (WT 8045)	Pen. Malaysia
Apuleia praecox	CFI 9706, 10723	No locality
Baudouinia fluggeiformis	Greve 224	Madagascar
Dicorynia guianensis	Basralokus 36A (TP 5192-36)	
	Y 45576	Surinam
	CFI 6344	"
Distemonanthus	FPRL 5746	Nigeria
	CFI 1588, 4294	"
	FPRL 18695	Sierre Leone
Eligmocarpus	McWhirter 204	Madagascar
Kalappia	Cel. 389	Celebes
Koompassia excelsa	FPRL 21631	Sabah
	CFI 7249, 7260	Pen. Malaysia
Koompassia grandiflora	FPRL 28726	W New Guinea
	Cramer & Schodde 1058a	" "
Koompassia malaccensis	FMS 1986, 2043	Pen. Malaysia
Martiodendron excelsa	CFI 13258	
	FPRL 15973 (B.G. 4299)	British Guiana
Mendoravia	McWhirter 213	Madagascar
Storckiella pancheri	Vieillard 402	New Caledonia
Storckiella grandiflora	Hyland 6717	Australia